NUTRITIONAL ASPECTS OF THE INTERACTION BETWEEN WINTER WHEAT (*TRITICUM AESTIVUM* L.) CV. AVALON AND THE WEEDS WILD OAT (*AVENA FATUA* L.) AND BARREN BROME (*BROMUS STERILIS* L.)

HAILE GHIORGHIS REDAI

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Department of Biochemistry and Biological Sciences

Wye College

University of London

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GENERAL ABSTRACT

Aspects of the competitive relationships between winter wheat (Triticum aestivum L. cv. Avalon), wild oat (Avena fatua L.) and barren brome (Bromus sterilis L.) were investigated under glasshouse conditions in pot experiments. In one experiment the Ethiopian cereal Tef (Eragrostis tef Zucc.) was also investigated. The outcome of both intra- and inter-specific competition was measured using several plant attributes relating to growth and the efficiency of nutrient uptake and utilization.

The responses of the species to a range of levels of five macro-nutrients (N, P, K, Ca and Mg) were studied in water culture experiments using the nutrient film technique. Both differences and similarities in the responses of the species were recorded which may suggest differences in their requirements for specific elements related to their evolutionary backgrounds. In general the weeds, particularly barren brome, contained higher concentrations of N, P, Ca and Mg and showed greater efficiency of ion uptake measured by uptake per unit dry weight of roots. The crop showed higher concentrations of K and it was as efficient as wild oat in utilizing these nutrients in terms of dry matter production per unit ion uptake. Barren brome was the least efficient in nutrient utilization and hence appeared to be an accumulator, showing higher tissue concentrations.

Wild oat was less responsive to variations in the levels of P, K and Mg than the other species, showing less reduction in dry matter production as the levels of these nutrients were reduced in solution. The amount of top growth produced by barren brome was always smaller than in wheat and wild oat, which were generally similar, although the crop was more responsive to higher levels of nutrients, especially N, P, and K, and thus grew larger than this weed.

Differences in root morphology of the species were obvious. Barren brome had a finer, denser and longer root system than the other species. The ratio of root to shoot weights was often higher for this species than for the others. The higher concentration of nutrients found in barren brome may be attributed to these features, especially at low levels of nutrients in the medium.

Attempts were made to study the kinetics of P and K absorption

using intact plants in continuously flowing water culture experiments where the concentration of nutrients was continuously depleted from the solution over a period of several hours. The uptake data were fitted to equations of the form $Y = A.1^{B.X}$ and $Y = A + BX$. However, plotting data for rate of uptake against concentration failed to produce satisfactory values of Vmax - the maximum rate of uptake and hence the Km - the concentration of the solution at which uptake was half Vmax. The probable reasons for failure to estimate these values in these experiments are discussed. Instead the three species were compared on the concentrations (mMol/l) of P and K remaining in solution at various intervals and uptake rates (mMol/g FW of roots). Lower P concentrations were found in solutions where wheat or wild oat plants were grown; however, uptake rates were higher for barren brome. In the K experiments, lower concentrations were found in the solution containing wheat plants. The crop also showed higher K uptake rates than either weed. Both wheat and wild oat also reduced the initial K concentration to zero earlier (6-7 hours) than barren brome. The weeds, especially barren brome, had the lowest value for P concentration remaining in solution after depletion (C min), showing ability to absorb the element from a lower level in solution.

The responses of the three species to P and K in pure stands and mixture were investigated using both the additive and replacement series models. The performances of the species were assessed by determining dry matter yield (g/plant), tissue nutrient concentrations and total amounts, relative yield (RYs) and relative yield totals (RYTs) and relative crowding coefficients (RCCs) and their products. Tissue nutrient concentrations were higher in the weeds, especially barren brome, than the crop. However, values for RYs and RCCs calculated for both yields of dry matter and nutrients were always smaller for this weed, showing generally a lower competitive ability than the other species. In the P experiments wild oat showed a higher competitive ability whilst the crop was more competitive than the weeds for K.

Separation of the effects of root and shoot competition generally showed that competition for underground resources (mainly nutrients) was more important than that for those above ground (mainly light). The effects of root and shoot competition were not additive and root effects were usually greater than the effects of full competition.

Aggressivity values gave an order of aggressiveness of WO W BB.

Root restriction experiments showed that barren brome was the species most affected by this treatment, probably as a result of root competition since the weed produced denser roots than the other species. The effects of intra-specific root competition appeared to be reduced by the addition of a higher level of P. The distribution of the roots of the species along a profile of soil in cylinders was quantified and photographed. The roots of wild oat grew deeper than those of the other species. Roots of barren brome were confined to the top 0-30 cm of the soil - a distribution very similar to that of the crop roots.

Throughout the thesis the results are discussed in relation to the literature of the subject and to the significance of mineral nutrients in competitive interaction between plants.

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4. GENERAL INTRODUCTION

4.1 Weed

In the Webster's International Dictionary of the English Language, a weed is defined as "an introduced plant growing in a ground that is or has been in cultivation usually to the detriment of the crop or to the disfigurement of the place". To the individual farmer, agronomist or even city dweller, the term means a class of plants that are unwanted, non-useful and a nuisance to man. In the scientific literature concerning the biology of weeds, however, one can see the existence of differences in opinion and difficulties in finding an objective and generally valid single definition of a weed (Harlan, 1965; Hill, 1977; Wells, 1978, cited by Holzner, 1982; Aldrich, 1984). Various definitions of a weed may be found in Harper (1961), Harlan and de Wit (1965), King (1966) and Klingman et al. (1975). Wells (1979) cited by Holzner (1982) wrote that the term is not a scientific one but 'public property' and the public as a whole has a very broad concept on 'what a weed is'. Holzner (1982) said that different people have different conceptions of weediness and that not only plants that are a nuisance for some reason, but simply most plants that are 'unsightly' or just good for nothing are considered as undesirable and thus classified as weeds. Wells (1979) also described one of the difficulties in defining a weed as the tendency of people to consider all plants as potential weeds. As man tries to utilize more and more of his environment he comes into conflict with more and more plants that he tends to regard as weeds. Some weeds are also closely related to valuable crop species, and a number of those that are weedy in certain situations may be useful plants in others. Therefore, the concept of weediness in plant species differs from person to person, area to area and even from year to year. Strictly speaking plant species are defined by the weed biologist as weeds when they interfere with man's activities, his objectives or requirements and thus the simplest and most common definition of a weed is "any plant growing where it is not wanted". Weeds are, therefore, non-invited guests in crop cultivation and tend to be adaptable to all man-made habitats.

Weeds encompass all types of undesirable plants and no one character is common to all weeds. They vary in their physiology and morphology and

their general habits of growth and range from parasites to independent vigorous plants.

Weeds seriously reduce the productive capacity of agricultural lands. In the United States alone the total annual cost to agriculture as a result of pests has been calculated at $12 billion. Of this amount, the annual cost resulting from plant diseases is about 17%, insects 28%, nematodes 3% and weeds 42% (Klingman et al., 1975). Probably the heaviest yield losses caused by weeds result from their competition with crops for soil nutrients, light, soil moisture and carbon dioxide. Weeds are generally vigorous and their demands for nutrients great. For example, one plant of yellow mustard (Brassica hirta) needs twice as much nitrogen and phosphorus, four times as much potassium and water as a well-developed oat plant. The average common ragweed (Ambrosia artemisufolia L.) is also said to require three times as much water as a maize plant (Zea mays).

Weeds directly or indirectly affect the cost of food and the health and comfort of people. They increase costs of labour and equipment; reduce the quantity and quality of livestock products; harbour insects and fungus pests that attack crop plants; may impair the health of human beings and cause depreciation of land values and reduce farm loans.

4.2 Competition

Crop plants are not grown in isolation, but in communities including many species that influence their growth and reproduction as a result of processes referred to as 'competition'. Although the term has a widespread significance in agriculture, its exact interpretation has been much debated in botanical literature. The term lacks an independent scientific meaning (Harper, 1961) and is often misused and thus several definitions have been proposed (e.g. Clements et al., 1929; Pavlychenko and Harrington, 1934; Bleasdale, 1960; Sakai, 1961; Mather, 1961; Milne, 1961; Harper, 1961; Donald, 1963; Fitter and Hay, 1983). A basic division exists among those who wish to define competition in terms of population dynamics to include plants, microbes and animals (Williamson, 1972) and those who use the word to include all deleterious effects on individuals, whatever the cause may be (e.g. Milne, 1961; Harper, 1961, 1964) and there are still others who confine competition to the situation

where the supply of a resource is less than the joint requirement of the two organisms (e.g. Clements et al., 1929; Harper, 1977; Glauninger and Holzner, 1982; Tarawali, 1983; Fitter and Hay, 1983; Begon et al., 1986; Johnson, 1987). In the plant world, the classical definition of competition remains that of F.E. Clements reported by Clements et al. (1929) and reiterated by Donald (1963) with some modifications to include animals. Clements states: 'Competition is purely a physical process. With few exceptions, such as the crowding of tuberous plants when grown too closely, an actual struggle between competing plants never occurs. Competition arises from the reaction of one plant upon the physical factors about it and the effect of the modified factors upon its competitors. In the exact sense, two plants do not compete with each other as long as the water content, the nutrient material, the light and the heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins'. Despite this straightforward definition Harper (1964; 1977) argued that the term does not embrace all the mutual influences of plants growing together and adopted 'plant interference' instead of competition to describe all changes in the environment brought about by the proximity of individuals. Consequently he divided interference into competitive influences - to include all neighbour effects due to the consumption of resources in limited supply and non-competitive processes - to include allelopathy and mutual or self-protection. He concluded that competition itself is only one facet of interference between plants, although at times it may be very dominating one. Allelopathy is different from competition. Allelopathy may be described as the production of substances by one plant injurious to another plant (Muller, 1970). One feature that distinguishes allelopathy from competition is that something is being added to the environment, as opposed to something being removed from it. Competition is always 'for something' and the competition among populations of plants of similar genotypes is referred to as 'intra-specific' and when different species are grown in mixtures it is 'inter-specific' (Harper, 1983). Plant nutrients, water and light are the main factors of competition among two or more plants. There are two obvious conditions in order for competition between species to occur: (i) Competition begins when one or more of these factors reaches limiting levels in the growing medium, and (ii) The environment in which the species grow is shared. In this investigation the sense in which competition is used refers to the

efficiency with which individuals, growing in association, secure from the environment the factors which are necessary for their growth and reproduction.

4.3 Project objectives

Weed species growing under poor fertility conditions may be capable of acquiring nutrients necessary for growth and reproduction more easily than crop species. This may help explain why weed infestation commonly occurs and may be severe on soils of low fertility status. The presence of weed species, in fact, has been used as an indicator of mineral deficiency of the soil (Schipstra, 1957, cited by Hoveland et al., 1976). Baker (1974) stated that one of the characteristics of many weeds is their ability to survive and reproduce in a wide range of environments. These include soils with low nutritional status and, because they have evolved in this way, weeds may be expected to show a greater efficiency in absorption and/or utilization of nutrients than crop plants which are often cultivated under artificially maintained higher fertility levels. Alkamper et al (1979) looked at the relationship between weed growth and fertility conditions and noted that these species often appear to absorb fertilizers faster and in relatively larger amounts than crops. More recently Tarawali (1983), Johnson (1987) and Qasem (1987) showed that some crop and weed species respond differently to varying levels of various nutrients and indicated that the latter were more efficient in the uptake and use of these when they were at deficient levels. Zimdahl (1980) pointed out that weeds are also capable of responding to increasing nutrient levels in the soil and suggested that the application of fertilizers may stimulate weed growth to the extent that crop loss may actually increase and that it would thus be impossible to achieve weed control through the use of fertilizers to stimulate crop growth.

The literature on crop/weed competitive interactions is plentiful. Such studies have, however, mostly been geared to reporting on the question of what happened rather than why it happened and in general surprisingly little information is available on the nutritional aspects of crop/weed interactions. These relate root morphological and physiological traits to differences in competitive abilities between the two groups of plants. Studies which deal with the examination of root

systems in particular, and growth and development of the competing plants as a whole, may identify and perhaps account for differences in efficiency of nutrient uptake and use. In the present studies, therefore, attempts are made to look for evidence that the weeds wild oat (Avena fatua L.) and barren brome (Bromus sterilis L.) are different from the crop (wheat) in their responses to different nutrients and especially in their efficiencies of uptake and use at deficient levels. No such comparisons have previously been made between wheat and barren brome and little information is available even on the crop and wild oat despite their long history of association.

The general objectives of the present study were:

(1) To understand the nature and extent of competition between the crop and the weeds and also between the weeds themselves.

(2) To demonstrate the importance of nutritional aspects of competition between the crop and the weeds.

(3) To study the importance of below ground and above ground competition and relate differences to features of the root system and/or dry matter production.

(4) To demonstrate the potential importance of barren brome compared to wild oat in relation particularly to nutrient concentration and accumulation as this weed has become increasingly important in some parts of England and Europe in recent years.

In the different sections of this report, investigations are therefore carried out to answer specific questions, as follows.

Section I

1. How do the three species respond to levels of a specific element in water culture? That is, whether the species differ in their response to increase or decrease in the levels of an element in terms of one or more of the following plant attributes:

(a) dry matter production and distribution

(b) Changes in root characteristics, i.e. root thickness, length, surface area, density, area/unit weight of roots etc.

(c) Nutrient concentration (mMol/g DW) and accumulation

(mMol/plant)

(d) Nutrient efficiency (uptake/unit dry weight of roots (mMol/g DW))

(e) Nutrient utilization efficiency (amount of dry matter produced per unit ion uptake (g DW/mMol))

If species are different, what are the possible implications of these findings in the light of soil nutrient status as an important ecological factor determining species adaptation and distribution?

Section II

Studies in the past have determined kinetics of ion uptake of some nutrient elements using excised roots (e.g. Nissen, 1973a, b, 1974 and 1983; Tarawali, 1983; Johnson, 1987) or intact plants (Claassen and Barber, 1974; Lee, 1982; Drew et al., 1984; Becceril-Roman, 1988). These determinations did not use continuously flowing nutrient solutions. One of the objectives of the present study was to develop a method to study differences in the kinetics of P and K uptake in the three species using plants grown in such solutions and if possible to use any differences to explain their responses in competitive and non-competitive situations.

Attempts were therefore made to answer the following specific questions.

(1) Are the species different in their rate of depletion of intial ion concentrations following periods of deprivation?

(2) Do the species differ in the minimum concentration to which they can reduce the solution (Cmin)?

(3) Are the species different in the values of the parameters - Vmax and Km in response to variables such as external ion concentration, duration of deprivation and age of plants?

Section III

Competition commonly occurs within and between species and the main objects of competition are the limiting resources of the environment, mainly light, soil nutrients and water. The ability of a successful species in competition depends mainly on the size of its root system and

the ability of its roots to deplete and cope with variations in nutrient levels in the medium. A species with a greater capacity to tolerate low nutrient levels in competition will reduce the growth of a competitor without this characteristic. Weed species in general are strong competitors in limiting conditions because of their adaptations to a wider range of habitats than crops. The present investigation was therefore structured to determine the competitive abilities of both weed species and the crop and attempts were made to look for evidence relating to the following questions.

(1) Are the species different in their response to intraspecific competition and levels of phosphorus?

(2) What are the effects of increasing population densities of either weed on the growth and nutrient content of the crop? What is the effect of increasing the level of P and K on the competitive ability of the weeds and the crop?

(3) Can de Wit's replacement series technique carried out at varying levels of P and K reveal specific aspects of the competitive inter-relationships between the species? Can we enhance the relative competitiveness of the crop by the addition of a specific nutrient? Are the weeds different in their competitive abilities especially for low levels of an element (P or K)?

Section IV

Differences in the size and morphology of the root systems of the species may have a profound effect on the extraction of nutrients from the soil. For a given mass of the root tissue, long thin roots will have a larger surface area than short thick roots and would be expected to explore the same volume of soil more effectively. Thus differences in the rooting densities of competing species can be a major factor determining the efficiency of uptake and utilization of resources, which may be the reason that one species succeeds at the expense of another.

Investigations in this section were directed towards answering the following questions:

(1) Can we attribute greater competitive abilities of the species to greater root or shoot competition i.e. are the weeds

different in the form of competition affecting the crop?

(2) Are the species different in their responses to root restriction? Do the three species react differently to this treatment in terms of:

(a) production of shoots and roots and their distributions

(b) concentrations, accumulation and distribution of nutrients between shoots and roots?

(c) nutrient uptake efficiency (mMol/unit root dry weight)?

(3) Can the application of a higher level of P compensate for root restriction in any or all of the species?

(4) Are the species different in the growth and distribution of their roots within the soil profile?

4.4 The Biology of *Avena fatua*

Amongst the most successful weed species in the world, as judged by their worldwide distribution and abundance, are wild oat (*Avena fatua* L.) and certain varieties or sub-species of *Avena sterilis* L. of which the sub-species *ludoviciana* is of the greatest agricultural importance (Thurston and Phillipson, 1976).

Avena fatua may have originated as a wild plant in the Pamirs in South West Asia. Its rapid spread by primitive man began in prehistory, continued with settlers from Europe taking their cereal seeds to North America and Australia and still goes on (Elliott *et al.*, 1979). At present *A. fatua* is the characteristic wild oat of Great Britain, North West Europe, North America, North Africa, Central Asia and other regions with a similar climate. In Britain, wild oats have become a serious menace to agriculture on a national scale and there are no longer any major cereal-growing areas free from them. A survey in 1951 (Thurston, 1954) in which 621 samples were examined showed that *A. fatua* was present in all wheat and barley-growing areas of England, in both winter and spring cereals and on all soil types. It was found in 97% of the samples. More recently Chancellor *et al.* (1984) carried out a survey of grass weeds of cereals in 1981 and 1982 in Central Southern England and

reported that Elymus (Agropyron) repens occurred in 35%, Avena fatua in 32%, Alopecurus myosuroides in 26%, Poa trivialis in 24% and Bromus sterilis in 12% of the 1021 fields of winter wheat, spring wheat and winter barley assessed. In the UK A. fatua appears mainly in spring and is therefore mainly associated with spring cereals. It is also present in late-sown winter wheat and winter rye.

Wild oats are annuals, depending on their seeds for survival, multiplication and invasion of new areas. They are capable of producing a large number of seeds. One plant can produce 6750 seeds or more under favourable conditions (Thurston, 1982), though under severe competition it may have only one or two seeds. An 'average' plant in a cereal crop probably bears 40-50 seeds (Cussans, 1976). Chancellor and Peters (1972) reported the total seed production for a wild oat population to be in the range between 944-28,512/m^2. The natural pressure on wild oat, as on other weed species, encourages the production of as many seeds as possible even under adverse conditions. For example Thurston (1951b) reported that under severe manganese deficiency these plants produced the same number of seeds per plant as with adequate manganese, although the average content of the element per seed was less.

Most ripe wild oat seeds have innate or primary dormancy (Johnston, 1935; Thurston, 1963). These seeds are shed directly into the soil and are subsequently ploughed in. Many remain months or years in the soil before germinating, thus avoiding control measures applied immediately following contamination. They produce seedlings in subsequent arable crops for several years, thus increasing the chance of some seedlings appearing in crops in which they can grow and seed freely again. The buried wild oat seed is capable of germinating and emerging from depth. Most seedlings (60-80%) emerge from seeds occurring in the top 7.5 cm of the soil; some can come from as deep as 19 cm (Holroyd, 1964a) or even 23 cm (Thurston, 1951a). Fyske (1970) cited by Chancellor (1976) found that wild oat seeds survived five years in dry soils and 6-9 years in wet, the longest survivals being in heavy soils. Under English conditions, Thurston (1961) reported A. fatua seeds surviving 5 years and 1 month in a heavy clay soil. In Canada, Banting (1962) reported that 5 years was the minimum period for elimination of seeds from heavy clay soils. In an arable field with a mean population of 663 A. fatua plants/m^2 Kurth, (1967; cited by Chancellor, 1976) found that when seeding was completely prevented, the population declined quickly. After

1 year the population was 385 plants per m^2, after 2 years 195/m^2, after 3 years 15/m^2, in the fourth year 0.5/m^2 and thereafter no more plants occurred. The persistence of seed banks in the soil under arable conditions is maintained by environmental conditions and cultural practices which prolong viability as well as dormancy. The burial of the seed by ploughing appeared to aid seed survival (Wilson and Cussans, 1972). Dry soil conditions encourage longer viability of these seeds. Light is known to be inhibitory to the germination of wild oat seed (Black and Naylor, 1957 quoted by Chancellor, 1976) but it did not greatly prolong seed survival. The dormancy of these seeds was also induced by low and high temperatures (Thurston, 1963), thus increasing the chance of seed survival in the soil. On the other hand, cultivation and both high and low temperatures can break dormancy and increase germination (Whybrew, 1964), thus increasing the rate at which the seed is depleted from the soil. The application of herbicides to the parent affected seed viability and dormancy as did other chemicals like nitrogenous fertilizers, gibberellic acid and sulphuric acid (Sexsmith and Pittman, 1963; Hay and Cumming, 1959) although none of these eradicated the seed in the soil.

4.5 The Biology of *Bromus sterilis*

The *Bromus* species (brome grasses) are believed to have originated in the Mediterranean region, but are predominantly distributed in the Northern temperate zone. They are found in Britain, Central and South Europe, South Scandinavia, South-West Asia, North and South America and some mountainous regions of the Tropics (Behrendt and Hanf, 1979). Some are valuable fodder grasses and a number of them are weeds of cereal crops among which *Bromus sterilis* (barren brome) is of agronomic importance. In the United Kingdom barren brome was described as an annual, occasionally biennial or rarely perennial grass of dry, shady and waste places (Love, 1862, cited by Froud-Williams *et al.*, 1980); field margins, hedgerows and headlands (Pollard, 1982; Froud-William, 1982; Hilton, 1982). Long (1910), Brenchley (1920) and Morze and Palmer (1925) classified barren brome as a weed of pastures. It has not until recently been considered an important arable weed in England although it was reported as a problem at Drayton Experimental Husbandry Farm in the mid-1960s (Anon, 1967; Whybrew, 1969). Broad (1952), Gooch (1963), Tonkin and

Phillipson (1973) and Budd (1981) reported the presence of barren brome seeds in cereal seed samples. Since the mid-1970s barren brome has become increasingly important as a weed of early-sown winter cereals established by minimal cultivation techniques (Froud-Williams et al, 1980). It encroached from field margins, partly as a consequence of moving straw from headlands during preparation of fire-breaks prior to stubble-burning. Its spread has been further facilitated by harvesting machinery (Anon, 1981). A survey of grass weeds in cereals in nine areas of Central Southern England was made by Froud-Williams and Chancellor (1982) in summer 1981 with the primary purpose of determining the importance of Bromus sterilis. Of the 2192 fields of winter cereals assessed in this survey 206 had B. sterilis growing within the area planted to the crop and a further 147 had the weed growing in the hedge or along the field margins outside the cropping area. This was 16% of all the fields surveyed. It was found to occur more frequently in wheat than in barley fields and this could be due to the greater competitive ability of the latter (Pavlychenko, 1937). Grime and Hunt (1975) described barren brome as a potential weed possessing relatively fast growth rate. Gray (1981) found it a competitive weed which could reduce yield and increase lodging and Gwynne et al. (1985) put it on a par with blackgrass. The weed may produce more than 200 seeds/plant in a crop and very few infertile seeds are produced (Froud-Williams et al., 1980). Most seeds of barren brome are shed from late June to early August and most germinate between late summer and early autumn, provided that soil moisture is adequate (Froud-Williams et al., 1980). The seed has little innate dormancy, but a small percentage of seed may have dormancy enforced as a result of exposure to moisture stress, low temperature or daylight (Froud-Williams, 1981a; Gray, 1981). In contrast to many weed seeds in which germination is reduced in the dark and promoted by light, barren brome has germination inhibited by light (Hulbert, 1955; Grime and Jarvis, 1975). Subsequently, Hilton (1982) demonstrated that light-enforced dormancy is an unusual response resulting from photo-inhibition of germination by Pfr (the active form of the plant pigment phytochrome). Unlike other dark-germinating species, she found that the seeds contained very little pre-existing Pfr and did not produce Pfr in darkness. Further, the inhibitory effect of Pfr is markedly increased by low moisture status and temperatures lower than 15°C (Hilton, 1984). Temperatures higher than 15°C were also inhibitory to germination, but at these temperatures Hilton did not find additional inhibitory effect mediated by Pfr. It was

concluded, therefore, that germination of barren brome seeds in the soil can be delayed greatly from the time they were shed in autumn until the following spring by the interaction of these environmental factors. Nonetheless, the seed does not persist longer than one year in the soil, forming only a transient seed bank (Thompson and Grime, 1979), unlike wild oat (Avena fatua and A. sterilis ssp. ludoviciana) which are capable of surviving or remaining dormant for several years if incorporated into the soil. Burial did not appear to enforce dormancy in barren brome and seeds buried below 13 cm were unable to emerge (Froud-Williams et al., 1980; Gray, 1981). Thus burial of seeds by ploughing to a depth of 20 cm should be an effective means of eradicating the weed in areas where farmers are not committed to minimal cultivation of systems (Froud-Williams , 1983). Where minimal cultivations are practised, crop rotation or the inclusion of a spring-sown crop which would break the seed's cycle had been considered as the only effective means of cultural control (Froud-Williams et al. 1980). The control of the weed by chemical means has been ineffective (Froud-Williams et al., 1980; Orson, 1981; Pollard and Richardson, 1981) because of its resistance to herbicides commonly employed to control blackgrass, wild oat and other grass weeds. In general, headland hygiene has been suggested as a very important means of preventing the spread of the weed throughout a crop field.

SECTION I



Plate 1 Invasion of a wheat field by barren brome plants. Drooping heads of the weed may be seen emerging from an infested crop

SECTION I

The Response of *Avena fatua*, *Bromus sterilis* and wheat to differential nutrition of phosphorus, potassium, calcium and magnesium in water culture experiments

5.1 ABSTRACT

The responses of winter wheat, wild oat, barren brome and tef to a range of different levels of N, P, K, Ca and Mg were studied in water culture experiments under glasshouse conditions.

N deficiency seriously reduced the dry matter yield of wheat, wild oat and barren brome. Wheat generally responded to increases in the levels of all nutrients except K, where it was more tolerant to low levels of the elements than barren brome. Wild oat was less responsive to variations in the levels of P, K and Mg whilst barren brome was more sensitive to these elements than the former. The response of tef to levels of Ca showed that the growth of the crop was seriously reduced and deficiency symptoms were observed at the lowest level. Although barren brome gave the smallest plants, it always produced finer roots and a greater length of roots per unit dry weight than wheat or wild oat.

Nutrient concentrations (mMol/g DW) and uptake efficiencies (mMol/g root DW) were generally higher for the weeds, especially barren brome. Total nutrient contents (mMol/plant) and utilization efficiencies (g/mMol) were however, generally greater for wheat and/or wild oat. The total amount of N, P, K, Ca and Mg in tef was greater than for wheat and barren brome.

The agronomic and ecological significance of these observations are discussed in relation to the requirement of the species and their ability to compete for limiting resources of these nutrients.

SECTION I

5.2. Introduction

The answers to questions such as why certain plant species live where they live and not in other places has been explained by the adaptive mechanisms of these organisms to soil nutrients and other related factors of the soil. Adaptive success implies that the plant uses the environment advantageously for its physiological needs and that it tolerates those features of the environment which are inimical to it (Epstein, 1972, Chapter 13). Plant adaptation and distribution is a function of both morphological and physiological mechanisms. For example, Bradshaw (1965) stated that plants have become adapted to their mineral habitats as they have become adapted to all conditions of life, through the evolution of a vast range of genotypes. It is commonly observed that when plants of the same species, naturally growing at different locations, are grown together in the same experimental area for several years, they retain the features characterising the plants in their original habitat. Chapin (1983) working with grasses and trees of both high-nutrient adapted and low-nutrient adapted species identified some adaptive mechanisms that could be important for effective growth in infertile soils. These were:

1. differences in nutrient metabolism and efficiency in use of nutrients to produce new biomass.
2. a high capacity to extract nutrients from soil.
3. a slow growth rate that minimizes nutrient requirement and prevents exhaustion of internal nutrient reserves.

Similar observations were also made by Grime and Hunt (1975) and Rorison (1968). Because of the adaptive mechanisms, populations of plants with distinct and marked responses to particular nutrients were found among and within species. A wide range of nutritional adaptations for uptake, translocation, utilization and distribution between species has been reported (e.g. Bradshaw and Snaydon, 1959; Bradshaw et al., 1958, 1960a,b, 1964; Gerloff, 1963, 1977; Ramakrishnan, 1968, 1969; Rorison, 1968; Turner, 1969; Antonovics et al., 1971; Epstein, 1972; Dunlop and Tomkins, 1976; Hoveland et al., 1976; Chapin, 1980, 1983). These

differences were also reported within species (e.g. Lyness, 1936; Jowett, 1959, 1964; Vose, 1963; Crossley and Bradshaw, 1968; Snaydon and Bradshaw, 1961, 1969; Davies and Snaydon, 1973a,b, 1974; Glass and Perley, 1980; Jensen and Petersson, 1980; Glass et al., 1981; Lafever, 1981) and among varieties i.e. genotypes and inbred lines of crop species (e.g. Gregory and Crowther, 1928; De Turk et al., 1933; Foy and Barber, 1958; Gorsline et al., 1964; Clark, 1975, 1978, 1983; Lafever, 1977; Nielsen and Schjorring, 1983).

One of the earliest citations of differential uptake and use of a nutrient was that of Boucet (1899) mentioned by Vose (1963) for iodine. Later specific and preferential requirements for nutrients were identified in many crop species. Examples include N, P and K in barley varieties by Gregory and Crowther (1928) and Fe in soybeans (Weiss, 1943).

In recent years high yields have been attained in food crops through the selection of varieties which demonstrated favourable responses to high fertilizer applications. However, because of the increasingly high cost of fertilizers, it was necessary to isolate strains of crop plants which possess mechanisms that enable the use of limited nutrient resource and effectively compete with weeds. Because competition exists between crop and weed plants, a relatively small difference between these species in response to a limiting nutrient may result in the replacement of one by the other. Crop plants are normally associated with soils of high fertility whilst it is one of the characteristics of weeds that they can grow and reproduce in a wide range of environmental conditions (Baker, 1974) including soils of very low fertility. Therefore, in crop-weed competition situations, particularly where such two species compete for the same limiting nutrient(s), a greater efficiency of uptake and use (expected of the weeds) will be of a competitive advantage (Dunlop and Tomkins, 1979 and Glass and Perley, 1980). Evidence of the fact that weeds are adapted to low fertility levels is plentiful in literature. For example, the presence and growth of some weed species in the field were used as indicators of 'nutritional disease'. Schipstra (1957) cited in Hoveland et al. (1976) reported that K deficiency in rye (Scale cereale 1.) was associated with the weeds Chrysanthemum leucanthemum L. and Ranunculus repens L. while P deficiency was associated with common lambsquarters (Chenopodium album L.). Singh and Singh (1939) noted that the weeds which belong to the genera Amaranthus, Cleome, Chenopodium and

Portulaca were particularly efficient in the uptake of potassium from low levels in the soil. Hoveland et al. (1976) found that in general weeds were sensitive to low soil K than were to low soil P and shifts in predominant weed species commonly occurred when a particular species was given only a slight competitive advantage through its response or lack of response to P or K. For example, the superior growth of showy crotalaria to Florida begger-weed (Desmodium tortuosum (Sw) Dc. in response to low P was an important competitive advantage to the former. Instances of differential responses of crop, pasture and weed species to specific nutrients and other soil factors like heavy metal presence and soil salinity, have been commonly reported and the mechanism(s) underlying these variations identified. Gerloff (1977) and Shenk and Barber (1980) indicated processes including absorption, translocation, utilization, detoxification and metabolic factors such as enzyme activity, together with root morphology (i.e. root branching, distribution patterns, surface area, volume and weight) as the factors responsible for difference between and among species in response to available nutrients. These plant characteristics which determine the efficiency or inefficiency of nutrient uptake and utilization are known to be under genetic control (Lyness, 1936; Vose, 1963; Shea et al., 1967; Jefferies et al., 1969; Dunlop and Tomkins, 1970; Epstein, 1972; Clark, 1978; Sarić, 1981; Nielson and Schjorring, 1982).

Gross differences in the morphology of roots of species growing together in solution cultures may be expected to result in parallel variations in the uptake of plant nutrients owing to the fact that the root characteristics are the chief determinants of uptake. Rorison (1968) grew four ecologically distinct species in solution cultures containing a range of phosphorus concentrations to determine whether they differed in their rates of growth and P uptake. He found that the four species differed in their relative growth rates, P absorption and concentration. These species were also found to vary in the number and extent of their secondary root systems and the development of root hairs. Species which had a higher content of P also produced larger numbers of root hairs, whilst others had thicker roots. Bradshaw et al. (1960b) reported the complete lack of response of Nardus stricta to phosphorus level in sand culture and correlated this with its ability to grow in the poorest soil conditions. Snaydon and Bradshaw (1962a) reported a marked correlation between the response of populations of Trifolium repens L. to

phosphate at low levels and the amount of phosphate in the native soil of these populations. They reported that populations from soils high in P showed larger reductions in growth at low P level than did those from low P soils. It was concluded that the response to P was one aspect of the physiological adaptation of the natural populations to particular conditions. They also found that populations tolerant to low P level had higher concentrations of P in the shoot material and a higher uptake of P per unit weight of roots than did those intolerant of low P. The differences between the populations in response to P were believed to be due to differences in uptake rather than to differences in metabolic requirements. The evidence that species differ in ability to absorb P from solution was also demonstrated by Noggle and Fried (1960). However, the results of Lawton and Davis (1956) and Nye and Foster (1958) indicated that species did not differ in ability to exploit relatively high P reserves, but only in ability to utilize P at low concentration in the soil solution. Hackett (1968) studied the root systems of barley varieties in response to P and K deficiencies and reported the number of axes and length of primary laterals to be greatly reduced by both nutrients. Johnson (1987) also reported differential response in root growth and morphology in wheat and blackgrass (A. myosuroides L.) induced by P supply in solution. He found that under low P in solution blackgrass had a lower shoot/root ratio, higher length to root weight ratio (density) and was generally more efficient in absorbing nutrients than wheat. At higher P concentration in solution he reported that the opposite was true for the crop. Tarawali (1983) working on the same two species reported a lower shoot/root ratio for blackgrass than wheat.

The available literature on the biology and control of wild oats (both A. fatua and A. ludoviciana) is extensive but reports on the requirements and general response of wild oats to the major nutrients are scarce. Thurston (1959) reported that the wild oat absorbed the same amount of N as winter wheat from nutrient solutions, but Koch and Kocher (1968) found that N absorption by wild oat from a solution culture was less than that of wheat. It was also reported that the nitrogen content of the nutrient solutions affected the root/shoot ratio of A. fatua. It was also found that wild oat assimilated less potassium than barley (Sinyagin, 1966, quoted by Chancellor and Peters, 1976).

The importance of barren brome as an economic weed problem has only recently developed, hence little is known about its nutritional

requirements and competitive ability with crops it infests. Grime and Hunt (1975) described it as a potential weed possessing a relatively fast growth rate. Gray (1981) reported it as a competitive weed which reduced wheat grain yield and increased lodging while Gwynne and Murray (1985) reported it to be at least on a par with blackgrass. The only evidence available about the nutrition of barren brome is that of Gray (1981) who carried out a series of competition experiments with winter wheat and barley for N, P and K. He found that wheat was competitively superior to brome for N and P, while brome was more competitive for K. However, he did not investigate the underlying mechanisms as the possible causes for the differences, which could have been due in part to the differential root growth response to these nutrients or differences in uptake kinetics.

The main aim of the present investigation was to look for evidence of differential responses of wheat, wild oat and barren brome to the levels of N, P, K, Ca and Mg in solution culture and relate where possible any observed differences to the nutritional backgrounds of these species. Hence, the amount of each of these major nutrients in the solution was considered as a factor which may alter the growth and inorganic composition of these species. It was reported (Fageria, 1973) that cell permeability, enzyme activities, respiration and growth rates were influenced to a greater or lesser extent by the inorganic composition of the medium, which in turn may affect the rate of ion absorption.

The experiments in this chapter were carried out to achieve the following specific objectives:

(1) To determine differences between responses of wheat, wild oat and barren brome in dry matter production.

(2) To look for differences in root characteristics of the species i.e. variations in root weight, length, surface area, density, etc.

(3) To determine differences in uptake and accumulation for N, P, K, Ca and Mg in the species demonstrated by:

(i) Concentrations in shoots, roots and whole plants.

(ii) Total contents in roots, shoots and whole plants.

(4) To determine 'root efficiency'. This may be expressed as the rate

of uptake per unit weight of root (Williams, 1948) but may also be expressed using root length, surface area, volume or even number (Hunt, 1978).

(5) To determine differences in responses to 'utilization efficiency'. A mineral efficient plant, as defined and used in this section, is a species which grows better, produces more dry matter for each unit of nutrient taken up and develops fewer deficiency symptoms than other species particularly when grown at low levels of a mineral element.

(6) To study the effect of varying independently the levels of N, P, K, Ca and Mg on the uptake of the others i.e. nutrient interactions.

5.3. Materials and Methods (General)

Wild oat seeds were obtained from B and S Weed Seed Supplies of Whatton - in - the - Vale, Nottinghamshire. Seeds of barren brome were collected from headlands and field margins in and around Wye College farm during the period September to November. Wheat (cv. Avalon) was purchased from a seed merchant. The majority of wild oat seeds failed to germinate initially while those of barren brome germinate freely. Increase in the number of germinating wild oat seeds was, therefore, obtained by treating with 50% H_2SO_4 for 3-3½ hours followed by thorough cleaning by violent shaking in a flask containing a large volume of water and a small handful of coarse grit. The remaining seeds were then washed with several changes of tap water to remove remaining particles of the husk and any residual acid. Prior to sowing free water on seeds was removed using paper towels. Nutrient-free soiless compost in seed trays was used as a medium for germination and distilled water applied when necessary. Germination and all subsequent stages took place in the glasshouse. Wild oat, barren brome and wheat seeds germinated and seedlings appeared at about the same time. The time to reach the transplanting stage (1-2 leaves) did differ. Barren brome seedlings grew at a slower rate than the other two species during the first few weeks and were therefore sown 5-7 days earlier.

When the seedlings reached the 1-2 leaf stage, they were transferred to a nutrient film technique (NFT) installation based on those described by Cooper (1979). The advantages and limitations of this technique are

given by Johnson (1987). The main parts of the NFT installation consisted of plastic channels (4 m by 10 cm) made from domestic guttering, 15 l capacity reservoirs made from buckets for holding the nutrient solutions and circulating pumps, each pumping the solution into a pair of channels. In order to facilitate the flow of the solution along the channels to the reservoirs and avoid any localized depressions, the entry end was raised about 5-7 cm above the bench. Nutrient solutions (10 l) prepared on the basis of Cooper's nutrient recipe (1979) were circulated at a flow rate of 1 l per minute.

Uniform seedlings from each of the species were selected and transplanted into 5 cm open-mesh plastic pots filled with Perlite as an absorbent and support. A polythene sheet covering the entire length of the channel allowed the placement and support of the pots in holes 15 cm apart. As the root grows, it passes through the perforated body of the pots into the channel, where it comes into direct contact with the shallow stream of recirculating solution. There were 24 plants, eight of each species per channel. The species were planted in the same systematic order along the length of the channel forming groups of three. Attempts were made to prevent algal growth on exposed top parts of the pots using pieces of the polythene sheet cut to fit and placed around the base of the plants. Plants were also periodically sprayed with "Milgo E", containing Ethirimol at 280 mg l^{-1} to control mildew which particularly affected the wheat.

The circulating solution consisted of all the required elements, at approximately optimum levels, except the nutrient under investigation which was varied to give a range of concentrations. Except for the first two weeks the solution was normally changed weekly. A daily estimate of the concentration of total elements in solution was obtained using a portable conductivity meter. When the conductivity (cF) fell below 2 mMhos at any time between solution changes, sufficient nutrients were added to increase it to a value around 2.5 mMhos. The pH of the solution was also adjusted daily to a value of 6 ± 0.2 using 0.1N H_2SO_4 or HNO_3 and NaOH. Distilled water was used to top up solutions between renewals, the quantity added depending on the growth of the plants.

The design of these experiments was of the completely randomized type with species, treatment levels and harvests as factors. Four replicates were used and enough plants were raised from each species to

allow three consecutive harvests. Unless otherwise stated the first harvest was taken four weeks after transplanting and the next two at weekly intervals. At each harvest four plants per species were selected at random and harvested. Roots and shoots were separated, washed with tap water and rinsed with distilled water. Unless otherwise mentioned plant attributes such as root and shoot fresh and dry weights and number of tillers were recorded at each harvest. Other root variates, including volume, radius, length, surface area etc. were obtained by direct measurement or calculated for the second harvest only. Root volume was determined by a displacement method using the apparatus described by Andrew (1966). The root length estimates were obtained either using a Comair root length scanner at the Institute of Horticultural Research, East Malling or the line intercept method explained by Tennant (1975). The mean root radius (r_o) was calculated from $r_o = (FW/\pi L)^{\frac{1}{2}}$, (Fontes et al., 1986); where FW was root fresh weight in grams and L the root length in cm. This formula was used on the assumption that roots were cylinders with specific gravity equal to 1.0. The root surface area (RSA) was calculated from $RSA = 2\pi r_o L$.

Unless otherwise specified for a particular experiment, analyses for nutrient concentrations of the roots and shoots were carried out for harvest 2 and 3 only.

Roots and shoots were oven-dried at 70°C for up to 3 days before dry weight was recorded. The dry plant material was finely ground in a small hammer (ball) mill to pass through a 0.5 mm sieve. Sub-samples of 150 to 200 mg of each ground sample were weighed into a glass vial and ashed in a muffle furnace at 450-480°C for 4-6 hours. The ashed sample was dissolved in a few drops of concentrated hydrochloric acid and transferred after dissolution was complete (approximately 10 min) into 100 cc volumetric flask. Deionized water only was used to transfer the sample and the solution was topped up to the mark. Samples were drawn from each solution to determine phosphorus, potassium, calcium and magnesium. Phosphorus was determined colorimetrically by the vanado-molybdate method and potassium by flame photometry. Calcium and magnesium were determined by atomic absorption spectrometry. In order to be able to remove any depressive effects due to interference from other elements such as aluminium phosphates ($PO_4^{\equiv}$) a releasing agent made up of strontium chloride/perchloric acid [60 g $SrCl_2 \cdot 6H_2O$+60% $HClO_4$ (100 ml/litre)] was added at a rate of 1:10 (v/v) to the samples and standards

before determining calcium and magnesium.

Materials and Methods Specific to Individual Experiments

Experiment 1.1: The response of wild oat, barren brome and wheat to low levels of nitrogen, phosphorus or potassium

Barren brome seeds were sown on 14/3/87 and those of wheat and wild oat on 19/3/87. Germinating seeds were kept in a glasshouse cubicle (25/25°C day/night mean temperatures) till seedling emergence and thereafter removed to a cubicle where the day/night mean temperatures were 16/14°C respectively. When the seedlings reached the transplanting stage, they were transferred to the NFT installation in the same cubicle on 29/3/87. The seedlings were treated with the following solutions.

(L1) NPK (full strength Cooper solution)
(L2) 1.43 mM (20 ppm N) - other elements at full strength
(L3) 0.06 mM (2 ppm P) - other elements at full strength
(L4) 0.38 mM (15 ppm K) - other elements at full strength

During the entire period of the experiment daily maximum, minimum and mean air temperatures of the cubicle were recorded and the overall means of each for the period were 32.2, 15.0 and 23.6°C respectively.

Three consecutive harvests were taken and at each harvest the root and shoot variates described earlier were determined.

Experiment 1.2: Response of Avena fatua, barren brome and wheat to levels of phosphorus

Barren brome seeds were sown on 18/6/87 and wild oat and wheat on 24/6/87. All seedlings were ready for transplanting 10 days after this date. Seeds were germinated and seedlings grown in the same cubicle whose maximum, minimum and mean air temperatures were 32.1, 18.9 and 25.5°C respectively for the period up to the last harvest. During this period plants were supplied with solutions containing four different phosphorus levels applied at two weeks intervals:

(L1) 1.94 mM (60 ppm P)
(L2) 0.97 mM (30 ppm P)
(L3) 0.48 mM (15 ppm P)
(L4) 0.06 mM (2 ppm P)

The concentrations were obtained by reducing the amount of KH_2PO_4 and replacing the potassium with K_2SO_4. The experiment ended on 18/8/87.

Experiment 1.3: Response to levels of potassium

The range of K concentrations used in this experiment extended both above and below that used as the low K treatment in Experiment 1. Treatments were thus:

(L1) 7.69 mM (300 ppm K)
(L2) 2.56 mM (100 ppm K)
(L3) 0.38 mM (15 ppm K)
(L4) 0.13 mM (5 ppm K)

These concentrations were obtained by reducing the amounts of KNO_3 or KH_2PO_4 and replacing the nitrate and phosphate with $NaNO_3$ and $NaH_2PO_4.2H_2O$ respectively.

Barren brome seeds were sown on 12/7/87 and five days later wheat and wild oat were planted. All seedlings were transplanted on 26/7/87. The cubicle air temperature for the entire growth period was recorded as 32.2, 17.5, and 24.9°C for maximum, minimum and mean daily temperatures respectively.

In this experiment solutions were renewed every two weeks. The experiment terminated at the end of the sixth week after transplanting.

Experiment 1.4: Response to levels of magnesium

Barren brome seeds were sown on 30/7/87 and wheat and wild oat on 3/8/87. On 12/8/87 a number of seedlings were transplanted to NFT channels. Three levels of Mg were used:

(L1) 2.08 mM (50 ppm Mg)
(L2) 1.04 mM (25 ppm Mg)
(L3) 0.21 mM (5 ppm Mg)

Levels 2 and 3 were obtained by reducing the amount of $MgSO_4.7H_2O$. Solutions were renewed once every two weeks. The air temperature in which the seedlings were grown was recorded as 30.4, 17.3 and 23.8°C for maximum, minimum and mean daily temperatures respectively. This experiment ended on 25/9/87.

Experiment 1.5: Response to levels of calcium

The response of the species to various concentrations of calcium in solution was studied in two separate experiments. The first experiment involved wheat, barren brome and tef (Eragrostis tef), a cereal crop indigenous to and of great importance in Ethiopia, and was carried out during the summer of 1986.

Barren brome and wheat seeds were sown on the same day (4/6/86) and tef seeds a week earlier on 27/5/86. Seedlings were transplanted on 24/6/86.

Four levels of calcium were obtained by making appropriate reductions in $Ca(NO_3)_2 \cdot 4H_2O$ and $NaNO_3$ was used to replace the reduced levels of nitrate. Levels used were:

(L1) 4.15 mM (170 ppm Ca)
(L2) 2.13 mM (85 ppm Ca)
(L3) 1.06 mM (42.5 ppm Ca)
(L4) 0.27 mM (10.6 ppm Ca)

The quantity of circulating solution was 14 l in this experiment and pH was maintained at between 5.8-6.2. The whole solution was changed whenever CF in any one of the containers fell below 2 mMhos or rose above 3 mMhos. This time varied between 7 and 10 days. Three consecutive harvests were made at weekly intervals commencing the end of the 4th week from transplanting. At each harvest, tiller number, shoot and root dry weights only were recorded.

Attempts were made to carry out tissue chemical analysis to determine nitrogen, phosphorus, potassium, calcium and magnesium from a single digest. The method was a modified version of that of Allen et al. (1986) and involved the addition of 5 ml of a 0.2% (w/v) solution of selenium dioxide in concentrated H_2SO_4 and then a drop of H_2O_2. Initially digestion had to proceed at low temperature (150-200°C) in heating blocks to avoid H_2SO_4 fumes. Eventually the temperature was increased to up to 320°C and the digestion continued until a clear solution was obtained. A total of 3-3½ hours was required for this. After the boiling tubes were removed and the solution cooled, 5 ml deionized water was added cautiously and tubes swirled. The solution was transferred into a volumetric flask (100 ml) and topped up to the mark with

deionized water. Solutions were sampled to determine the different plant nutrients. Total nitrogen was determined colorimetrically by the salicylate method (AOAC, 1984). Phosphorus, potassium, calcium and magnesium were determined in the same manner as in the dry ashing method. A releasing agent (1:10) made up of lanthanum oxide/hydrochloric acid (4.7 g La_2O_3 + 25 ml HCl/litre) was added to prevent refractory compounds of aluminium, phosphorus and other elements interfering. The determination of phosphorus in this method involved a routine and time-consuming practice of adjusting pH of sample solutions; the dry ash method was used in all other experiments for this reason. Nitrogen was, therefore, determined only in this experiment.

5.4. Results

It was the initial intention to present the data for all three harvests. Eventually it was decided to present only those for the second harvest because (1) results in all harvests showed similar trends in most cases, and (2) the data were so extensive that a full presentation would have been excessively long. Differences between harvests, where they occurred, are noted in the text.

The nutrient requirements of plants may be determined by observing the effects of added nutrients on their growth and measuring the quantities (both concentration and amount) of inorganic substances present in their tissues. The responses of whole plants of wheat, wild oat and barren brome and especially their root systems, were examined by growing without nutrient stress and when certain nutrients were limiting. In the text below the notation -N, -P, etc. is used to refer to the stressed treatments, though these did not involve the total absence of the relevant nutrient from the medium.

Experiment 1

Shoots: The deficiency of N more seriously retarded the growth of shoots than P and K deficiencies (Table 1.1), though reduction in all three nutrients had a significant effect. When these nutrients were supplied at optimum levels, wheat plants were larger than those of the other species. Barren brome was the species most affected and wild oat was least sensitive, particularly to P and K deficiencies. In P and K

Table 1.1 Effects of N, P, K nutrition on some growth variates of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT (Harvest II)

	Shoot dry weight (g/plant)	Root dry weight (g/plant)	Whole plant weight (g/plant)	Root/shoot ratio	Root radius(cm)	Total root length (m/plant)	Total surface area (cm^2/plant)	Root length/root dry weight	Surface area/root dry weight
C (complete)									
W	12.67	4.16	16.83	0.33	0.013	884.0	7380.0	214.0	1779.0
WO	8.15	2.07	10.22	0.26	0.013	472.7	3788.0	230.6	1840.0
BB	4.63	1.49	6.12	0.32	0.010	511.0	3111.0	345.1	2094.0
-N ($\frac{1}{20}$)									
W	1.76	1.38	3.14	0.79	0.011	377.5	2591.0	312.5	2100.0
WO	1.22	0.74	1.96	0.55	0.011	204.1	1378.0	292.9	1910.0
BB	0.48	0.66	1.14	1.39	0.008	308.4	1617.0	485.9	2557.0
-P ($\frac{1}{20}$)									
W	4.68	1.98	6.66	0.42	0.014	311.8	2817.0	157.3	1421.0
WO	5.04	1.41	6.45	0.31	0.014	316.4	2680.0	240.3	2042.0
BB	0.81	0.37	1.18	0.46	0.010	109.8	692.0	308.6	1957.0
-K ($\frac{1}{20}$)									
W	5.26	2.11	7.37	0.40	0.016	361.1	3633.0	179.0	1805.0
WO	6.43	1.20	7.63	0.19	0.017	192.2	2057.0	163.4	1761.0
BB	1.58	0.37	1.95	0.23	0.009	174.7	983.0	488.8	2722.0
Significance level									
SP.	***	***	***	***	***	***	***	***	***
Nut.	***	***	***	***	***	***	***	***	NS
SP*Nut.	***	***	***	***	***	***	***	***	NS
LSD ($P < 0.05$)									
SP.	0.51	0.22	0.51	0.11	0.001	30.1	230.1	48.8	274.4
Nut.	0.58	0.25	0.59	0.13	0.001	34.8	265.8	56.4	-
SP*Nut.	1.01	0.44	1.02	0.22	0.002	60.2	460.4	97.7	-

deficient solutions, the mean dry matter yield of wheat was similar while those of wild oat and barren brome were different. At the first harvest all three species were more affected by -K than -N.

Roots: Root weights showed trends very similar to those of shoots and were most affected by N supply. The species produced well below 50% of the control growth when N was deficient. In contrast to the shoot results root weight in barren brome was less affected by N deficiency than wheat and wild oat, but was the species most affected when P and K were limiting.

Whole plant weight: The mean whole plant yield of barren brome was less than that of wheat and wild oat, except in -N where it was similar to that of wild oat. Where P or K were deficient weights of wheat were similar to those of wild oat. The mean yield per plant of barren brome was similar in each of the deficient solutions as was wheat mean yield in -P or -K treatments. Wild oat, however, differed between nutrient deficiencies.

Root/shoot ratio: The species had similar ratios in the complete -P and -K treatments, but when N was deficient all were different and that of barren brome was about 2 and 2.5 times larger than that of wheat and wild oat respectively. At the first harvest the -K treatment differed from the second in that barren brome showed a significantly lower ratio.

Root radius: The estimates for root thickness varied with species, treatments and their interactions (Table 1.1). The thinnest roots were produced by barren brome in all treatments. All species had their thinnest roots in P deficient solution. The root thicknesses of wheat and wild oat were similar in all treatments, that of barren brome always being less than either.

Total root length: The species differed in total root length per plant (Table 1.1). Wheat produced the longest root system in all treatment combinations, except -P where wheat and wild oat were similar. The two weeds had similar lengths of root in the complete and -K treatments, but differed in -N and -P. Barren brome produced longer roots in -N than wild oat, while the latter had a greater root system in -P than the former. At the first harvest barren brome had the smallest root system in all the treatments. In -N and -P treatments wild oat was greater in root length than wheat, but in the control and -K, that of wheat was

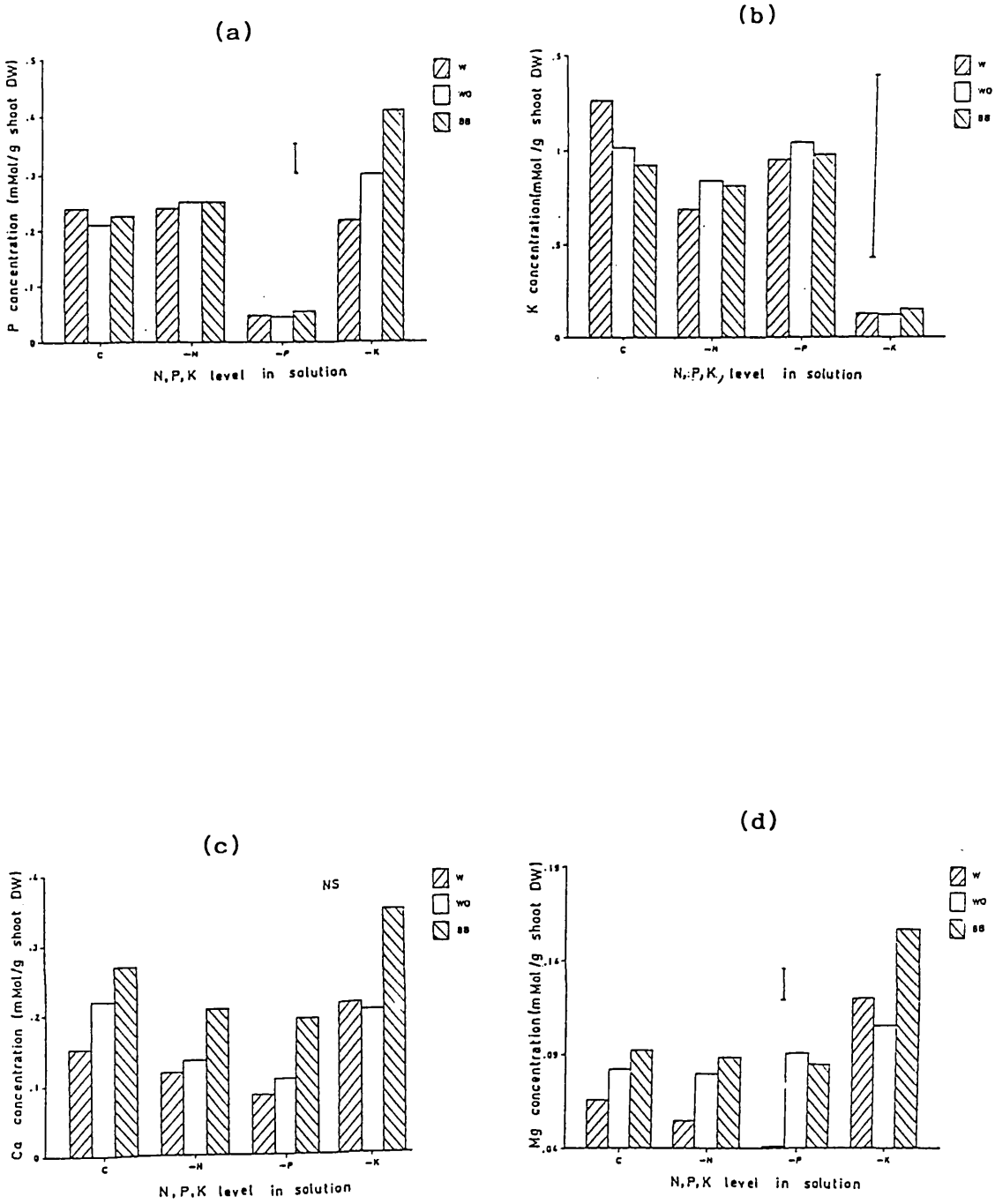


Figure 1.1 (a-d) Effects of N, P and K nutrition on the concentrations (mMol/g shoot DW) of P, K, Ca and Mg in wheat (W), wild oat (WO) and barren brome grown in NFT (Harvest II)

Vertical bars represent LSD at 5% level of probability

NS = no significant different

greater.

Total root surface area: The species differed in their total area of root surface produced (Table 1.1). Wheat again had a greater surface area of root than wild oat or barren brome except at -P where it was similar to wild oat. Barren brome was the smallest at all treatments, except -P where it was similar to the other species. At the first and the third harvests, wild oat significantly exceeded wheat in surface area in the -P treatment.

Total root length/unit root dry weight: Similar responses of the species were noted as for their root radii, i.e. the species which had the thinnest roots (barren brome) produced the longest root system per unit root dry weight. The thinnest roots observed for -P treatments in all the species also correspond to the longest root per unit weight. Wheat and wild oat which were similar in root thickness, also had similar length of root per unit root dry weight.

Root surface area per unit root dry weight: Barren brome produced the largest surface area/unit dry weight of roots. Wild oat also had a greater area per unit weight of root than wheat, although the difference was not statistically significant. In all the treatments except -P, where both weeds were similar, barren brome had longer roots than wild oat, although the differences did not reach statistical significance. At the third harvest wild oat produced greater area per unit dry weight than barren brome, while the latter had more surface area than the former when the treatments were -N and -K.

Nutrient concentration

P: Summed over all treatments barren brome had the highest P tissue concentration (Figure 1.1a). Wild oat was higher than wheat, but not significantly. Except in the -K treatment the species did not differ. At harvest 3, barren brome and wheat were similar but higher than wild oat. In the -P treatment, P concentrations were similar in all species and wheat and wild oat were similar in -N and -K, whilst barren brome and wild oat also were similar in C and -N. P concentration in -K was different for barren brome and in C wheat had the highest concentration.

K: The K concentration of the species was similar in all treatments except the control where it was greater in wheat than in barren brome. At the third harvest wheat had a higher K concentration than either of

Table 1.2 Effects of N, P and K nutrition on the total uptake (mMol/plant) of P, K, Ca and Mg in wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

	C (complete)			-N			-P			-K			Significance level			LSD (P 0.05)		
	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB	SP	Nut	SP*Nut	SP	Nut	SP*Nut
P	4.06	2.17	1.39	0.75	0.47	0.28	0.33	0.30	0.06	1.62	2.34	0.81	***	***	***	0.247	0.285	0.493
K	21.27	10.23	5.67	2.20	1.54	0.94	6.59	6.76	1.13	0.96	0.91	0.29	***	***	***	0.637	0.734	1.271
Ca	2.55	2.24	1.65	0.37	0.26	0.24	0.58	0.70	0.23	1.58	1.57	0.67	***	***	*	0.182	0.210	0.364
Mg	1.11	0.84	0.56	0.18	0.15	0.10	0.28	0.59	0.10	0.89	0.81	0.31	***	***	***	0.073	0.085	0.147

the weeds in the control.

Ca: Summed over all treatments the species differed in Ca concentration. Both weeds and especially barren brome had higher concentration than wheat. In all species Ca concentrations were highest in either the -K or the control treatment (Figure 1.1c).

Mg: Summed over all the treatments both weeds had higher Mg concentration than the crop with barren brome being the highest. The weeds contained similar Mg tissue concentrations in all treatments except when K was limiting where barren brome exceeded wild oat. The crop was similar to wild oat in the control and -K treatments.

Total nutrient content

P: The crop acumulated more P than either weed (Table 1.2). The highest amounts in all the species occurred in the control and -K treatments. The species did not differ in total P in -N and -P treatments but at the third harvet all differed in all the treatments except -P.

K: Summed over all treatments total K in wheat was the greatest. This occurred in the control treatment where the weeds also had their greatest amounts (Table 1.2). In -N and -K treatments all had similar amounts of K, though at the third harvest, all differed except in -K where wheat and wild oat were similar.

Ca: Summed over all treatments barren brome had the lowest total calcium. Wheat and wild oat had higher, but similar amounts in all treatments (Table 1.2). At the third harvest wild oat accumulated more than the other species except in -N where all were similar. All species accumulated more calcium in control and -K treatments. The lowest total Ca in all species occurred when the treatment was -N.

Mg: Summed over all treatments wheat and wild oat were similar in total Mg, but at the third harvest wild oat had significantly higher contents than wheat. Barren brome always had the lowest Mg except in -N where all were similar and had the lowest concentrations of any treatment (Table 1.2). At the third harvest, barren brome had the lowest amount in all treatments. The species had their highest Mg amounts in the control.

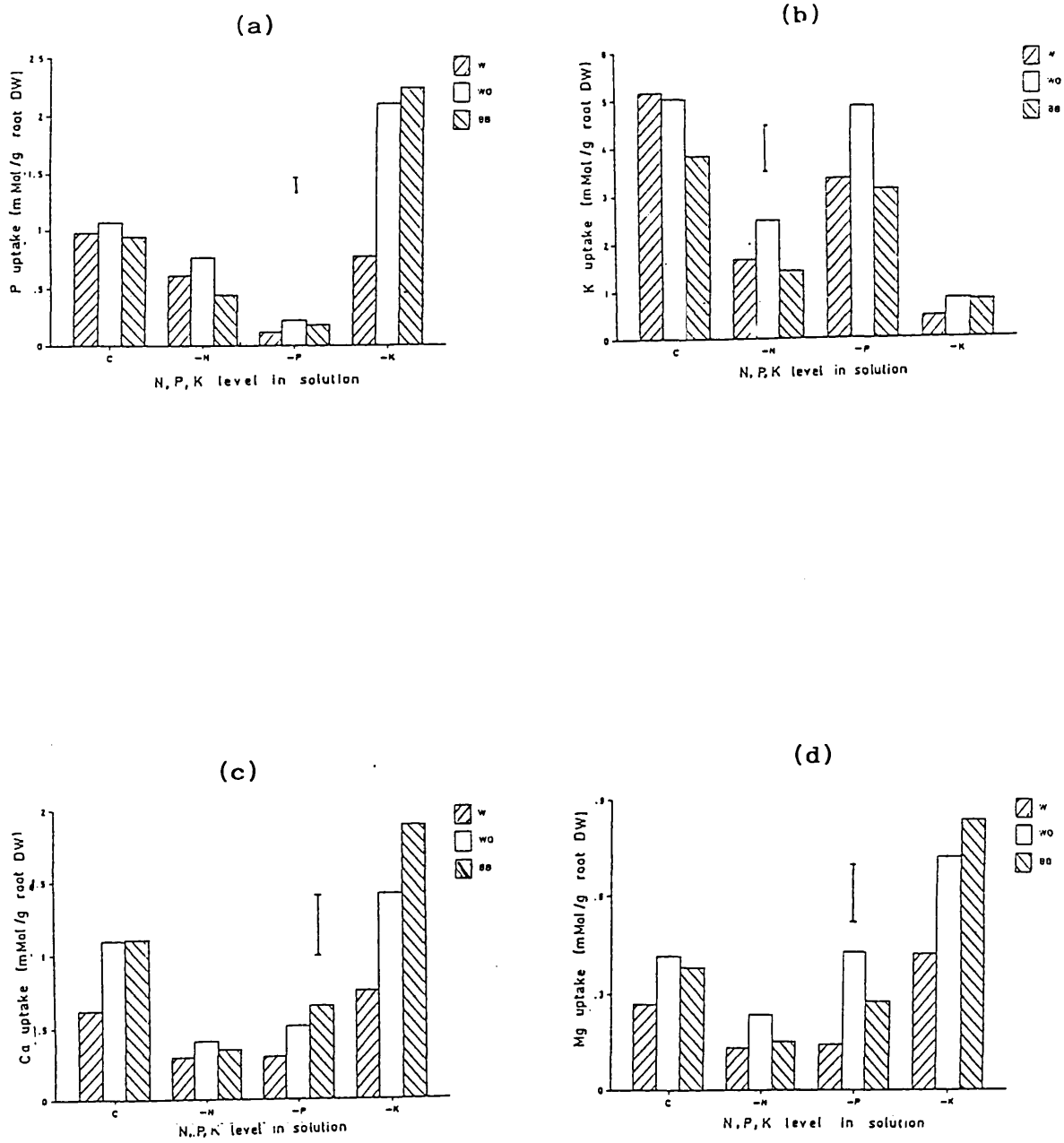


Figure 1.2 (a–d) Effects of N, P and K nutrition on the efficiency of uptake (mMol/g root DW) of P, K, Ca and Mg of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT (Harvest II)
Vertical bars represent LSD at 5% level

Nutrient uptake efficiency of roots

P: Summed over all treatments, in harvests 2 and 3, the weed species were more efficient than the crop (Figure 1.2a). When K was deficient P uptake efficiency of the weeds greatly exceeded the crop. In the other treatments all species were similar. Summed over all treatments the weeds were more efficient than the crop. Species did not differ in uptake efficiency when N and P were reduced. In the -K treatment barren brome absorbed more P per unit root weight than either wheat or wild oat.

K: Summed over all treatments, wild oat was the most efficient species. When K was deficient species did not differ significantly in efficiencies though the weeds had higher efficiency values than the crop (Figure 1.2b). Species efficiencies also differed when P was reduced and wild oat was the most efficient. Wheat and wild oat had similar efficiencies in C and -N treatments. At the third harvest, all species were equally efficient in the -N and -P treatments.

Ca: Summed over all treatments the weeds were more efficient than the crop in taking up Ca. Species did not differ in reduced N and P treatments whereas their efficiencies increased when K was limiting (Figure 1.2c). The efficiency of Ca uptake in barren brome in the -K treatment was particularly high at both harvests 2 and 3.

Mg: The weeds were more efficient than the crop in -P an especially -K treatments, but not in -N or the control (Figure 1.2d). F the 3rd harvest only -N treatment showed no difference.

Nutrient utilization efficiency

P: Summed over all treatments efficiency of wheat and wild oat as similar at the second harvest, but by the third harvest wild oat was re efficient than wheat. The species were most efficient in utilizi g P when it was limiting in solution (Figure 1.3a). In this treatment eat and wild oat had similar efficiencies, but both were more efficien than barren brome. The two weeds were similar when K was deficient a l all three species were similar in the control and -N. At the third rvest all were similar for -K and -N treatment where wheat was less ef icient than both weeds.

K: At the second harvest neither differences between sp ies nor

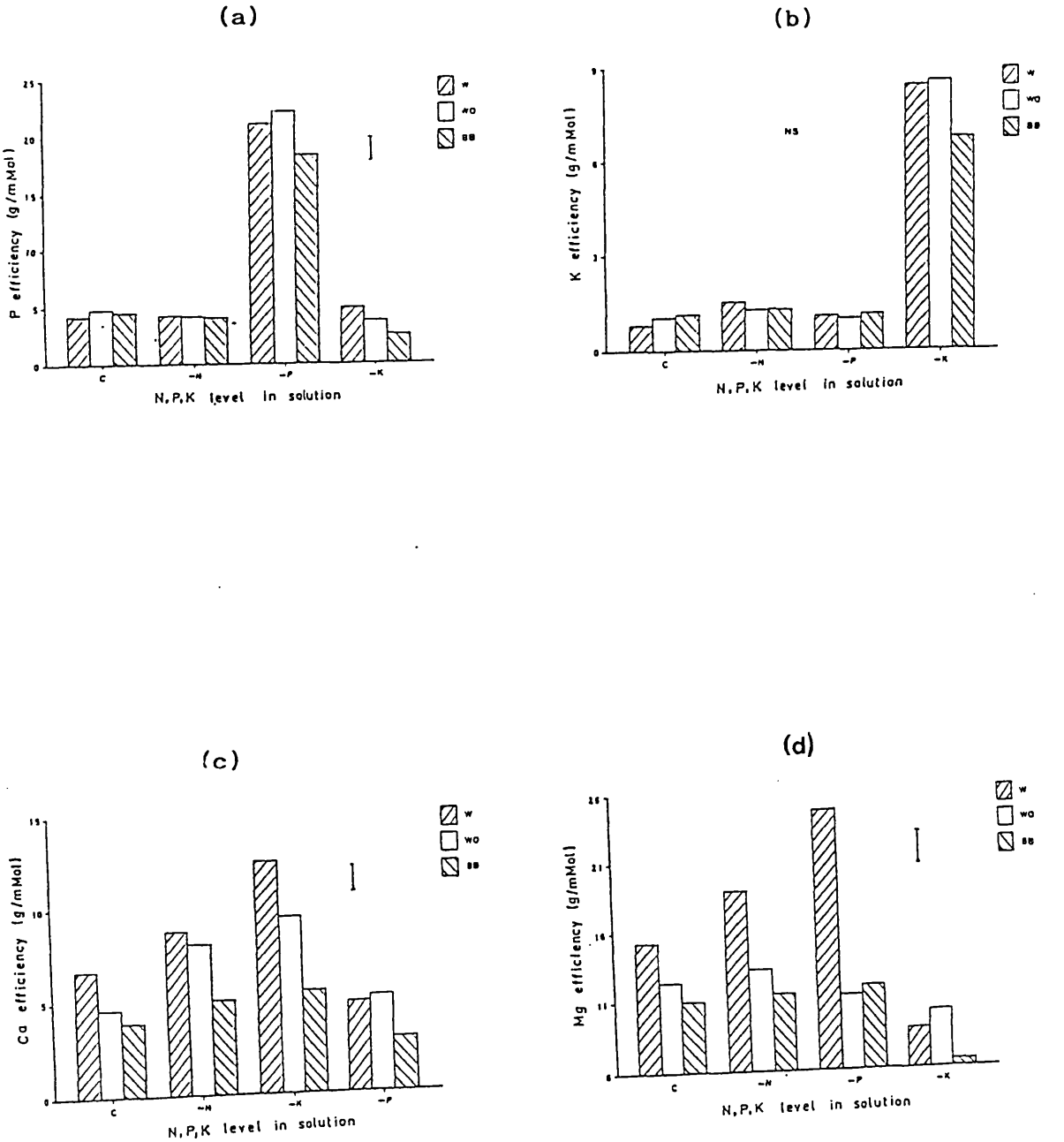


Figure 1.3 (a–d) Effects of N, P and K nutrition on the efficiency of utilization (g/mMol) of P, K, Ca and Mg in wheat (W), wild oat (WO) and barren brome (BB) grown in NFT (Harvest II)

Vertical bars represent LSD at 5% level

NS = no significant differences

interactions of species with nutrient were significant (Figure 1.3b). The differences between treatments was highly significant and all species were most efficient in the -K treatment. At the third harvest, the species as well as the interaction between species and nutrients were significant and wild oat was the most efficient in utilizing K.

Ca: Summed over all treatments wheat and wild oat were similar in their Ca utilization efficiencies. Barren brome was the least efficient species, though it had the highest concentration of Ca in its tissues. In the control treatment, barren brome was as efficient as wild oat. It was also similar to wild oat at the third harvest for -P but never as efficient as the crop at any harvest.

Mg: Summed over all treatments the crop was the most efficient in utilizing Mg. This was particularly noticeable at the 3rd harvest. The weeds were similar except in the -K treatment where wild oat was more efficient than barren brome. At the third harvest the species had similar efficiencies.

5.5. Discussion

Experiment 1.1: N, P and K nutrition of wheat, wild oat and barren brome

Dry matter yields

Shoot and root dry matter yield, weight of the whole plant and the ratio between the root and shoot were considered (Table 1.1). The three species showed marked differences in their responses to the levels of N, P and K. For all the species the mean dry matter yield was always higher when the nutrients were available at higher concentrations than when any one was limiting. The crop always accumulated the highest total dry matter and barren brome the lowest. The total dry matter in wild oat was more similar to wheat than to barren brome. The ability to respond strongly to fertilizers is an important aspect in crop yield. High dry matter production in wheat in the nutrient solution high in N, P or K concentration is to be expected, because crop plants and in particular, cereals have been selected and bred for dry matter accumulation and the ability to respond to higher fertiliser levels. The superior growth of the crop under high nutrient levels may give it an advantage in

competitive situations, because it is generally assumed that high yield is a character of strong selective advantage and that high yield may be equated with success in a given environment. In the past numerous investigators have attributed the dominance of strong competitors to early emergence and faster growth leading to larger plants (e.g. Black et al., 1969; Harper, 1983; Pavlychenko and Harrington, 1934). However, others (e.g. Van Keuren, 1961; Knight, 1960 and Sakai, 1961) have shown a very poor correlation between competitive ability and overall yield. On the other hand, the ability of wild oat to grow almost as large as the crop may suggest that there exists a physiological basis for its success as a serious weed of crops growing under relatively high soil fertility levels. Clapham et al. (1952) described wild oat as a weed naturalised in arable fields, generally disturbed and often common in suitable habitats.

The results also show that the dry matter yield of barren brome was always the smallest in any treatment and stage of harvest. This may be significant and have important ecological and agronomic implications. This weed has, in the past, tended to be restricted to areas low in fertility levels, such as waste places, roadsides, hedgerow and headlands of fields and as a garden weed. The ability to grow and to yield, even at a low level, in infertile soils may be considered a selective advantage, since such species may not outstrip the available nutrient supply and would therefore grow more or less normally. Fitter and Hay (1983) reported low relative growth rate as typical characteristics of low nutrient species and stated that since the maximum uptake that can be achieved in infertile soil is restricted, it is advantageous for the plant to place a small demand on the uptake process. However, such species may not be competitive for light and will tend to be overshadowed by faster growing species like wheat or wild oat. Although wheat produced the largest amount of dry matter under higher N, P and K conditions its yield tended to be the most reduced by deficient levels of N and P. All species were more seriously retarded by N than by P or K deficiencies, though the reduction in all three nutrients had a significant effect. It is noteworthy that the yield of wild oat was the least affected by P and K deficiencies, whilst that of barren brome was the most reduced. The crop was less affected by -K than barren brome.

The fact that nitrogen deficiency seriously affected the growth of the species indicates that it may be the most important nutrient

determining performance in competition. In this respect the weeds appeared physiologically adapted in similar ways to the crop and exhibited similar response to the limiting level of N in the soil. Chadwick and Obeid (1963) studied the responses of five weed species and two crop plants grown at five N levels in sand culture. They found that the dry matter yield of the weeds increased linearly with increase in N concentration as did that of the crop. They suggested that adaptation on the part of the weeds involved a yield response similar to that of the crop with which they are usually associated.

Hoener and De Turk (1938) found differential growth response of high- and low-protein maize varieties when grown at different N levels in nutrient culture. The low-protein variety yielded more at the lowest level of N, but with high N the high-protein variety yielded much more. The high-protein line absorbed and assimilated more nitrate, while the low-protein line accumulated only 49, 48 and 71% of total nitrogen, nitrate and dry matter respectively as the most effective line. They suggested that the differential growth response of maize varieties to different N levels might be due to the high-protein plants having a greater enzymatic capacity for reducing nitrate than low-protein plants.

The relative insensitivity of wild oat particularly to low levels of P and K could be a very important feature of the weed and may reflect adaptation to soils low in these elements. This may suggest that in competition between wild oat and either or both of the other species in soils deficient in these nutrients, wild oat might be expected to outcompete either.

Changes in the relative competitiveness of crops and wild oat through the use of fertilizers have been reported. For example, Koch (1967) noted that in pot experiments the deleterious effects of wild oat on barley were partly overcome at high nutrient levels and not at low ones when wild oats were removed at the onset of tillering. Contrary to this, the reduction in wild oat yields as a result of adding fertilizer had also been reported (e.g. Molberg and Leggett, 1955). Other reports indicated that added fertilizer had similar effects on the crop and wild oat (both A. fatua and A. ludoviciana (Thurston, 1959a). Sexsmith and Russell (1963) also noted that P had no effect on the growth and seed production of wild oat. Pawlik (1957 quoted by Chancellor, 1976) reported wild oat as being relatively insensitive to potassium. When

wild oat was grown in competition with barley and wheat, no differences in plant height, weight and K content in high or low levels were found (Halloin and Sudia, 1967, also quoted by Chancellor, 1976). This is in agreement with the observation on the present experiments where mean yield of wild oat was less affected by P and K than wheat or barren brome. There are some weed species which are less affected by low availability of some nutrients in the soil than certain crops and wild oat could be one of these. Contrary to wild oat, the yield of barren brome was significantly reduced by both nutrient deficiencies. Visual symptoms of K deficiency were also observed on this weed at the second harvest and persisted up to the last harvest.

Other workers have also observed the differential resonses of various plant species to levels of nutrients and attributed such differences to the natural habitats of the species. For example, Tarawali (1983) studied the responses of A. myosuroides and wheat to various levels of P, K, Ca and Mg in NFT and observed that the weed was relatively insensitive to P, Ca and Mg whilst the crop was markedly responsive to all these. He concluded that the observed difference between the two species could be related to the evolutionary background or the native habitats of the species. Johnson (1987) also investigated the responses of these species to a range of P levels and found both species responsive to high levels of the nutrients. Johnson's observation contradicted that of Tarawali and he attributed the differences partly to variations in methodology and type of nutrient solutions used in their respective experiments. The differential susceptibility of plants to nutrient deficiencies has also been shown by various other workers (Snaydon and Bradshaw, 1961, 1969; Clarkson, 1967; Shukla and Hans Raja, 1974; Clark, 1975, 1978). Bunting (1960) suggested that some weed species may show some physiological adaptation to differing levels of soil nutrients. He stated that weeds are essentially plants of secondary successions and are among the first colonizers of the open communities created by man. Under these conditions they often encounter a flush of soil nutrients due either to the removal of the previous plant cover or to fertilization accompanying agricultural practices. However, these nutrients soon become leached from or fixed in the soil, resulting in a deficiency of plant nutrients to which the weeds will be adapted. Hence, weeds in general are characterised by the ability to grow and reproduce in a wide range of

environmental conditions including soils of low fertility (Baker, 1974). It is thus possible that wild oat and barren brome have developed the ability to produce maximum or minimum growth respectively at very low levels of soil nutrients. It would appear, therefore, that overall yield is a character of ecological importance and that a high yielding ability may be a particular advantage under high nutrient levels, as may be low yield under conditions of low environmental potential.

Root/shoot ratio

The differences between the species in root/shoot ratios may also show significant difference between these plants in their adaptation to deficient levels of N, P and K. A number of authors reported changes in root/shoot ratios with decrease in environmental resources (e.g. Bradshaw et al., 1964; Atkinson, 1973; Tarawali, 1983; Johnson, 1987; Qasem, 1987). Chapin (1980) stated that plants from infertile habitats maximize nutrient intake more through a high root/shoot ratio and mycorrhizal associations than root absorption capacity predicated by Nye (1977) and Nye and Tinker (1977). High root/shoot ratios reported for species from infertile habitats was considered in part as a phenotyic response to reduced nutrient availability (Christie and Moorby, 1975; Loneragan and Asher, 1967 and White, 1972).

Barren brome gave the highest root/shoot ratio in the present experiments when N was limiting. This may explain its adaptability to a poor, infertile waste land where it grows normally and completes its life cycle. This suggests that barren brome may have the ability to compensate for N stress in the soil by switching its resources from shoot to root growth. It also implies that in soils where N is limiting barren brome would be expected to survive and grow more normally than wheat. If the two species were to compete for this resource, the weed may be able to limit the growth of the crop, as a result of the proportionately larger root system. At early stages of growth, all three species showed similarities in root/shoot ratios for all treatments except -K. The differences among the species especially in -N became clear as plants grew older. By the second harvest the root/shoot ratio of barren brome was 2 and 2.5 times greater than that of wheat and wild oat respectively under low N. The older plants of barren brome and wild oat at the third harvest showed similarities in having slightly higher root/shoot ratio characteristics, indicating the ability of both weeds to adapt to N

limiting soils by producing a greater proportion of roots.

Potassium deficiency reduced the growth of shoots much more than roots. This is in agreement with the observation of Asher and Ozanne (1967) on pasture species. They suggested that the ability to increase the relative size of the root system under nutrient deficient conditions would have a survival value, since it would increase the likelihood of the plant's obtaining sufficient nutrients to complete its life cycle.

Other investigators have demonstrated the importance of N nutrition as a crucial growth factor which determines ecology and yield of species (e.g. Frey, 1959; Antonovics et al., 1967). Koch and Kocher (1968 cited by Chancellor and Peters, 1976) found that N content of nutrient solutions affected the root/shoot ratio of A. fatua. That is, this species responded to a decrease in N availability by increasing its root/shoot ratio. Welbank (1962) showed that added N had a greater effect on the growth of Impatiens parviflora when its roots were competing with those of Agropyron repens than when they were in monoculture.

The distribution of roots and shoots of the species in low P showed similarities at all harvests, though the ratio was the smallest for wild oat. The lowest ratio in wild oat may suggest that P requirement of this species may not be so high that it is not necessary to invest more of its leaf photosynthates for the growth of a relatively larger root system. Its tissue concentration was lower than the other two species suggesting that its requirement for P may be lower.

Differences in root/shoot ratios of the species in -K were not statistically different except at the first harvest where that of wild oat and wheat were similar and higher than barren brome. The ratio in all species, especially the weeds, decreased with age. Thus in early growth low K reduced top growth more than that of the roots. This is an important strategy of some plant species in competition and many investigators have described such a characteristic as typical of competitive weeds. For example, Ennik and Baan Hofman (1983) showed that investment in greater root mass in Lolium clones in competition with Elytrigia repens was related to enhanced competitive effectiveness. Nye and Tinker (1977) observed that when plants are growing in monoculture they can alter the proportion of roots to shoots. If soils are deficient in moisture or nutrients, many plants apportion more biomass to the root

system. Noordwijk (1983) estimated the rooting density necessary to acquire moisture and nutrients in some species and concluded that as the abundance of a soil resources decreases or the resistance to its movement in the soil or into the root increases, the required rooting density for adequate supply increases.

An important ecological implication that arises is that the weeds in the present study may have developed a strategy typical of that of the most competitive weeds, which produce more root dry matter at early stages and more shoots later. Another assumption that may be made is that if the weeds were made to compete with the crop for limited K, they would outcompete the crop at early stages through the effects of intensive root competition and later by shading, as is the case with wild oat. Results of experiments on the separation of the effects of roots and shoots (Section IV) suggested that the main effect of barren brome is through its root competition while that of wild oat is as a result of direct shading by its shoots.

The marked reduction in root/shoot ratio of the species observed in -K at the 2nd and third harvest conflicts with the findings of Asher and Ozanne (1967). They found an increase in root/top ratio of species at the final harvest at K concentrations of 1 or 8 µM as compared to 24, 95 or 1000 µM. However, in the present experiments, the lowest level of K considered deficient was much higher (i.e. 0.38 mM) than the lowest concentration used by these authors, and there were also differences both in the species studied and in methodology.

Many investigators have reported difficulties in interpreting root/shoot ratio since it has little apparent relationship to overall yield, response to nutrients or the ecological distribution of the species (Bradshaw et al., 1964). High heritability estimates for root/shoot ratio have also been reported (Troughton and Whittington, 1969) in spite of the fact that it is influenced by many environmental variables (Troughton, 1960).

Root morphology

Fitter and Hay (1983) pointed out that differences between species in root/shoot ratios could be seen as the stabilization of a switching process at a value optimal to the fertility to which the species is normally adapted. They pointed out that differences in the amount of

root produced in response to the deficiency of a particular nutrient element have been widely considered, but that variations in root morphology may be more important in explaining species adaptab ility to soil environmental deficiencies. The differential growth of lateral roots in zones of high nutrient supply in soil is now a well established phenomenon (Drew and Saker, 1975, 1978). Hackett (1968) showed that closely related varieties of one species of barley (Hordeum vulgare) responded to P and K deficiencies in contrasting ways. In the present experiments examination of root growth and some morphological characteristics showed that the species clearly differed in their response to the limiting conditions of N, P and K nutrients in solution culture. The total length and surface area of roots per plant varied between species and harvests. All species responded by producing the largest root system at the higher N, P and K levels, the crop always producing larger values than the weeds. Differences were also obvious when nutrients were limiting, the weeds also producing smaller root systems than wheat in -N and -K treatments. In -P both wheat and wild oat were similar and larger than barren brome for total root length and surface area per plant. The weeds also differed in these respects. In -N barren brome had a larger root system than wild oat, but the latter was larger in -P treatment. Clear differences in the thickness of roots was also noted among the species. Barren brome produced the finest roots in all treatments and all stages of growth. Wheat and wild oat had a similar root thickness especially in the control.

In the study of Hackett (1968) referred to earlier, it was reported that the number of axes and length of the primary laterals were greatly reduced by both P or K deficiencies, but by comparison, the mean length of the axes, the number of all primary laterals per axis and the diameter of all types of roots were little affected. In the present study barren brome was clearly different from wheat and wild oat in features such as thickness, total length and surface area. The larger root system in wheat especially at the higher levels of N, P and K may be expected to be an advantage in competitive situation with the weeds in such circumstances. Barren brome, having the smallest root system might be at a particular disadvantage. It is important, however, that the weeds, particularly barren brome, produced the largest surface area and the longest roots per unit root dry in all treatments. This suggests that barren brome produces a root system with many branches and may therefore

have the ability to 'mine' a larger volume of soil than wheat or wild oat. In terms of ecological adaptations barren brome plants may, therefore, survive and grow normally if any one of these elements is deficient in the soil. In competition barren brome would undoubtedly be expected to be in a better position to continue its normal growth and reproduction processes reducing the growth of or even eliminating wheat, especially if barren brome is at high density. At higher population densities of barren brome of course, intraspecific competition may lead to a decrease in the size of individual plants.

Nutrient uptake of plants growing in the soil is clearly influenced by root length and radius. Silverbush and Barber (1984) demonstrated the influence of root morphology i.e. length, radius and surface area, on nutrient uptake. They reported that total nutrient uptake depends on root surface area, its rate of increase and on the uptake per unit surface area. It has also been documented that roots respond to a lower shoot nutrient status by developing a higher absorption capacity leading to a greater uptake (Lindgren, Gabelman and Geroff, 1977; Drew and Saker, 1978). The capacity to absorb in general, differs among species (Noggle and Fried, 1960) and varieties (Vose, 1963; Gerloff, 1977; Nielsen and Barber, 1978). Varieties and species with low relative growth rates generally have a high root/shoot ratio (Nielsen and Barber, 1978) and a low root absorption capacity (Hunt and Burnett, 1973; Lingren et al., 1977; Nielsen and Barber, 1978). The mean uptake per unit root surface or weight depends both on the uptake kinetics of the root (see Section II) and nutrient supply in the solution culture.

Johnson (1987) reported differences in the responses of wheat and blackgrass in terms of root length and length/weight ratio. He noted that root length in blackgrass was less reduced at the lowest concentration (0.07 mM P) than wheat. Blackgrass also had a higher length/weight ratio at the lowest concentration. These observations suggested that P supply can induce changes in root morphology which in turn can affect the efficiency of P uptake. Qasem (1987) grew tomato, fat-hen and groundsel in NFT in Cooper's full strength solution to study differences in root morphological characteristics. He reported higher root weight, volume, length and surface area for tomato than the weeds, but when length and surface area were calculated per unit dry weight or unit root volume, he found higher ratios in the weeds. The root diameter in the weeds was also much smaller than the crop.

Drew and Saker (1978) found compensatory increases in the growth of lateral roots and in rates of uptake of phosphate in solution when parts of the root systems of barley were deprived of phosphate. Bowen and Rovira (1971) used a technique of pulse labelling of wheat roots with radioactive P to study uptake. Lateral roots accounted for 81% of P uptake and also for most of the P translocated. Working with maize varieties, Smith (1934) and Lyness (1936) found some correlation between efficiency of P uptake and the number of secondary roots. There are major differences when root development in water culture and soil are compared, particularly in root hair production and in responses linked with the presence or absence of mechanical resistance. In many respects, however, the form of the root system can be very similar in the two media. It may therefore, be assumed that the use of water culture for studies of root growth can provide some information which is relevant to the field situation, though it is clearly desirable for predictions based on water culture studies to be confirmed in other media, including field studies. Some such studies are reported later in this thesis.

Nutrient uptake and accumulation

The results of the present work also showed the mineral nutrition of the species to be different especially when such differences are expressed in terms of nutrient concentration and accumulation, efficiency of nutrient uptake and utilization (Figure 1·1, 1·2, 1·3, 1·4a, b, c, and d). Where the supply of N, P or K was limiting, the weeds had significantly higher or similar tissue concentrations and accumulation to the crop. The crop exceeded the weeds in both respects when concentration of N, P and K in solution was higher. The concentrations of Ca and Mg in barren brome were the highest in all treatments and both harvests. The weeds were also more efficient than the crop in taking up P, K, Ca and Mg per unit dry weight, and the difference was still significant at the third harvest. Differences in utilization efficiency for P, Ca and Mg were also noted. Barren brome was less efficient in the case of these elements than wheat or wild oat. Wheat consistently showed the highest utilization efficiencies for Ca and Mg. Though barren brome showed higher or similar concentrations for all elements than the other species it contained the lowest total amount of all. This is because nutrient accumulation follows total dry matter accumulation. However, it is interesting that barren brome accumulated similar amounts to the other species of P, K, Ca and Mg when the supply of N was limiting. The total

amount of Ca and Mg in wild oat when P was deficient was greater than in wheat. Total P was also greater for wild oat in -K, but wheat exceeded wild oat in total accumulation of P and K in the control.

Variation between populations in their adaptation to different nutrient levels has been commonly investigated and there is a recognition of correlations between species distribution in the field and soil nutrient status. The observed differences between wheat, wild oat and barren brome in the present investigation are not surprising because of the genetic differences in the general nutrient requirements and differences in the level of nutrients of the soil where they are found.

Several authors have shown that weeds are able to take up nutrients better than crops when the levels of certain nutrients in the media are low (Blackman and Templeman, 1938; ; Alkamper et al., 1979; Johnson, 1987; Qasem, 1987).

The marked differences between the crops and the weeds in tissue P, K, Ca and Mg concentrations suggests variations in their responses to deficient levels of N, P or K. The crop required high levels of N, P and K to grow much bigger than the weeds. It had the highest concentration and accumulation of P and K when the levels of N, P and K were high in the medium. Thurston (1971) found that the growth of winter wheat as well as blackgrass was stimulated by the application of fertilizers and that wheat usually responded to a much greater extent than blackgrass. Johnson (1987) also found that the crop responded to higher concentrations of P. In field fertilization studies, Jefferies and Perkins (1977) showed the greater growth response to improved nutrient availability by rapidly growing species from fertile sites as contrasted with slowly growing species.

The higher Ca and Mg concentration in barren brome at all deficient levels may indicate that its requirement for these elements is greater than wheat or wild oat and/or that its ability to take them up is superior. In competition between wheat and barren brome or wild oat and barren brome, where the supply of Ca or Mg in the soil is limited, one might expect barren brome to dominate because of its ability to absorb more of these elements than the other species. On the other hand one may also argue that because of their lower requirements wheat and wild oat may be able to outcompete barren brome especially at deficient levels of these elements.

The marked reduction in Mg concentration in wheat at the deficient level of P in solution in the present experiments has also been noted by Johnson (1987), who partly attributed it to the effect of a lower P uptake by the crop. The observed similarities in the tissue concentration of P and K in wheat and wild oat at the higher level of NPK in the medium, may imply that the weed is, like the crop, well adapted to the fertile habitat. Wild oat however, also appears adapted to soils poor in P and K, particularly because of its ability to grow unhindered by the deficient level of P. It also accumulated the greatest total amount of P, K, Ca and Mg at this level. The fact that the growth of wild oat was little affected by high and deficient levels of P and K may be a bonus in any competitive situation in the field where variation in the soil nutrients can be large, with possibly regular exposure to very high as well as to low nutrient levels.

The greater the capacity of a plant to tolerate variations in soil nutrient levels, the greater its chance to survive the effects of competition from other species and also to spread into a range of habitats. A number of authors (e.g. Bradshaw et al., 1960a; Crossley and Bradshaw, 1968; Rorison, 1968; Davies and Snaydon, 1973b) compared the responses of species to different levels of nutrients and concluded that the observed differences were related to their evolutionary background and distribution in the field. Others claimed variations in nutrient concentration and accumulation between species to be due to their competitive abilities (Chambers and Holm, 1965; Pandey et al., 1971).

Root nutrient uptake efficiency

The observed differences in the efficiency of the weeds, particulary barren brome, in taking up nutrients from deficient levels may be of significant importance in competitive situations. Higher efficiency in nutrient uptake in barren brome may be due partly to the greater density of the root system referred to earlier, with its finer roots compared to the other two species.

The higher efficiency (i.e. $mM_o\ell$/g root dry weight) noted for the weeds in taking up P, K, Ca and Mg in the solutions deficient in P or K is in agreement with the higher length/dry weight and surface area/dry weight ratios in the weeds. Johnson (1987) found a constant pattern in the specific absorption ratios of wheat and blackgrass in relation to P level. Though he found that differences were not statistically

significant he concluded that the agreement of results over two periods suggested that the differences between the two species might be a true reflection of their efficiencies in nutrient absorption. He found that, under low P levels, blackgrass was relatively more efficient in absorbing nutrient than wheat. At higher P levels the opposite was true. He suggested that higher absorption efficiencies found in the weeds than the crop under low P could be due to the greater density of roots. Root morphology, density and distribution are important characteristics of a plant which affect the uptake of nutrients from the media. When two species exploit the same soil volume the resulting overlapping of the depletion zones will result in mutual interference in the uptake of nutrients. The species whose roots can exploit the greater volume of soil may be expected to benefit from such a situation. Drew (1979) and Drew and Saker (1975) showed that lateral roots and root hairs enhance absorption of nutrients. The high root/shoot ratios of barren brome may also show the importance of a large root system for the efficient uptake of nutrients from the soil. The fact that barren brome absorbed more Ca and Mg and was also less affected in the absorption of P, Ca, K and Mg than were wheat and wild oat under low N may suggest that it may be better adapted to such conditions than the other species. It has been reported earlier that under -N the root/shoot ratio in barren brome increased considerably above that of wheat or wild oat. It may therefore, be concluded that adaptation to low N conditions in this species is achieved by producing more roots in comparison to shoots. The ecological implication is that under competitive conditions where N is limiting barren brome may dominate to the exclusion of either species or both because of its large root system.

Nutrient utilization efficiency

In the present experiment, the species also differed in their utilization efficiency of the various nutrients. The crop was the most efficient in utilization of Mg and Ca in all treatments except -K, where it was similar to wild oat, but more efficient than barren brome. The three species did not differ in K utilization, but their highest dry matter per unit K was produced at the deficient level of this element. P utilization efficiency of the species also differed and the highest values were also produced at the lowest level of P. Under -P, the crop and wild oat showed similar efficiencies, and were higher than barren brome. Similar trends of results were found at the third harvest and may

therefore suggest that the differences may be a true reflection of their efficiency of absorption and utilization. Koch and Kocher (1968) also reported that wild oat utilized less P than winter wheat and barley. Wild oat have also been reported to assimilate less potassium than barley (Sinyagin, 1966).

A number of authors have investigated the differential responses of species to various levels of nutrients and compared in terms of ion uptake and/or ion utilization in nutritional studies (e.g. Harvey, 1936; Gableman and Gerloff, 1982; Tarawali, 1983; Johnson, 1987; Qasem, 1987). Vose and Breeze (1964) found in ryegrass, Lolium perenne, that different genotypes varied in their efficiency of N utilization, some tending towards high dry matter yield and relatively low N content (termed efficient), or lower yielding types with high N content, regarded as basically inefficient converters of N. Johnson (1987) reported that blackgrass was more efficient in utilizing P, K and Ca at the highest P concentration (1.94 mM P) whilst the opposite was true for Mg. Earlier, Tarawali (1983) noted that blackgrass was significantly more efficient than wheat in utilizing P, K, Ca and Mg.

The highest utilization efficiency shown by wheat and wild oat for Ca and Mg may cause both direct and indirect effects on barren brome plants when the species are grown in proximity to each other. As wheat and wild oat plants appeared to be unaffected by low tissue concentration of Ca and Mg, their demand for the other soil nutrients increases. Such nutrients which may be required by barren brome may be absorbed by wheat and wild oat and deprive the former species. In such circumstances barren brome may suffer the overshadowing effects caused by either species or both. The combined effects may lead to reduced growth of barren brome plants. On the other hand it has been shown earlier that barren brome showed the higher concentrations of these nutrients and may therefore be able to survive severe competition from both species.

In the present analyses of results instantaneous efficiencies of nutrient uptake and utilization were calculated by dividing the total nutrient and dry weight accumulated by the root dry weight and total nutrient respectively. Other investigators calculated the specific absorption rate (SAR) and utilization rate (SUR) (e.g. William, 1948; Welbank, 1962; Barrow, 1975; Johnson, 1987). Johnson, (1987) stated that although the use of these ratios could be a useful tool in nutritional

studies, there is a major weakness inherent in the calculations. In order for the calculations to be valid, there should be a linear relationship between root growth as measured by root weight and nutrient uptake throughout the period considered.

Others have proposed the use of a modified approach to the estimation of both. Siddiqui and Glass, (1981) proposed the calculation of 'Utilization Index' instead of estimating utilization efficiency as biomass produced per unit amount of nutrient absorbed. The authors claimed that the former method of estimating utilization efficiency does not describe adequately a dynamic system like growing plants since the relationship between biomass and nutrient concentration is complex.

Experiment 1.2

5.6. Results

Shoots: Species differed in shoot production at all P levels, except the lowest where wheat and wild oat were similar (Table 1.3). Shoot production within species also varied with P levels, and all species had the lowest shoot dry matter at the lowest P level. At harvest 3 all species had similar shoot weights at the lowest P.

Roots: The species differed in root weight at all P levels except the highest, where wheat and wild oat were similar. Differences within species were sometimes also obvious. For example, at L2 and L3 wild oat and barren brome produced similar amounts of root. The weeds also had their heaviest roots at these levels and wild oat roots were heavier than those of wheat and barren brome.

Whole plant: At any one P level, the species were different in their weights and the heaviest plants being wild oat (Table 1.3). At harvest 3 all species had similar weights at L4. Within the species whole plant weights were affected by P level. The dry matter yield of wheat was varied with P level, while the weeds had similar amounts in L1 and L3 treatments. At harvest 3 wheat and barren brome produced similar amounts of dry matter at L1 and L2.

Root/shoot ratio: The species had similar ratios at the highest level of P, and at the other levels both differences and similarities were observed. Differences within species were also obvious. Ratios were

Table 1.3 The effects of phosphorus levels on some growth variates of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

P level	Shoot dry weight (g/plant)	Root dry weight (g/plant)	Whole plant weight (g/plant)	Root/shoot ratio	Root radius(cm)	Total root length (m/plant)	Total surface area (cm^2/plant)	Root length/root dry weight	Surface area/root dry weight
L1									
W	7.76	1.52	9.28	0.198	0.016	228.1	143351.0	150.5	94580.0
WO	8.90	1.42	10.32	0.161	0.014	310.2	194935.0	218.0	136959.0
BB	2.52	0.40	2.92	0.163	0.010	107.0	67230.0	269.9	169552.0
L2									
W	6.22	1.50	7.72	0.243	0.013	271.7	170698.0	180.9	113637.0
WO	9.47	3.34	12.81	0.354	0.015	627.4	394238.0	188.4	118352.0
BB	1.92	0.72	2.64	0.376	0.010	195.1	122569.0	275.9	173344.0
L3									
W	4.69	1.47	6.16	0.401	0.012	392.2	246410.0	210.3	132137.0
WO	7.35	2.46	9.81	0.338	0.014	552.1	346894.0	224.8	141267.0
BB	2.31	0.66	2.97	0.284	0.011	135.4	85059.0	206.7	129887.0
L4									
W	1.77	0.64	2.41	0.362	0.013	127.1	79843.0	201.5	126613.0
WO	1.22	0.41	1.63	0.338	0.012	96.4	60539.0	238.8	150067.0
BB	0.53	0.25	0.78	0.475	0.011	74.0	46496.0	313.8	197137.0
Significance level									
SP.	***	***	***	NS	***	***	***	*	*
P	***	***	***	***	***	***	***	***	***
SP*P	***	***	***	***	***	***	***	**	**
LSD ($P < 0.05$)									
SP.	0.371	0.070	0.366	-	0.00035	14.933	9383.9	23.46	14734.6
P	0.429	0.081	0.424	0.044	0.0004	17.247	10834.9	27.09	17014.4
P*SP	0.743	0.136	0.734	0.077	0.0007	29.867	18767.6	46.91	29470.0

higher for all species at the lowest level of P, where barren brome had the highest value. The root/shoot ratios of wheat and wild oat were less affected by P levels than that of barren brome.

Root radius: The species were different in root thickness (Table 1.3). The thinnest roots were produced by barren brome plants at all P levels. Root radius within species varied with P level in wheat and wild oat, but that of barren brome was similar in the different treatments.

Total root length (m/plant): The species were different in their total root length at all except the lowest levels where the weeds had similar lengths (Table 1.3). The longest root systems occurred at the second and third levels of P in all species. Root length in wheat was more reduced by high available P than it was in the weeds. At the lowest P level, total root length of species particularly that of wild oat was greatly reduced. At all levels of P except the lowest wild oat produced the greatest total root length.

Root surface area per plant: The root surface area of species was different at the various P levels except at the lowest where the two weeds had similar areas. Root surface area for wild oat was greater at all levels (Table 1.3). Within the species the effect of P levels resulted in differences in root surface area. In all the species the largest surface areas were produced at L2 or L3.

Total root length/unit root weight: The length of root per unit dry weight varied significantly with species (Table 1.3). The weeds, particularly barren brome, had larger roots per unit root weight than wheat at all P levels, except 3, where all were similar. At the 2nd level wheat and wild oat were also similar. In both weeds, the largest root per unit root dry weight was produced at the lowest P.

Root surface area/unit root dry weight: Again the weeds had a greater surface area/unit dry weight of root than the crop, and barren brome exceeded wild oat. In both weeds, the greatest area per unit root weight occurred at the lowest P level. At the 3rd level all species had similar values. Wheat and wild oat also gave similar values at L2 and L4.

Nutrient concentration:

P: At the highest P level the crop had a slightly higher P concentration than the weeds, but at the lowest level the reverse was the

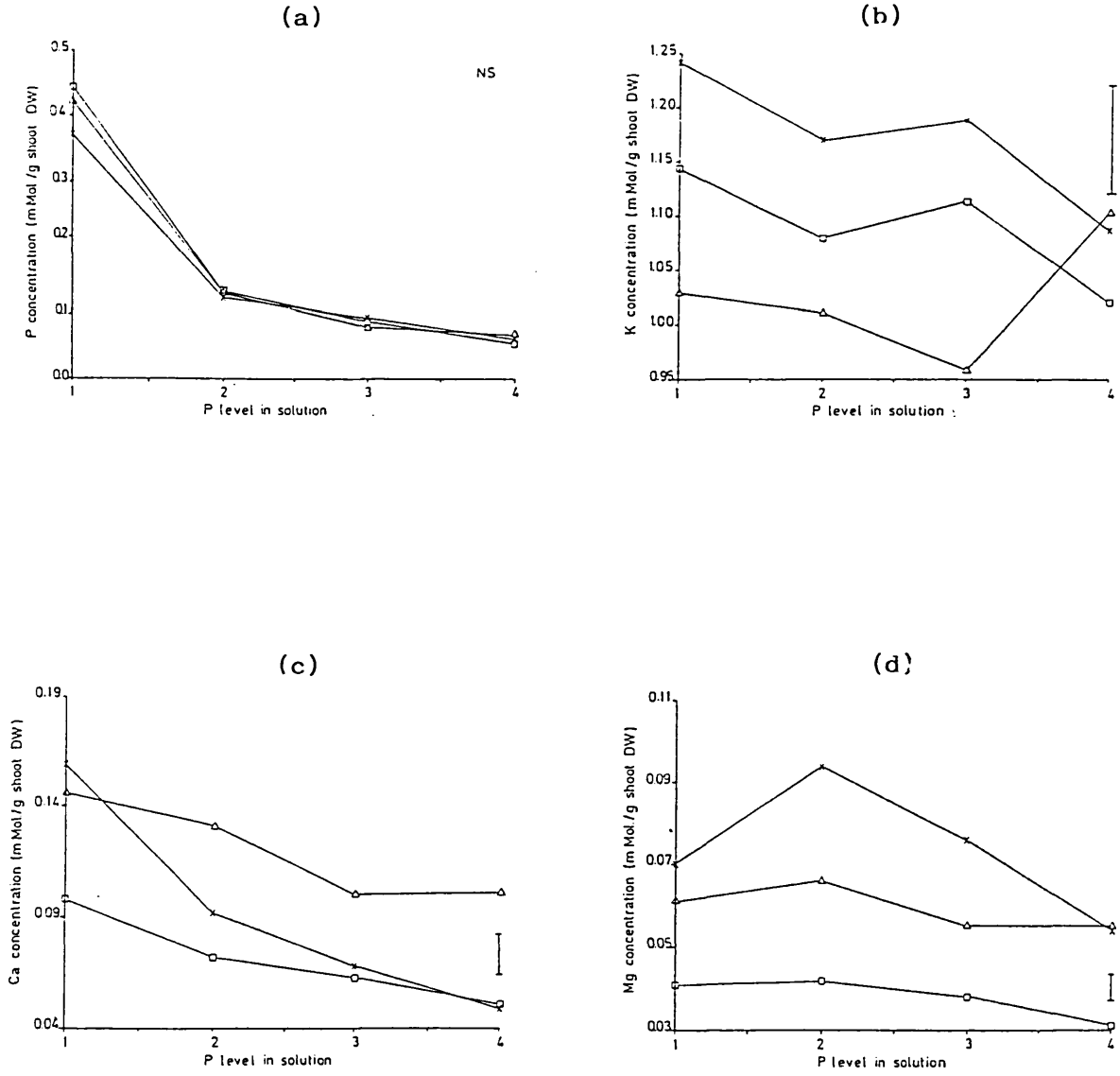


Figure 1.4 (a-d) Effects of phosphorus level on the concentrations (mMol/g DW) of P, K, Ca and Mg in wheat (□), wild oat (X) and barren brome (Δ) grown in NFT (Harvest II)
Vertical bars represent LSD at 5% level of probability
NS = no significant differences

case. By the third harvest, barren brome had a higher P concentration than wheat and wild oat, except at the highest P level where it was slightly lower than wheat. Interactions between P levels and species were not significant (Figure 1.4a).

K: At the second harvest K was more concentrated in wild oat than wheat, but they were similar at the third harvest. At the lowest level all species were similar. Wheat and wild oat were also similar in K concentration at all the other P levels. The lowest K concentration was always found in barren brome (Figure 1.4b). At harvest 3, all species had the lowest K concentrations in L2 and L3. The concentration of K in wild oat was less affected by P levels than in wheat or barren brome.

Ca: Concentration in the species varied with level of P in solution, except in L3 and L4 where both wheat and wild oat had similar concentrations. Barren brome plants had higher Ca concentration than wheat or wild oat, except at L1 where it was similar to the latter. At the third harvest the weeds had similar concentrations in L1 and L2. At the other levels of P barren brome had the highest concentration.

Mg: The weeds, particularly wild oat, had a higher tissue Mg than the crop (Figure 1.4d). At L3 and L4, both weeds had similar concentrations. Within species Mg absorption was affected by P levels. Concentration was reduced with reduced P in solution, except in wild oat which was less sensitive to changes in P level particularly at harvest 3. At the lowest level of P the weeds did not differ in Mg concentration. At the 3rd harvest both wild oat and barren brome were similar in Mg concentration at L2 and L4.

Total Nutrient Uptake

P: Total P in wild oat was slightly higher than in wheat, but by the third harvest wild oat had accumulated much more P than wheat. Barren brome had the smallest amount of P at both harvests. At the lowest P level all species accumulated similar quantities of P. Barren brome was the species least affected by reduction in P solution.

K: The species differed in total K content, wild oat having the highest and barren brome the lowest amounts (Table 1.4). As P was reduced in solution the total in species was also reduced, except in wild oat at the 3rd harvest where the reduction was not significant up to the third level of P. Wild oat and barren brome had similar contents of K at

Table 1.4 Effects of P levels on the total uptake (mMol/plant) of P, K, Ca and Mg of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

	L1			L2			L3			L4			Significance level			LSD (P 0.05)		
	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB	SP	Nut	SP*Nut	SP	Nut	SP*Nut
P	4.20	3.91	1.25	1.08	1.67	0.36	0.61	0.97	0.25	0.14	0.11	0.06	***	***	***	0.174	0.201	0.349
K	10.62	12.76	2.99	8.33	14.98	2.66	7.31	11.66	2.84	2.45	1.77	0.86	***	***	***	0.509	0.586	1.017
Ca	0.91	1.65	0.43	0.56	1.17	0.35	0.41	0.67	0.30	0.12	0.08	0.08	***	***	***	0.071	0.082	0.142
Mg	0.38	0.72	0.18	0.32	1.20	0.17	0.25	0.74	0.16	0.07	0.09	0.04	***	***	***	0.031	0.036	0.062

the lowest P level but the crop was higher than barren brome. At the third harvest all species were similar in the lowest P treatment.

Ca: Total Ca was higher in wild oat than in wheat and barren brome had the smallest amount (Table 1.4). The total amount of Ca in all species decreased with decrease in P concentration, and the reduction was the greatest in wild oat. The species all had similar quantities of Ca at the lowest of P.

Mg: Species differed in total Mg at all levels of P except the lowest, where all were similar. Wild oat had about 2½ and 5 times more Mg than wheat and barren brome respectively. In general total Mg in species decreased with P level, wild oat being the most affected and barren brome the least.

Efficiency of Nutrient Uptake of Roots

P: Summing over all concentrations species did not differ significantly in the efficiency of P uptake (Figure 1.5a). At the 3rd harvest wild oat was the most efficient species while wheat and barren brome were similar to each other. The effect of P levels on the P uptake efficiency of roots was such that roots were most efficient at the highest levels.

K: Wild oat was the most efficient species in absorbing K (Figure 1.5b). In general K uptake of the species decreased as P level was reduced. At L3 and L4 all species had similar efficiencies, although wild oat was slightly more efficient than wheat and barren brome. At the highest P level, wheat and barren brome did not differ and they also had similar efficiencies at all levels of P at the 3rd harvest. Wild oat and wheat at this stage were also similar at L1 and L2.

Ca: The weeds were more efficient than the crop in taking up calcium. All had similar efficiencies at the lowest P (Figure 1.5c). Wheat and wild oat also were similar in L2 and L3 and the weeds in the 2nd level in solution. At the 3rd harvest all the species had similar efficiencies in L3 and L4, whereas the weeds were similar in L1 and L2 solutions as well. In general, root efficiency decreased with a decrease in P level.

Mg: Summing over all concentrations the weeds, particularly wild oat, were more efficient than the crop (Figure 1.5d). The weeds had

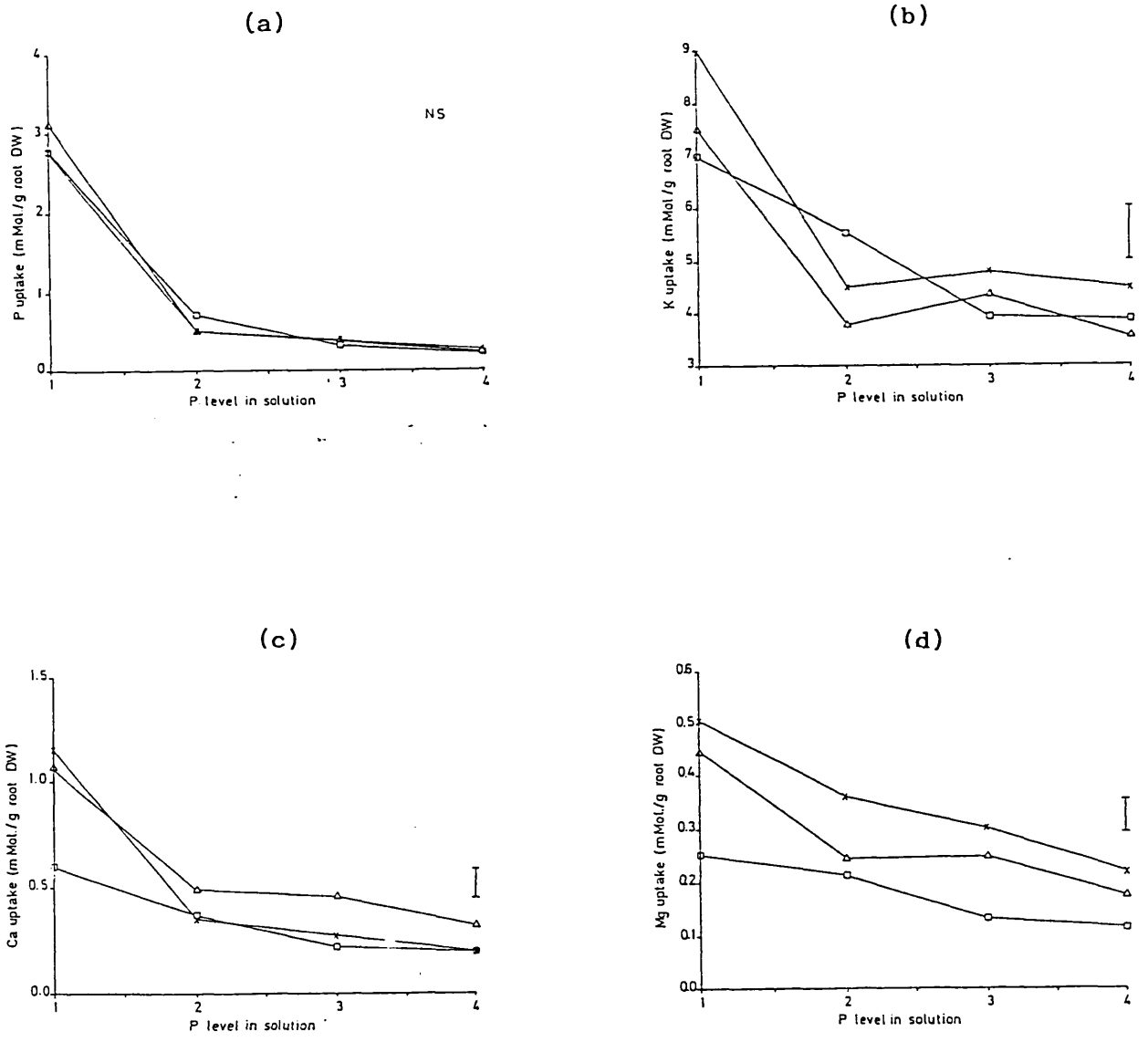


Figure 1.5 (a-d) Effects of phosphorus level on the efficiency of uptake (mMol/g root DW) of P, K, Ca and Mg in wheat (□), wild oat (X) and barren brome (△) grown in NFT (Harvest II)

Vertical bars represent LSD at 5% level

NS = no significant differences

similar efficiencies at all levels of P except the lowest, where wild oat was more efficient than barren brome. At the 3rd harvest wheat and barren brome had similar efficiencies at L3 and L4. In all species Mg uptake declined with a reduction in P.

Nutrient Utilization Efficiency of Species

P: Species effects and interactions between species P levels were not statistically significant (Figure 1.6a). In all species, P utilization efficiency increased with decrease in P concentration in the feeding solution. Greater efficiency was shown at the lower (L3 and L4), than at the higher (L1 and L2) levels. At harvest three wild oat was the most efficient species in production per unit of P, particularly at lower levels.

K: Barren brome was the most efficient species at both harvests. P level in solution had no influence on the efficiency of the species in utilization of K at harvest two (Figure 1.6b) but by the third harvest the influence of P on K was very evident. The utilization efficiency increased with a decrease in P level but at harvest three no clear trend was found. At the lowest P all species had similar efficiencies and at the other levels wheat and wild oat were also similar. At the third harvest all species were similar at L2 and L3.

Ca: Wheat was the most efficient species and barren brome was the least efficient (Figure 1.6c). Wheat and wild oat had similar efficiencies at L3 and L4 and both weeds were similar only at L1. At the 3rd harvest all were different, except in treatment L1 where wheat and wild oat were again similar. All species increased their efficiency of utilization at lower level of P.

Mg: Summing over all concentrations the crop was the most efficient species in utilizing Mg (Figure 1.6d). Efficiency increased with a decrease in P. The weeds were similar in their efficiencies at the lowest P level but at the 3rd harvest barren brome was more efficient at all P levels. The crop produced the largest amount of dry matter per unit Mg at all P treatment levels.

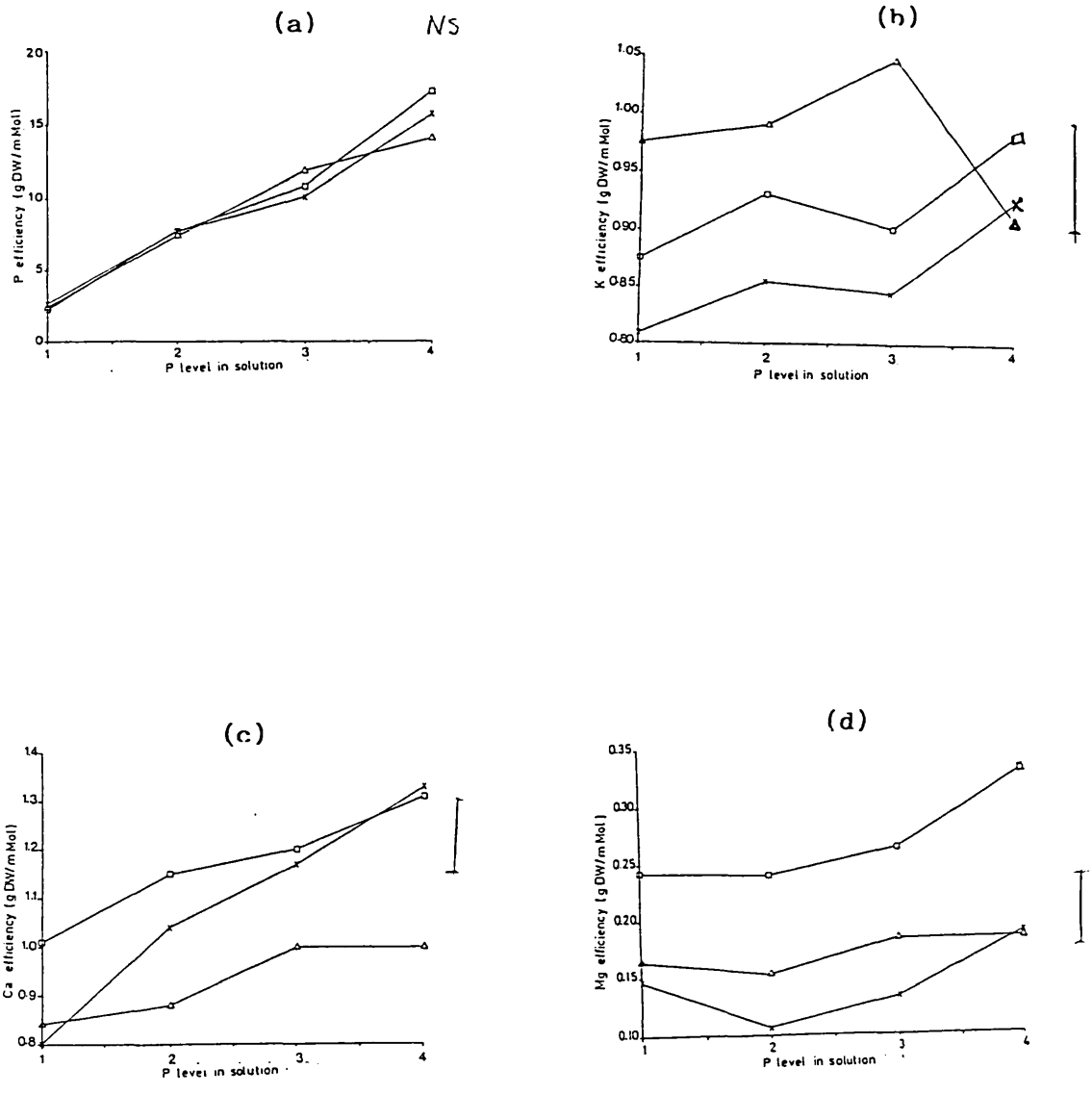


Figure 1.6 (a-d) Effects of phosphorus level on the efficiency utilization (g/mMol) of P, K, Ca and Mg in wheat (□), wild oat (X) and barren brome (△) grown in NFT (Harvest II)
Vertical bars represent LSD at 5% level

Experiment 2

5.7. Discussion

Dry Matter Yield

The results indicate that there were marked differences within and between the species in dry matter yield (Table 1.3) in response to the various levels of P in solution. The differences were also consistent at different stages and for various P levels. Except at the lowest P level (L4) wild oat accumulated the greatest amount of dry matter and barren brome the smallest. The dry matter accumulation of the weeds fell slightly at the highest P (L1) and was greatest for the crop at this level. It may be that wheat would respond to P concentrations above the highest level considered in the present experiment. It was also the species with the highest dry matter production at L4. The yields of the weeds increased or remained similar as P concentration was reduced down to the third level (L3). At the lowest level the yields of both weeds were significantly lower than that of the crop.

The observation . . in the previous experiment that the dry matter yield of wild oat was little affected by reduction in P level are confirmed by the fact that in the present experiment its yield was either increased, remained similar or decreased very little as P was reduced to the third level (L3). However, the yields of wild oat as well as barren brome were significantly lower than the crop at the lowest P level (L4). The ultimate reduction in the yield of wild oat to a lower level than the crop may indicate that the weed has a threshold level for P beyond which its ability to survive is at stake. In experiment 1 the level of P considered deficient was somewhat higher than the amount applied as the lowest level in the present experiment (3 ppm as opposed to 2 ppm). The frequency of replenishment in the two experiments was also different, this being done at weekly intervals in experiment 1 and every 2 weeks in the present experiment. Although a general trend of decrease in the total dry matter yield of the crop is obvious with reduction in P and its yield was always smaller than wild oat down to the third level, it is of particular interest that wheat actually exceeded wild oat at the lowest P level. One of the reasons for greater dry matter production of the crop at the lowest P than either weeds may probably well be that wheat seed is much bigger than that of either weed

seeds and may therefore contain more P. Under such conditions where the availability of P is seriously reduced in the medium the species with the highest reserve would be expected to perform better. Hoveland et al. (1976) reported that crop species were generally less sensitive to P and K of the soil than were a number of weed species studied in glasshouse conditions in fine sand loam soil. They suggested that this can probably be explained on the basis that crop species such as corn, soybean and cotton have larger seeds, and given a 'one-to-one' situation competition would favour the crop.

One explanation for better growth response of the crop than the weeds at such a low P level may be the interaction of environmental factors, particularly temperature, with P which may have favoured the crop. This means that the responses of the two species to variation in temperature may be different. Experiment 1 was conducted in the spring and experiment 2 in the summer of 1987, during which cubicle temperatures were very high. Unfortunately specific experiments to investigate such differences were not designed and may therefore be worth consideration, as temperature is one of the more important environmental factors controlling plant growth and development. In this laboratory, Johnson (1987) looked at the responses of wheat and blackgrass in relation to temperature and explained the dry matter accumulation of both species in terms of the relative growth rates. He found that under high day/night temperatures (24/16°C) or high shoot/root temperatures (20/20°C) the mean relative growth rate of blackgrass was slightly higher than the crop, and under low day/night temperatures (15/16°C) or high shoot/low root temperatures (20/10°C) the differences in relative growth rates of the two species were not significant, though blackgrass maintained a consistently higher relative growth rate than wheat. Numerous authors (e.g. Gregory et al., 1979; Hawton, 1980; Macduff and Wild, 1986) have studied the responses of species to temperatures and invariably concluded that root temperature exerts a greater influence on plant growth than shoot temperature. A number of other investigators also concluded that the harmful effects of low temperature on plant growth cannot be overcome by nutrition (e.g. Patterson et al., 1972; Fowler and Gusta, 1982).

The three species also differed in response to the highest P level. As previously indicated the total dry matter yield of wheat was the highest at this level of P and this suggests that the crop may respond to higher levels than the highest used. The yield of wild oat at this level

was lower than that at L2 and L3 and may suggest this level may have been high enough to interfere with growth. The amount of root produced at L1 was 2.4 and 1.7 times lower than those produced at L2 and L3 respectively. Phosphate toxicity at that level may be suggested for wild oat. Similar remarks can be made for barren brome, since its total yield at the highest P level remained similar to those at the 2nd and 3rd. Snaydon and Bradshaw (1962) demonstrated that natural populations of Trifolium repens from contrasting soil types differed in their comparative growth when grown on each of the parent soil types, each doing best in the type from which it had been obtained. He concluded that the observed differences in the comparative growth of each population was related to the soil conditions of its native habitat. Similar explanations may also be offered for the observed differences between the weeds and the crop in the present experiment. Crop plants are normally associated with soils of high fertility whilst it is one of the characteristics of the weeds that they can grow and reproduce under soils low in fertility. Antonovics et al. (1967) have also shown that ecotypes varying in their response to mineral nutrients are often found on soils differing in fertility. Tarawali (1983) compared the response of winter wheat and blackgrass to P and reported the insensitivity of the weed while the crop responded markedly to all levels of the element. Johnson (1987) also investigated the responses of the two species to a range of P levels in NFT. He found that increasing P supply in solution resulted in increased dry matter production in crop species. Wheat, however, responded to the full range of P concentration whilst A. myosuroides did not respond above 0.66 mM P.

Rorison (1968) conducted similar studies with four ecologically distinct plant species and came to the conclusion that the differences in their responses to P supply were related to their observed distribution in the field. The author found Rumex acetosa L. responded to a whole range of P levels in keeping with its wide distribution. Deschampsia flexuosa L. Trin. and Scabiosa columbaria L., which survive on acid and calcareous soils respectively, showed the least responses to increases in P whilst Urtica dioica L., commonly found in fertile soils, responded only at higher level of P.

Bradshaw et al. (1960a) also investigated the responses of a number of grass species to levels of P which ranged from deficient to toxic in sand culture. The species were collected from very fertile as well as

habitats poor in P. They reported that the species differed markedly in their responses to available P. The species from soils high in P responded to increase in P while those from the P deficient habitats lacked responses to the element. It was concluded that lack of response was a clear reflection of the ability of these plants to grow in the poorest soil conditions where the level of P is very low.

Root/Shoot Ratios

The dry matter distribution of the species also varied between and within the species, though trends of responses were similar, i.e. root/shoot ratios markedly increased with decreases in P levels. The lowest ratios for all three species occurred at the highest level at all three harvests. The highest ratios were not consistent, except that of barren brome which always occurred at the lowest level of P. The higher root/shoot ratio observed in barren brome compared to the crop and wild oat at the lowest P level may be a characteristic of the weed which could be related to its ability to grow and reproduce under very low soil fertility conditions. The lower root/shoot ratio observed for wheat is because of the fact that crop species have been selected and bred for greater distribution of dry matter to the tops under relatively high fertility. It is interesting that root/shoot ratios for wild oat did not follow a consistent trend in response to P level and this may show its adaptability to a range of soil conditions, including low fertility.

A number of authors have studied plant root systems in relation to their ability to compete for soil resources. Baan Hofman and Ennik (1980; 1982) and Ennik and Baan Hofman (1983) studied the competitive abilities of genetically different lines of perennial ryegrass, Lolium perenne grown with a highly competitive grass, Elytrigia repens. They found that the most competitive lines were consistently those with greater root mass and large root/shoot ratios. In the present experiments the fact that wild oat produced the greatest root mass and barren brome the higher root/shoot ratio may be expected to make them more competitive than the crop under field conditions. The more massive root system in wild oat may enable the species to occupy more of the soil volume, than the root system of the crop. The highest root/shoot ratio in the second weed may also enable it more effectively to deplete soil resources in localised zones, especially because of its much branched root system.

Root Morphology

The absolute values for the total root length and surface area per plant were the greatest for wild oat at all P levels except the lowest, where wheat exceeded both weeds. The values of these variates were the smallest for barren brome. However, the ratios of root length to root dry weight, and area to root dry weight were greatest for barren brome. Though both ratios increased with decrease in P, the highest ratio at almost all levels occurred for barren brome. The highest ratios for barren brome suggests a more branched root system which could be an advantage for the weed in a solid medium since such a root system may be expected to exploit a greater volume of the substrate, as already discussed in relation to experiment 1. Phosphorus is a non-mobile element in the soil, and this root morphological feature of the weed may enable it better to meet its demands for this ion. This could be a very significant advantage under competitive conditions with the crop and wild oat in the field. Johnson (1987) also reported a higher length/weight ratio for blackgrass than wheat at the lowest P concentration (0.07 mM P) and stated that this observation strongly suggested that P supply can induce changes in root morphology which in turn could affect the efficiency of P uptake. Support for such suggestions comes from investigations by Drew and Saker (1978). They reported compensatory increases in the growth of lateral roots and in the rates of uptake of P in solution when parts of the root systems of barley were deprived of phosphate. Bradshaw *et al.* (1960a) in general found a reduction in the relative amount of rooting at higher phosphate levels and hence lower root/shoot ratios for some species than at the lower levels.

Vose (1962) grew, in solution culture, three varieties of ryegrass known to give progenies varying widely in yield when grown as spaced plants in the field. He found that although the relative order of the varieties in yield remained the same as in the field, the actual relative difference in yield between them was very small in solution culture. It was suggested that the large root system of the highest yielding variety enabled it to take advantage of the soil volume. Troughton (1959), cited by Vose (1963) found in perennial ryegrass that the uptake of radioactive P by branched roots can be as much as 30% greater than the uptake by unbranched roots, thus emphasising the importance of variations in root type in varietal difference in nutrition. Smith (1934), using sand solution culture and sand/soil

mixtures, found marked differential responses in maize inbreeds and hybrids to low P. He concluded that the ability to grow relatively well on a low level of P is inherited and it is dominant over lack of such ability. Lyness (1936) found both a differential yield response and a difference in P-absorbing capacity when he grew 21 varieties of maize at different levels of P in sand culture and nutrient solution. One variety which had a high P requirement apparently had only a limited capacity for P absorption from low P concentrations. Both Lyness and Smith found that there was also a direct correlation between P efficiency and the number of secondary roots in relation to primary roots. Schenk and Barber (1980) have found that P-acquisition in maize can be increased by development and selection of hybrids with more fibrous root systems. Nye (1977) has emphasised that when a nutrient is at a low concentration in the medium, root surface area is the factor most likely to be limiting in ion absorption. It is suggested therefore, that the observed differences in the accumulation efficiency of P, by wheat, wild oat and barren brome may be due partly to differences in size and type of roots and rooting patterns. It is emphasized that such features of the root systems of plants are important in nutrient uptake and are especially relevant to P where root interception, and contact, plus diffusion are the mechanisms of supply for this element.

The number and type of roots may clearly have an influence on the nutrition of plants in soil, because an extensive root system is important in order to take advantage of volume of soil available for exploitation and for increased competitive effectiveness.

A study of the absorption of ^{32}P by two inbred lines of maize and their hybrids showed that the hybrid with the largest root system absorbed the greatest amount of radioactive P (Rabideau et al., 1950). Uptake and accumulation of P by maize have been studied extensively by Baker et al. (1970) and Gorsline et al. (1964). Differences among maize genotypes with high and low P accumulation properties were attributed to root size, the ability to compete effectively for P, the ability to tolerate detrimental effects of competing or harmful elements like Al, and to root phosphatase activities. Phillips et al. (1971) also attributed differences in uptake and accumulation of P to the differences in the type and size (dry weights and lengths) of their roots, maximum rates of uptake (Vmax), Km and P concentration remaining in solution when net influx was zero (Nielsen and Barber, 1978).

Nutrient Concentration and Accumulation

The present species differed extensively in nutrient concentrations and total content and in the dry matter produced per unit element. The weeds, in general, showed higher concentrations and contents than the crop (Figures 1.4a, b, c and d; Table 1.4). Both weeds, especially barren brome, contained slightly higher P. Barren brome also showed significantly higher concentration of Ca at all P levels, except the highest, where it was similar to wild oat. Wild oat contained the highest K and Mg at all P levels except the lowest where it had similar amounts of K to wheat. It was also similar to both species for total Mg and the lowest P. In general, highest total amounts of P, K, Ca and Mg were found in wild oat, the lowest being in barren brome. At L4 the three species did not differ in the total accumulation of these elements. In general, nutrient concentration, accumulation and uptake per unit root weight decreased with decrease in P level in solution. The reverse was true for dry matter production per unit nutrient absorbed.

The efficiency of the roots in taking up P did not differ significantly with species, though there were some consistent trends with the weeds tending to have higher values than the crop. Wild oat showed the highest root efficiency in taking up Mg and K at all levels of P except L2, where the crop was higher than both in K uptake efficiency. At any level of P, except the highest, where wild oat was more efficient than barren brome, the latter was the most efficient in Ca rate of uptake.

Nutrient Uptake and Utilization Efficiencies

The crop appeared to be slightly more efficient than the weeds in the amount of dry matter produced per unit tissue P. It was the most efficient species in the utilization of Ca and Mg at any P level. Barren brome produced the highest dry matter for every unit of K absorbed except at the lowest P where it was similar to the other two species. Although wild oat showed higher contents and uptake efficiencies for K and Mg and slightly for P, its efficiency in utilizing these elements was the lowest. This may suggest that the weed absorbs these nutrients even if they are not required (i.e. luxury consumption). A number of investigators have found uptake of nutrients greater than the immediate requirement in some species. For example, the work of Jeffrey (1964) with Banksia ornata suggests that young plants were able to absorb

orthophosphate at high rates in time of plenty, store it as inorganic polyphosphate and release it within the plant when the external supply was low. This is of obvious ecological importance since it enables the species to survive under low P conditions after prior absorption under more favourable conditions. Rorison (1968) also found excess P uptake in Scabiosa columbaria and concluded that the ability to take up more than the immediate requirement is ecologically valuable and the accumulation of a tissue mobile element at flush times may be adequate to ensure steady growth during times of stress.

It may thus be suggested that the high uptake rates observed for P, K and Mg and their low utilization efficiency in wild oat may explain the ability of the weed to guard itself against times of deficiencies of these elements. It may also indicate the ability of the weed to adapt to a wide range of soil nutrient conditions in its habitat. The fact that wild oat showed the lowest utilization efficiencies for P, K and Mg may suggest that the demand for these nutrients and thus their high uptake and concentrations in its tissues may simply be the result of the activity of its large root system.

It is interesting that the weed with the highest tissue concentration of the element showed the highest efficiency of uptake for that element. Barren brome showed the highest concentration of Ca and was also more efficient than wild oat. Tissue concentrations for K and Mg were higher in wild oat as were their uptake efficiencies. Both weeds also showed slightly higher P concentrations and higher efficiencies than the crop. It is likely that the high concentrations of these nutrients found in the weeds may be due partly to changes in the features of the roots described earlier.

Johnson (1987) found that the mean tissue concentrations of K and P were significantly higher in wheat than blackgrass, whilst the opposite was true for Ca and Mg. He also reported that P supply affected the uptake of N, P, K, Ca and Mg in both species, and that increasing the supply of P in solution resulted in increased tissue concentration of these elements. This is in agreement with the results of the present experiments where nutrient uptake, concentration and accumulation showed increases with increase in P level in the solution. In other studies of plant nutrition, synergistic effects have been reported. For example, Robinson and Jones (1972) found that both P and S fertilization increased

dry matter and tissue concentrations of N, P and S of all plant parts.

In the previous experiment, the species did not show significant differences in P tissue concentrations, although barren brome was slightly higher than the other species. The weeds were higher in Ca and Mg, whilst the crop in K. The uptake of K, Ca and Mg in both experiments was affected similarly i.e. at low P levels uptake of these elements was in general reduced and vice versa.

Experiment 3

5.8. Results

Shoots: Wheat and wild oat produced similar amounts of shoot dry matter at all K levels; barren brome always produced less (Table 1.5). In all species shoot production was reduced with reduction in K level. The most affected species was barren brome, which produced less than 20% of its control level of dry matter at the lowest K concentration.

Roots: The results for root dry weight paralleled those observed for the shoot (Table 1.5), and results for the whole plant naturally follow from this.

Root/shoot ratio: Species and the interaction between species and K levels were not statistically different but the ratios did depend on K concentration (Table 1.5). At the first and third harvest interactions were significant. In general the ratio between roots/shoots increased in all species as the K level was reduced.

Root radius: Summed over all levels the finest roots were produced in barren brome (Table 1.5). Wheat and wild oat had similar diameters, which generally increased as the level of K was reduced. Roots of barren brome either remained the same or grew thinner with reduced K.

Total root length: Summed over all levels the total length of root was the longest in wild oat plants and smallest in barren brome (Table 1.5). All species had the same length of root at L2 of K. Wheat and wild oat also had similar root length at L1. At L3 and L4 wild oat produced longer roots than wheat. In all species, root length was reduced by reduction in K level.

Table 1.5 Effects of K level on growth variates of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

K level	Shoot dry weight (g/plant)	Root dry weight (g/plant)	Whole plant weight (g/plant)	Root/shoot ratio	Root radius(cm)	Total root length (m/plant)	Total surface area (cm^2/plant)	Root length/root dry weight	Surface area/root dry weight
L1									
W	5.37	1.10	6.47	0.20	0.013	238.9	1938.0	221.0(1.66)	1782.0
WO	5.40	1.02	6.42	0.19	0.014	227.9	2028.0	226.0(1.67)	1997.0
BB	2.04	0.38	2.42	0.19	0.011	116.1	802.0	311.0(1.77)	2133.0
L2									
W	3.39	0.57	3.96	0.18	0.016	92.5	948.0	172.0(1.46)	1789.0
WO	3.28	0.49	3.77	0.15	0.015	96.0	911.0	199.0(1.48)	1886.0
BB	1.67	0.28	1.95	0.18	0.011	80.4	559.0	290.0(1.70)	2021.0
L3									
W	2.59	0.60	3.19	0.23	0.017	93.0	1010.0	162.0(1.57)	1761.0
WO	2.47	0.54	3.01	0.22	0.015	160.6	1479.0	308.0(1.82)	2831.0
BB	0.68	0.14	0.82	0.20	0.011	43.6	282.0	325.0(1.82)	2095.0
L4									
W	1.91	0.45	2.36	0.24	0.015	94.7	905.0	214.0(1.63)	2049.0
WO	1.90	0.47	2.37	0.25	0.016	128.6	1314.0	282.0(1.84)	2883.0
BB	0.32	0.12	0.44	0.27	0.007	46.0	200.0	659.0(2.15)	2812.0
Significance level									
SP.	***	***	***	NS	***	***	***	***	***
Nut.	***	***	***	***	***	*	***	***	***
SP.Nut.	***	***	***	NS	***	**	***	***	NS
LSD ($P < 0.05$)									
SP.	0.29	0.07	0.32	-	0.001	8.60	87.7	(0.05)	277.0
Nut.	0.34	0.08	0.37	0.03	0.001	9.94	101.3	(0.06)	319.8
SP*Nut.	0.58	0.14	0.64	-	0.002	17.21	175.1	(0.10)	-

Values in brackets are for Log_{10} transformed data

Total root surface area: Wild oat had the largest and barren brome the smallest surface area of roots (Table 1.5). Wheat and wild oat produced similar areas of root at L1 and L2. The surface area of the species decreased with a decrease in K level.

Root length/root dry weight: The length of root per unit root dry weight was greatest for barren brome at all levels of K (Table 1.5). All species had similar ratios at L1. Except at L3 wheat and wild oat were similar. The weeds were also similar at L2 and L3 on all the species, particularly barren brome the ratio increased with a decrease in K levels.

Root surface area/root dry weight: The weeds had larger area per unit root weight than the crop at all levels of K (Table 1.5). The largest ratio was found at the lowest K level in solution.

Nutrient concentration

P: Summed over all levels, barren brome had the highest P concentration, the highest occurring at L3 and L4 (Figure 1.7a). Wheat and wild oat were similar at all levels of K except the lowest where wild oat had a higher concentration than the crop. P concentration in all species increased with a decrease in the levels of K.

K: Summed over all levels the crop had a higher concentration of K than either weed. All species were similar at the two lower K concentrations though values for barren brome were slightly higher than for the other two (Figure 1.7b). The weeds were also similar at L1 and L2.

Ca: Summed over all levels barren brome had the highest concentration of Ca. Wheat and wild oat were similar (Figure 1.7c), except at the third K level, where wheat had a higher concentration than wild oat. At all levels except L3 where wheat was similar to barren brome, the latter had higher Ca concentrations. Ca concentration increased up to the third level of K and decreased at L4 in all species.

Mg: Summed over all treatment levels, the weeds contained a higher concentration of Mg than the crop and barren brome was slightly higher than wild oat (Figure 1.7d) (much higher at the third harvest). The weeds, particularly barren brome, were more efficient than the crop in taking up Mg when the K level was reduced. At higher levels of K, barren

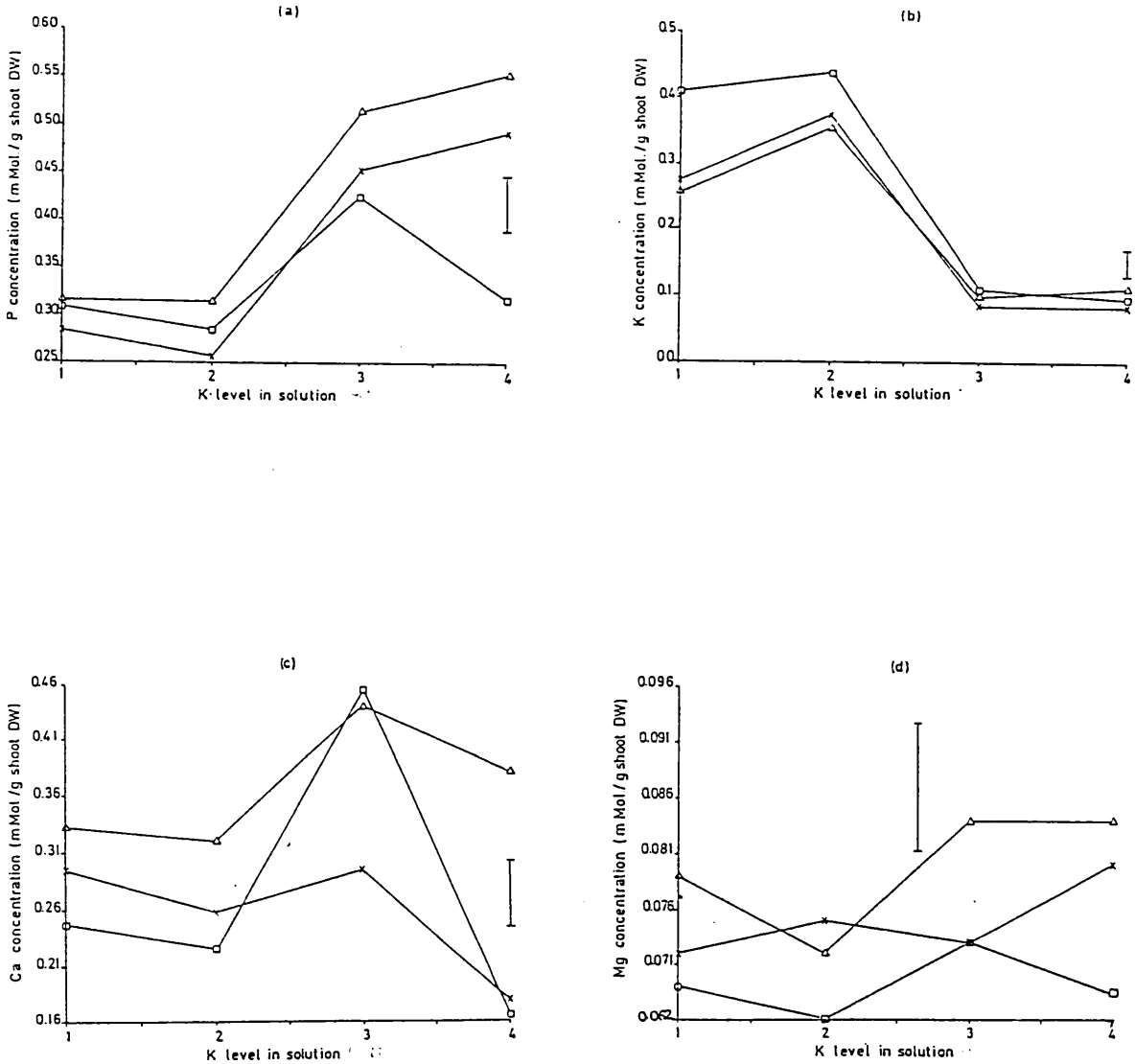


Figure 1.7 (a–d) Effects of potassium level on the concentrations (mMol/g DW) of P, K, Ca and Mg in wheat (□) and wild oat (×) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at 5% level of probability
NS = no significant differences

brome was more similar to wheat that to wild oat. At harvest 3, however, the species showed similar efficiencies at all K levels.

Total nutrient content

P: Summed over all K levels the total P contents of wild oat and wheat were similar and greater than that of barren brome (Table 1.6), but at the third harvest wild oat contained more P than wheat or barren brome. Generally P contents of wheat were reduced with K concentration, but wild oat was only slightly affected.

K: Summed over all levels the total amount of K found in wheat was greater than both weeds (Table 1.6). Differences among the species occurred only at the two higher levels of K. The total K in all species was reduced by reduction of K in solution, wild oat being the least affected species.

Ca: Summed over all treatment levels the amount of Ca in wheat and wild oat was similar and barren brome had the smallest content at all levels of K (Table 1.6). By the third harvest wild oat had the largest amount and barren brome the smallest. In all species the amount accumulated was reduced with reduced K.

Mg: At the second harvest wheat and wild oat did not differ in total Mg (Table 1.6), barren brome values again being lower. By the third harvest wild oat contained more than both wheat or barren brome. The total Mg in the species was also reduced as K level in solution was reduced.

Efficiency of nutrient uptake of roots

P: Summed over all K levels there was a significant effect of species in efficiency in taking up P per unit root weight. Interactions were not statistically different at harvest 2, but were by harvest 3. P efficiency also increased with a decrease in K level in solution in all the species.

K: The species did not differ in the uptake efficiency of K at harvest 2, but at the third harvest barren brome was less efficient than the two species. The K uptake efficiencies of all species declined as the availability of K in the feeding solution was reduced and this was more pronounced in the third harvest than in the second.

Table 1.6 Effects of K levels on the total uptake (mMol/plant) of P, K, Ca and Mg of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

	L1			L2			L3			L4			Significance level			LSD (P 0.05)		
	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB	SP	K	SP*K	SP	K	SP*K
P	1.99	1.81	0.76	1.11	0.97	0.62	1.39	1.36	0.42	0.74	1.14	0.21	***	***	***	0.169	0.195	0.338
K	2.65	1.77	0.62	1.74	1.42	0.70	0.35	0.25	0.08	0.23	0.20	0.04	***	***	***	0.168	0.182	0.316
Ca	1.60	1.89	0.80	0.87	0.98	0.64	1.48	0.88	0.36	0.38	0.43	0.15	***	***	***	0.163	0.189	0.327
Mg	0.45	0.46	0.19	0.24	0.28	0.14	0.23	0.24	0.07	0.16	0.19	0.07	***	***	***	0.028	0.032	0.056

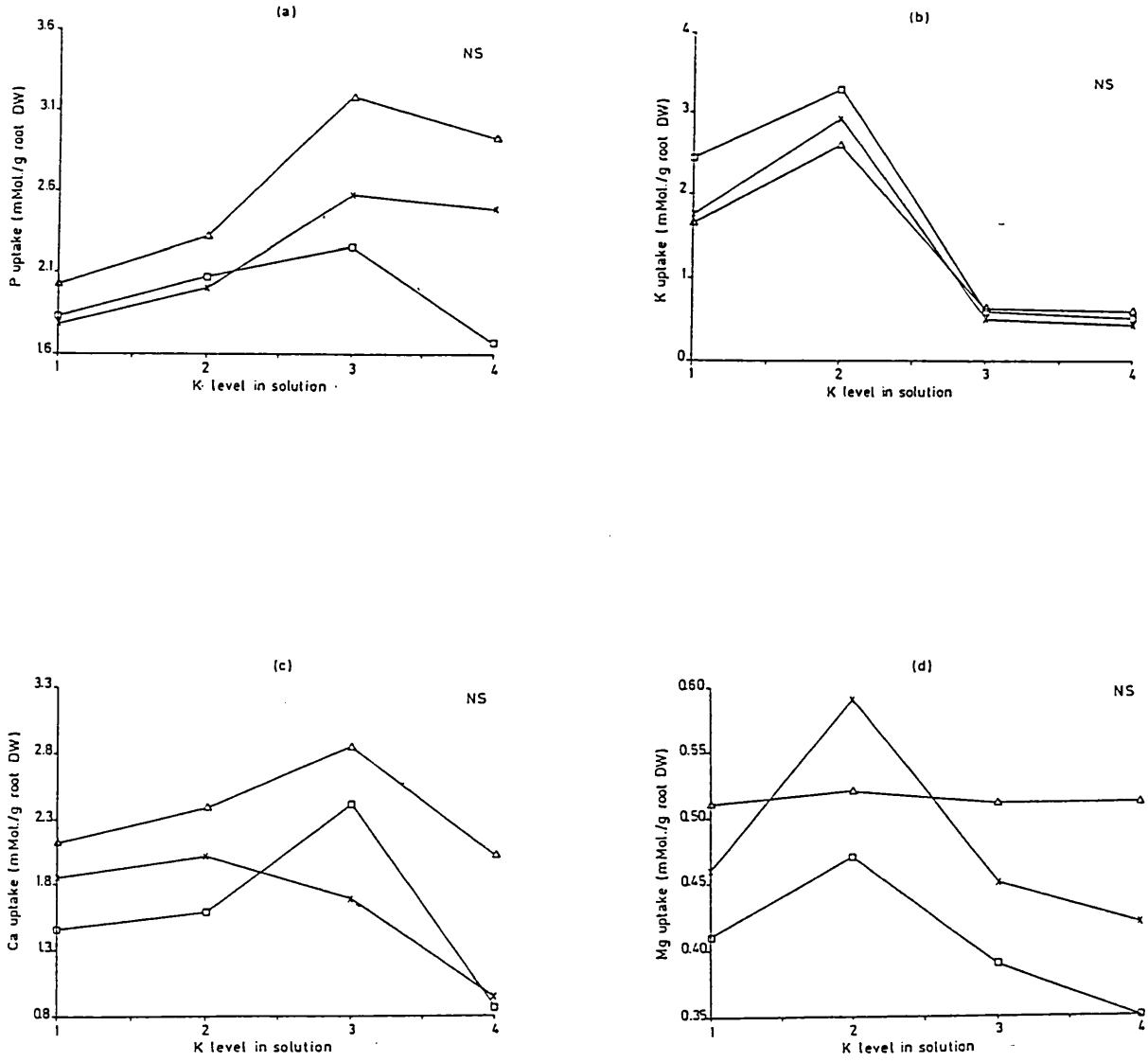


Figure 1.8 (a-d) Effects of potassium level on the efficiency of uptake (mMol/g root DW) of P, K, Ca and Mg of wheat (□), wild oat (✗) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at 5% level of probability
NS = no significant differences

Ca: Efficiencies varied with both species and K levels, but interactions were not significant. Summed over all levels the most efficient species was barren brome, whilst wheat and wild oat did not differ (Figure 1.8c). At the third harvest interactions were significant and the weeds, especially, barren brome, were very efficient in Ca uptake. In all species except barren brome, the efficiency of Ca uptake decreased with decreasing K concentration.

Mg: Summed over all levels wheat and wild oat had similar efficiencies and barren brome was the most efficient. At the third harvest the weeds were also more efficient than the crop. The efficiency of Mg uptake was reduced in all species as K was reduced except that at the third harvest that of barren brome increased, while wheat and wild oat showed similar trends of decrease.

Nutrient utilization efficiency of species

P: Summed over all K levels wheat and wild oat showed similar efficiencies which were greater than that of barren brome (Figure 1.9a). Species utilization efficiency decreased as the level of K was reduced, although the reduction in wild oat was less than that in both wheat and barren brome. By the third harvest the crop was more efficient than either weed.

K: Summed over all levels wild oat was the most efficient species (Figure 1.9b), whilst wheat and barren brome did not differ from each other. In all the species efficiency was higher at the lowest levels of K. By harvest 3 all species showed similar values.

Ca: Summed over all treatment levels, wheat and wild oat showed similar efficiencies. All species were not greatly affected by reduction in available K, although both wheat and wild oat increased efficiency at the lowest K level and barren brome utilization efficiency continued to decline from the second level of K, particularly at harvest 3.

Mg: Wheat was the most efficient species, particularly at lower levels of K. The weeds were similar in their utilization efficiencies, although at the third harvest wild oat was more efficient than barren brome. Mg utilization efficiencies of all species generally decreased as the level of K was reduced (Figure 1.9b).

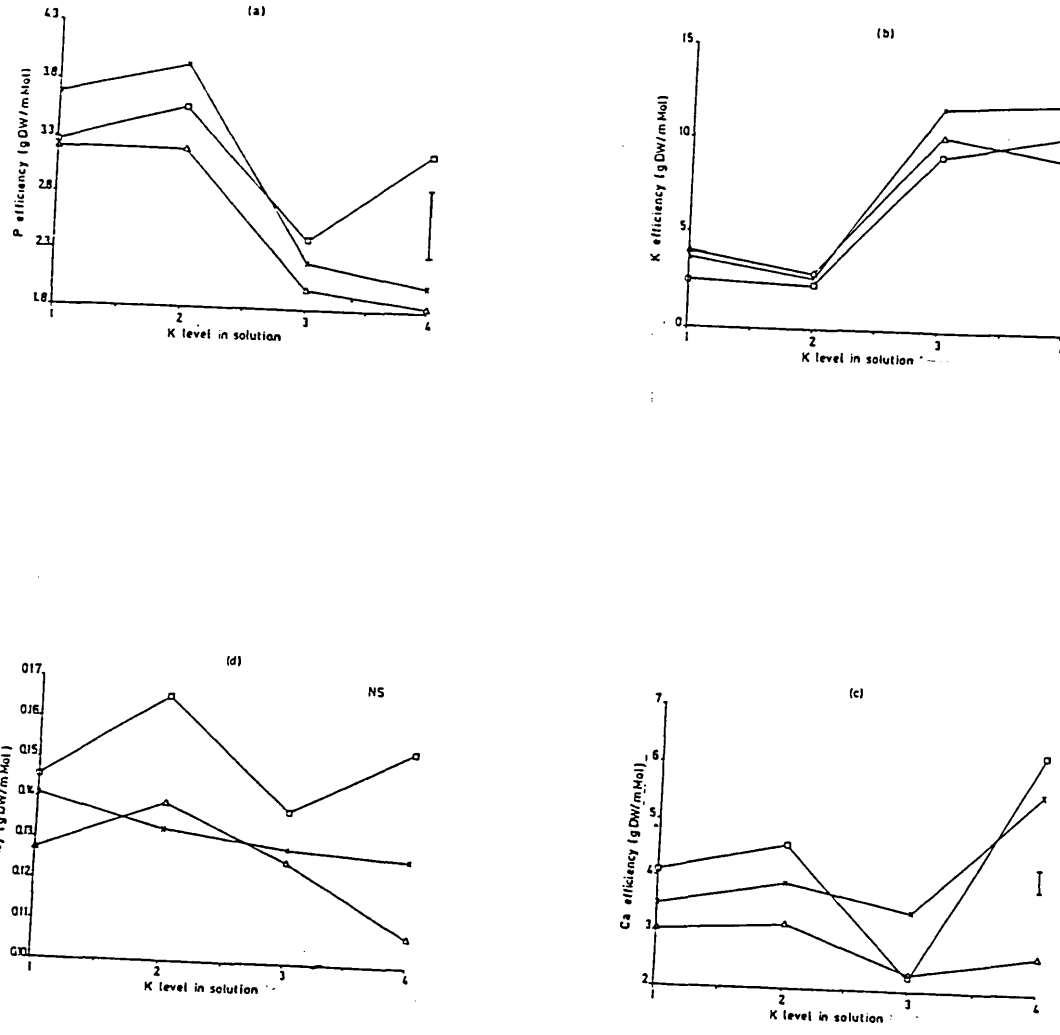


Figure 1.9 (a–d) Effects of potassium level on the efficiency utilization (g DW/mMol) of P, K, Ca and Mg in wheat (□), wild oat (×) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at 5% level of probability
NS = no significant differences

Experiment 1.3: Responses of wheat, wild oat and barren brome to K

5.9. Discussion

Dry matter yields

In all three species, total dry matter accumulation was significantly reduced by reduction in the level of K (Table 1.5). Barren brome was the most affected species, at the lowest level of K only producing about 20% of its yield at the highest K. This result agrees with that of the first experiment, where barren brome was more seriously affected than the other species. The deficient level of K used in the previous experiment was also included in the present one and mean reduction in barren brome yield in both was similar, confirming the susceptibility of the species to low K. In all species, and particularly in barren brome, shoots were more reduced than roots. The relative shoot dry matter reduction between L1 and L4 was 84% in barren brome compared with 64 and 65% in wheat and wild oat respectively. The root dry matter reduction over this range of K was 59, 54 and 68% in wheat, wild oat and barren brome respectively.

The total dry matter yield of barren brome was the lowest at all levels of K, whilst those of wheat and wild oat were similar to each other. These results clearly indicate that the species, especially barren brome, were markedly different in response to levels of K in the medium. The sensitivity of barren brome to K level was also shown by the fact that the weed showed a 5.50-fold increase in dry matter production over the range of K levels as compared to wheat and wild oat which were 2.74- and 2.71-fold respectively.

In experiment 1 the relative increases in dry matter production from the deficient to the higher level were 2.28, 1.34 and 3.14-fold for wheat, wild oat and barren brome respectively. In that experiment it was concluded that wild oat was the least sensitive species and barren brome the most. Although barren brome responded similarly to experiment 1 in the present experiment the responses of wheat and wild oat were similar over the entire range of K used. The two experiments together may or may not suggest that the two species have similar requirements for the element. The differences in the results may be attributed, among other

factors, to differences in methodology and season. Experiment 1 was carried out in the spring of 1987. During this period individual plants of each species were much heavier than those in the present experiment, which was conducted during the hottest part of the year i.e. early July to early September. Barren brome occurs as an important weed of early-sown winter cereals, as the seeds germinate between late summer and early autumn (Froud-Williams et al., 1980). Wild oat in England and Canada germinates in the spring with a lesser flush in autumn, but in some parts of France and America the autumn flush may be the main one (Chancellor, 1976). In experiment 1 nutrients were replenished on a weekly basis while in the present experiment this was done fortnightly. Extremes of temperature may affect the incidence and development of wild oat whilst mild conditions appear to favour its rapid growth. It may be that these factors influenced the magnitude of the responses of wheat and wild oat, resulting in smaller differences between them compared with those observed in Experiment 1.

Several investigators have studied the responses of various species to levels of K and differences within and between plants have been reported (e.g. Hoveland et al., 1976; Minotti, 1977; Zimdahl, 1980).

Asher and Ozanne (1967) studied the response of 14 different plant species to different concentrations of K in water culture. They reported differences in the response of the different species to changes in K concentration. They also found that the species differed in their requirements for K for optimum growth in the nutrient solution.

Wild et al. (1979) compared, under similar environmental conditions, the response of four herbage species to a range of K concentrations in flowing nutrient solution and in sand culture. The species investigated included the grasses Anthoxanthum odoratum L. and Dactylis glomerata L. and the legumes Trifolium pratense L. and Medicago lupulina L. In both culture systems they found consistent differences in the behaviour of the two grasses. They reported that the yield of A. odoratum was greater than that of D. glomerata at low K concentrations whereas at high K concentrations the relationship was reversed. They suggested that the observed differences between the grass species paralleled differences in their ecological distribution: A. odoratum is common in natural grasslands where nutrient supplies are comparatively low, whereas D. glomerata has been bred for high yields at a higher fertility. They also

found consistent differences between the two leguminous species. In sand culture, T. pratense responded more to increasing K concentrations than did M. lupulina, but in flowing nutrient solutions the reverse was recorded. They suggested that the difference between the results from the two techniques may be due to T. pratense being more self-shading in the flowing solution than in sand culture.

Geloff (1977) also reported wide differences in the K response of two tomato lines. When an adequate amount of K was supplied to both lines, one of them strain 94, yielded 25% more than the second (strain 98). He concluded that the former had a requirement for higher substrate K.

Qasem (1987) studied the responses of tomato, fat-hen and groundsel to K in a series of pot and water culture experiments and noted marked differences in response to levels of this element. He found fat-hen to be the most responsive and sensitive species to levels of K particularly at early stages of its growth. He suggested that observed differences in the growth of the species under the various K levels may mean that high levels of the element may be advantageous to fat-hen when the species are grown in competition.

Thurston (1972) reported a low K-requirement for blackgrass and suggested that this may be one reason why the weed invades wheat in K-deficient soils. Tarawali (1983) also found blackgrass less responsive to K in solution culture than wheat. The relative insensitivity of wild oat to K reported by Pawlik (1957) has been mentioned earlier in Experiment 1. Chancellor (1969) reported that increasing K caused only a slight weight increase in the top growth of wild oat.

Root/shoot ratios

Despite the fact that the species differed dramatically in their yield responses to levels of K, differences in their root/shoot ratios did not reach statistical significance at the second harvest (Table 1.5). Summed over all species, however, significantly higher root/shoot ratios were observed for the lower K levels (L3 and L4) than for the higher (L1 and L2). At the first harvest interactions were significant but differences between the species at any level were not significant. Differences within species were noted in wheat and wild oat, whilst barren brome produced similar ratios at all levels of K. Both wheat and

wild oat produced their lowest ratios at the 2nd level of K. This was also noted at the third harvest and interactions between species and K levels were also significant at this stage. In both harvests 2 and 3, the ratio between roots and shoots increased as the level of K was reduced in all species, except for barren brome at the 3rd harvest which showed the lowest at the lowest level. An increase in root/shoot with decrease in K in solution was also noted in Experiment 1, especially for wheat and wild oat. It has been noted (Christie and Moorby, 1975; Grime and Curtis, 1976 and White, 1972) that rapidly growing species from high-nutrient habitats show considerable plasticity in root/shoot ratio and generally have a higher ratio at low availability and lower ratio at higher availability than do species from a low-nutrient habitat. In general, species from infertile habitats increase their uptake of nutrients through high root/shoot ratios. Barren brome may thus conform to the general behaviour of species from low nutrient habitats. The similarities in dry matter production and their distribution in wheat and wild oat at all stages of harvest and K levels may also suggest that the two species have developed similar adaptation to K levels in the soil, because of their long historical association in agricultural fields.

In the studies of Qasem (1987) already referred to, he observed that at low K levels, the ratio between roots and shoots significantly increased in fat-hen, whilst in groundsel it decreased and in tomato it was not significantly changed. He inferred species difference in their adaptation to such nutrient depression. He also noted more shoot than root reduction in fat-hen, but in the other two species roots were more reduced than shoots. He also suggested that this may imply that under nutrient stress conditions groundsel roots became more efficient in the uptake and transport of nutrients. In the present experiment, the shoots of the three species were more reduced than the roots, although the magnitude of reduction in barren brome was greater than in wheat or wild oat. Although the trends of responses are similar in all three species, and may imply similarity in adaptability to low K, barren brome might clearly be less efficient in the uptake and utilization of K than the other species, whilst the latter may share similar degrees of efficiency for this element. It may also be that the greater reduction in barren brome roots and shoots at low K levels does not necessarily indicate its inability to extract the nutrient, but a high requirement for K, as clearly shown by its greater increase in size with increase in levels of K.

Although a larger root/shoot ratio has been associated with higher efficiency in species (see Snaydon and Bradshaw, 1962a), authors differ on the ecological importance of this ratio, because it does not always reflect the actual performance of a plant as it is genetically controlled. For example, in the present experiment, wheat and wild oat were significantly different from barren brome in the production of total dry matter, but did not significantly differ in their root/shoot ratios. Similar observations were made by Tarawali (1983) who reported greater dry matter production in blackgrass than in wheat, but found similar root/shoot ratios in both species. The observations made by Snaydon and Bradshaw in relation to root/shoot ratios are often quoted in literature. They showed that varieties of Trifolium repens which were efficient in taking up K from low levels had a higher root/shoot ratio. In another study Bradshaw et al. (1964) found that Agrostis stolonifera L. and Lolium perenne L showed similar yields in response to N level but were markedly different in their changes in root/shoot ratios. On the other hand, although Nardus stricta L. and A. stolonifera had extremely different yield responses to N, they gave similar changes in root/shoot ratio. In general, although their data showed a clear increase in root/shoot with decrease in N, there was no evidence of any correlation with the habitat. Fageria (1973) studied the absorption of K as influenced by its concentration in nutrient solution by rice plants and its relation to growth. He found that K deficiency generally reduced the growth of tops more than of roots. This is in agreement with the present results and those of Asher and Ozanne (1967) in solution culture in various plant species. The results of the present experiment are also consistent with the general observation that a shortage of mineral nutrients or water tends to reduce shoot growth more than root growth (Brouwer, 1962). It is suggested that the ability to increase the relative size of root system under conditions of K deficiency may have survival value, since it may increase the ability of the plant to obtain enough of the element to complete its life cycle, even in the case of an element which is relatively mobile in the soil.

Root morphology

In general the total root length and surface area were reduced with decrease in K in solution (Table 1.5). At higher K levels (L1 and L2)

wheat and wild oat showed similarities for the two variates but a lower levels (L3 and L4) wild oat had significantly higher values. The finest roots were produced by barren brome at all levels of K. Root thicknesses in wheat and wild oat were similar except at 3rd level where wheat roots were thicker than wild oat. Thickness of the roots in both showed a significant increase as concentration decreased, but that of barren brome remain unchanged down to the 3rd level and significantly declined at the lowest level. Root length and surface area per unit dry weight was the highest for barren brome at all levels of K. Wheat and wild oat were similar in both variates at higher K levels, but at lower levels values for both were higher for wild oat. In all three species, root length and root surface are/unit dry weight increased significantly as K level was reduced.

It has already been emphasised that root system size and morphology may be important factors which determine the responses of species to nutrients. In the present experiment, the observed differences, particularly between barren brome and the other two species in their responses to levels of K, may be attributed to differences in root morphology. Several authors have attributed higher performance of species especially under nutrient deficient conditions to differences in root systems. For example, Vose (1963) found superiority in the field of a high yielding strain A over a low yielding strain C of ryegrass to be primarily due to enhanced root growth. It follows that plants with a large or rapidly growing root system, will tend to appear superior under these conditions to plants with a less extensive root system.

The work of Rabideau et al. (1950) relating ^{32}P uptake to size of the root systems of maize has already been mentioned. Nye (1973) has emphasised that when a nutrient is at low concentration in the medium, root surface area is most likely to be the limiting factor in ion absorption. Raper and Barber (1970 I and II) found that although the soybean variety Harosoy 63 had a more extensive root system than that of Aoda, the capacity of each variety to absorb nutrients was about the same. However, Evans (1938) found no relationship between the absorbing surface and total length or weight of roots although there were large differences in the total absorbing surface of different varieties.

Some of the most aggressive weeds show a faster and more extensive root development than most crops. Wiese (1968) mentioned wild oat as an

example of a weed having a much more extensive root system than all cereal species. Much earlier, Pavlychenko and Harrington (1934) listed wild oat as a serious competitive weed, based on the extensive root system it produced. In the present experiment the ability of wild oat to produce the largest root system especially at low levels of a specific element in water culture, is confirmed. However in NFT, where nutrients are readily available, the large root system in wild oat may not be a great advantage. Under soil conditions this may enable the weed to utilize high nutrient levels by luxuriant growth, combining the effects of high competition for light and other nutrients. When nutrients are limiting, wild oat may be able to exploit immobile elements like P, as well as moisture in deeper soil. Barren brome on the other hand, may be able intensively to exploit the soil at shallower depths for nutrients and moisture because of density of roots. Snaydon (1962) noted that a 2- to 3-fold variation in soil solution nutrient concentration within a few centimetres is not uncommon and species with finer roots may have some advantage in gathering these nutrients. The ability of plants to exploit pockets of high nutrient concentration of a limiting nutrient by localized proliferation of lateral roots in zones of high availability, demonstrated by Drew and Saker (1978) has also been mentioned previously. There was a clear difference between species in the uptake of P but not in the case of K.

Nutrient uptake and content

The weeds, particularly barren brome, showed greater concentrations of P, Ca and Mg than the crop. The crop had the highest K concentration at higher levels. At the lower levels all three species were similar (Figure 1.7 9a, b, c and d). The concentration of P and Mg tended to increase with decreased in K levels in all species.

The crop accumulated the greatest total amount of K at higher levels, but at lower levels all species were similar. Both wheat and wild oat showed similar accumulations of P, but at the lowest level wild oat contained more P than wheat. Barren brome had the lowest total contents of P, K, Ca and Mg. Wheat and wild oat had a similar quantity of Ca at all levels except L3, where wheat was higher. These two species also had similar amounts of Mg at all levels of K (Table 1.6).

Interactions between K levels and the species were not significant for the uptake rate of P, K, Ca and Mg (Figure 1.8 1a, b, c and d). In

general the species which showed higher tissue concentration for a specific nutrient also showed a slightly higher efficiency of uptake for that nutrient; for example, barren brome was more efficient in the uptake of P, Ca and Mg and had the highest tissue concentrations. The crop also appeared to be slightly higher than the weeds in its efficiency of K uptake, especially at higher levels, but at lower levels barren brome was slightly more efficient than the other species. Summed over all species, K uptake was higher at higher than lower levels. The uptake efficiency for Mg was influenced by K levels. At higher levels the uptake was greater than at lower levels. Uptake efficiency for Ca appeared to decrease in wheat and wild oat while that of barren brome slightly increased as K level decreased. The species differed significantly in the utilization efficiency for P, K, and Ca (Figure 1.9 2a, b, c and d). They were not significantly different at any one K level, but summed over all levels the crop was the most efficient. K level in solution did not appear to have any influence on Mg utilization rate in any species. However, summed over all K treatment levels wheat was the most efficient and wild oat was more efficient than barren brome.

It has been shown that the observed differences among the species in their nutrient concentrations and total contents may depend on the uptake efficiency and/or on the efficiency of utilization of the abosrbed nutrients. Although both factors may be genetically controlled (Vose, 1963, 1984; Gorsline et al., 1964) variation in the level of K in solution may have caused differences in the efficiences of uptake of the species for P, K, Ca and Mg. For example barren brome had the highest tissue concentrations for P, Ca and Mg and showed the highest rate of uptake for these elements. Its efficiency of uptake also appeared to be slightly increased as the level of K decreased. However, barren brome did not exceed wheat or wild oat in total content due to its smaller size. The amounts in these two species were similar to each other or different, depending on the specific element for which root efficiency was higher. For example, wheat showed high root efficiency for K and thus had higher concentration and total content of the element. Both had a similar total content of P except at the lowest K level where wild oat exceeded the crop. The two did not differ in root efficiency.

Wild oat had slightly higher Ca concentration than wheat at all K levels except at L3 where wheat was higher. The three species did not differ in their root efficiencies for this element. Wheat and wild oat

were also similar for total Ca content, except at L3 where the crop was higher than the weed. The wild oat also was higher in total Mg than wheat, despite their similarities in root uptake efficiencies and total dry matter accumulation.

The higher concentration and greater root efficiency for P, Ca and Mg in barren brome may reflect a higher requirement for these nutrients by the weed, and that its needs are fulfilled because of the characteristics of its roots already discussed. The fact that both wheat and wild oat grew large and accumulated larger quantities of P, K, Ca and Mg may not imply that they perform better than barren brome in competition. Given the same number of plants the latter may be expected to compete better than both, especially at lower levels of K in the soil. At greater densities, barren brome may undoubtedly be expected to reduce the growth and nutrient yields of wheat and wild oat. Because of wheat's greater efficiency and thus higher concentration and contents for K, particularly at higher K levels, it may be suggested that the crop has a higher requirement for this element than the weeds. At lower levels however, barren brome exceeded wheat both in root efficiency and K concentration, and may thus compete more strongly than it might do when the element is present at higher levels in the soil. The agronomic implication may be that higher K may favour the crop in competitive situations, whilst lower and deficient K situations may favour its competitors. Weeds in general are found to be better competitors under low soil nutrient conditions (e.g. Hoveland et al., 1976; Tarawali, 1983; Qasem, 1987; Johnson, 1987). Many weeds, because of their adaptive mechanisms, may possess higher nutrient concentrations at the expense of crop plants, e.g. Cheopodium album accumulated N and K at the expense of several crop species; Amaranthus netroflexus accumulated seven times as much P as associated bean plants (Vengris et al., 1955). Alkamper's study (1976) emphasised that weeds usually absorbed fertilizer faster and in relatively larger amounts than crops and therefore derive greater benefit. The results of the present experiment gives some supporting evidence to this, with the weeds, especially barren brome, showing higher rates of uptake and concentrations of P, Ca and Mg than the crop. Other studies have also shown that fertility control falls short of being an effective weed control technique, because weeds respond to added nutrients in the same manner as the crops. Thurston (1962) showed that added N increased yields of both cereals and wild oat, in competition.

In the present experiments the yield of the weeds, particularly barren brome, responded more strongly to added K than the crop in NFT.

Shea et al. (1967) studied the efficiency of K-utilization in strains of Phaseolus vulgaris. They also grew the plants at stress (5 ppm) and high (200 ppm) levels of K and reported that differential response to low K nutrition appeared to be associated with efficiency of K utilization at the metabolic level. They also found that variation in efficiency of K utilization was not associated with higher levels of K in the efficient plants. Wheat in the present experiment had the highest efficiency of uptake and the greatest amounts of K, especially at higher K levels, but it was inefficient in K utilization, especially at those levels. Similarly, barren brome was less efficient in utilizing P, Ca and Mg than both other species although it showed higher concentrations and slightly greater efficiency in taking up these elements. An increase in uptake rate above that needed for maximum growth will result in accumulation of these elements in 'luxury' concentrations. It has been reported from a number of sources that plants seem to show this feature for K. For example Bartholomew (1928, cited by Fageria, 1973) reported results that indicated a large consumption of K by alfalfa, oat and Sudan grass above their actual needs.

The efficiency of weeds in removing nutrients more efficiently from the soil than the crop has been noted by Pandey et al. (1971). The study of Vengris et al. (1953) concerning weed-crop associations showed that weeds in general had higher concentrations of nutrients than associated crops.

In the study of Qasem referred to earlier, he found that fat-hen was most responsive to and showed a high requirement for potassium. It contained a higher concentration of the element than tomato and groundsel and Qasem concluded that high K levels could be advantageous to this weed in competition. Similar remarks may be made for wheat which showed specific requirement for K. However, a decrease in K in soslution resulted in lower P concentration in the crop than the weeds. At lower levels of K in the soil the crop may thus be at a disadvantage because of such indirect effects.

The response to and accumulation of individual minerals by individual species may be affected by shortages of specific elements in the growing media. K shortage increased the concentration of P and Ca in

all species, especially in barren brome; but did not alter Mg tissue concentration in this species significantly. Total uptake decreased for all three elements as K was reduced. The efficiency of the three species in taking up P, Ca and Mg was not influenced by the level of K, although this increased in the weeds for P. Several authors have reported such effects. For example, Qasem (1987) reported a decline in P concentration in fat-hen as K in solution was reduced in media. Johnson (1987) also found an increase in K concentration as P level in solution was increased. Lat ies (1960) has shown a marked decrease in K content of calcifuge lupin at high concentration of Ca. The uptake of K by a population from a calcareous site was increased as Ca supply increased, while the acidic population showed lower K content at higher levels of Ca.

The lower uptake of Ca at the highest level of K clearly suggests a competitive effect. The higher uptake of P at lower levels of K may be similarly explained. The level of K did not show any significant influence on the uptake of Mg.

Experiment 1.4

5.10. Results

Shoots: Summed over all levels wild oat produced the highest shoot dry matter (Table 1.7). It was also the species least affected by low Mg in solution. Barren brome was the most affected species and produced only 40% of its control yield; wheat and wild oat yielding about 57 and 88% respectively.

Roots: The root dry weight of the weeds was reduced at the highest Mg level and significantly increased at the second level, but at the third level that of wild oat slightly icreased while that of barren brome decreased. Yield of wheat decreased by about 55% at the lowest Mg level.

Whole plant dry weight: The trends for this variate closely followed those given above for the tops of the plants.

Root/shoot ratio: The species were different in their root/shoot ratios (Table 1.7), both weeds having higher values than the crop

Table 1.7 Effects of Mg level on some growth variates of wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

Mg level	Shoot dry weight (g/plant)	Root dry weight (g/plant)	Whole plant weight (g/plant)	Root/shoot ratio	Root radius(cm)	Total root length (m/plant)	Total surface area (cm^2/plant)	Root length/root dry weight	Surface area/root dry weight
L1									
W	4.77	1.06	5.83	(-0.65)	0.010	380.0	2461.0	359.0	517.0
WO	4.62	0.94	5.56	(-0.70)	0.011	448.7	3029.0	504.0	657.0
BB	2.18	0.30	2.48	(-0.86)	0.005	566.3	1747.0	1885.0	809.0
L2									
W	3.50	0.59	4.09	(-0.78)	0.008	453.6	2188.0	744.0	589.0
WO	4.36	1.24	5.90	(-0.55)	0.009	548.0	3035.0	443.0	697.0
BB	2.36	0.66	3.02	(-0.59)	0.006	475.4	1694.0	843.0	739.0
L3									
W	2.74	0.48	3.22	(-0.75)	0.007	415.6	1930.0	861.0	718.0
WO	4.05	1.02	5.07	(-0.60)	0.012	464.7	3454.0	470.0	871.0
BB	0.89	0.23	1.12	(-0.58)	0.005	272.2	854.0	1244.0	1066.0
Significance level									
SP.	***	***	***	NS	***	***	***	***	**
Nut.	***	***	***	NS	***	***	*	**	*
SP.Nut.	*	**	***	*	***	***	***	***	NS
LSD ($P < 0.05$)									
SP.	0.42	0.14	0.45	-	0.0006	34.1	254.2	139.2	157.5
Nut.	0.42	0.14	0.45	-	0.0006	34.1	254.2	139.2	157.5
SP*Nut.	0.73	0.25	0.78	(0.19)	0.0011	59.11	439.1	241.1	-

Values in brackets are for Log_{10} transformed data

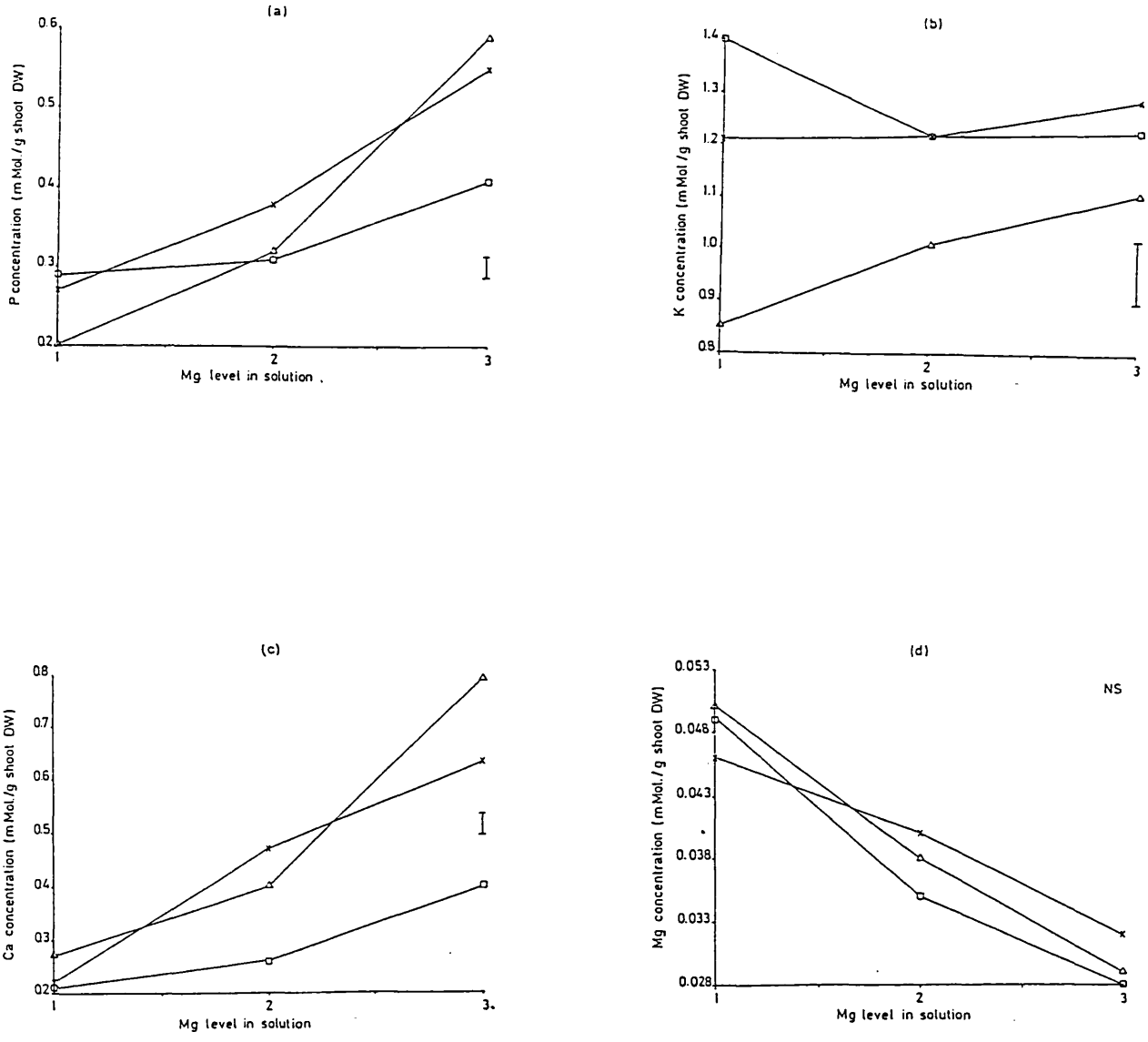


Figure 1.10 (a–d) Effects of magnesium level in solution on the concentration (mMol/g DW) of P, K, Ca and Mg in wheat (□), wild oat (X) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at the 5% level of probability
NS = no significant differences

although the difference did not reach statistical significance at harvest 3.

Root radius: Thinnest roots were, as usual, produced by barren brome. Wheat roots were thinner than those of wild oat, except at the highest level (L1) of magnesium. Barren brome root radius was not affected by Mg level. Wheat roots were similar at the second and third levels of Mg, whilst wild oat roots differed in thickness in all treatments. The thickness of roots in wheat was reduced as the level of Mg in solution was reduced and that of wild oat did not show any regular trend (Table 1.7).

Total root length: This was similar for all the species at the second level (L2) of Mg. Wheat and wild oat were also similar at the third level (Table 1.7). At the highest level (L1) barren brome had the longest root system while that wheat and wild oat occurred at the second level. Root length in barren brome was severely reduced by reduction in Mg level in solution while that of wheat and wild oat remain similar to their control.

Total surface area: The total surface area of roots differed with Mg levels for all species. Total surface area for barren brome was always the smallest and that of wild oat was the largest (Table 1.7). Surface was reduced in wheat and barren brome by reduction in Mg level, and that of wild oat increased, although treatment means were not significantly different.

Total root length/root dry weight: Summed over all levels the length of root produced per root dry weight was the highest in barren brome. The value increased with decreasing Mg in wheat whilst that of barren brome decreased. Wild oat did not show a clear trend.

Root surface area/unit dry weight: Barren brome also had the largest surface area/unit weight of root in all Mg treatment levels (Table 1.7). In all the species this variate increased as the level of Mg was reduced.

Nutrient Concentration

P: Summed over all treatment levels, the weeds, particularly wild oat, had higher concentrations than the crop. The species differed at every level of Mg (Figure 1.10a), except the second, where wheat and

barren brome were similar. In all species P concentration increased as the level of Mg decreased. At the lowest Mg level barren brome had the highest concentration; at the third harvest, wild oat had the highest.

K: Wheat and wild oat were similar in their K concentrations, except at the highest Mg level where that of the crop exceeded that in wild oat. Except in the lowest Mg concentration where all were similar, barren brome had the lowest K concentration (Figure 1.10b). When the level of Mg was reduced K concentration in both weeds slightly increased, while that of wheat decreased significantly.

Ca: All species absorbed most Ca in the lowest Mg level. Barren brome had the highest concentration and wheat the lowest (Figure 1.10c).

Mg: Summed over all treatments all species had similar concentrations of Mg at the second harvest, but by the third harvest the weeds, especially wild oat, exceeded the crop. The amount of Mg in uptake solution had little effect on the concentration in plant tissue (Figure 1.10d).

Total nutrient contents: Summed over all treatments the total P found in wild oat was the highest and that of barren brome the lowest. Total P in wild oat and barren brome increased as Mg was reduced; the reverse was true for wheat.

K: Summed over all treatments K accumulation in wild oat was the highest, and in barren brome the lowest (Table 1.8). Total K in wheat and barren brome was reduced by decreasing levels of magnesium. The value in wild oat was similar in all Mg treatments.

Ca: The total amount of Ca in wild oat was 2 and 2.5 times larger than that in wheat and barren brome respectively. As Mg level in solution was reduced the total Ca in the weeds, especially in wild oat, increased significantly (Table 1.8d).

Mg: Wild oat accumulated the highest amount of Mg at L2 and L3. At L1 its content was similar to wheat. Barren brome was the lowest in total Mg at any level (Table 1.8d).

Nutrient uptake efficiency of roots

P: Summed over all treatment levels the uptake efficiencies did not differ significantly at the second harvest, but at the third harvest the

Table 1.8 Effects of Mg levels on the total uptake of P, K, Ca and Mg (mMol/plant) in wheat (W), wild oat (WO) and barren brome (BB) grown in NFT at Harvest II

	L1			L2			L3			Significance level			LSD (P 0.05)		
	W	WO	BB	W	WO	BB	W	WO	BB	SP	K	SP*K	SP	K	SP*K
P	1.71	1.52	0.50	1.26	2.13	0.88	1.11	2.80	0.66	***	*	***	0.18	0.18	0.32
K	8.11	6.71	2.12	4.78	6.81	2.81	3.41	6.57	1.24	***	***	***	0.68	0.68	1.18
Ca	1.21	1.26	0.67	1.07	2.65	1.10	1.09	3.19	0.87	***	***	***	0.21	0.21	0.37
Mg	0.28	0.26	0.13	0.15	0.22	0.11	0.08	0.16	0.032	***	***	***	0.017	0.017	0.030

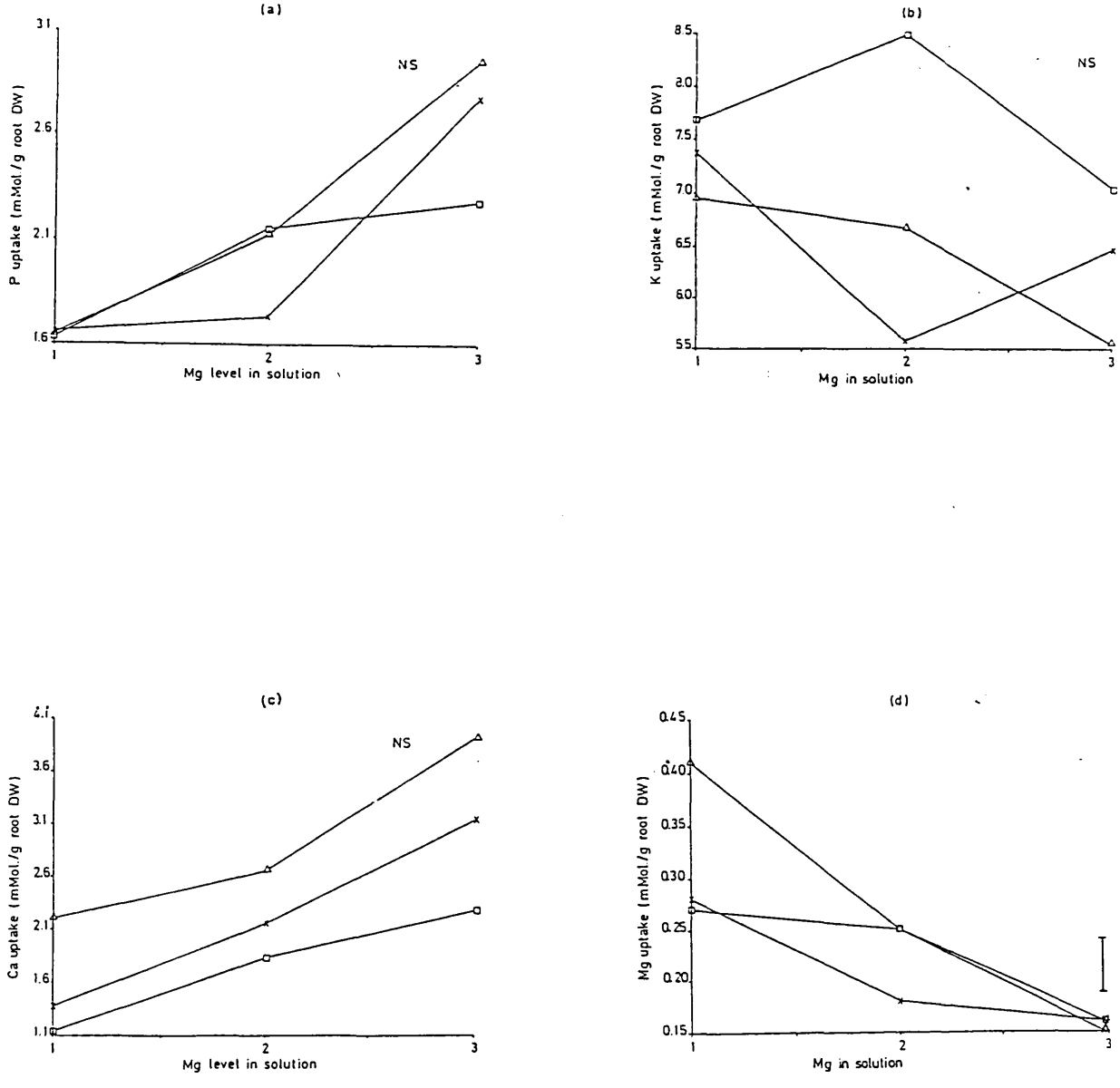


Figure 1.11 (a–d) Effects of magnesium level in solution on the efficiency of uptake (mMol/g root DW) of P, K, Ca and Mg of wheat (□), wild oat (X) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at the 5% level of probability
NS = no significant differences

weeds were less efficient than the crop. In all three species P uptake efficiency increased as the level of Mg decreased, and the value at the lowest Mg was the highest for barren brome.

K: Wheat was the most efficient species at all levels of Mg and the weeds were similar (Figure 1.11b). At harvest 3, species and the species X nutrient interactions were statistically significant. At this stage of plant growth all species had similar efficiencies of K uptake at the second level (L2) of Mg. At other Mg levels the weeds were similar and the crop was the most efficient.

Ca: The efficiency of all species in taking up Ca increased as the level of Mg was reduced (Figure 1.11c). Barren brome was the most efficient species, particularly at the lowest Mg level.

Mg: Summed over all treatments barren brome was the most efficient species. Wheat and wild oat had similar efficiencies except at the second level where wheat was more efficient. Wheat and barren brome had similar efficiencies in L2 and L3 Mg. In all species, efficiency decreased as the level of Mg was reduced (Figure 1.11d).

Nutrient Utilization Efficiency

P: Summed over all treatments barren brome was the most efficient species in utilizing P to produce dry matter. All species produced higher dry matter per unit P when Mg level was high in the medium and efficiency fell with the level of Mg (Figure 1.12a).

K: Barren brome was the most efficient species. Efficiency of K utilization was higher at L1, except in wheat, which showed a significant increase at lower Mg levels. At the third harvest the species did not differ significantly in K utilization efficiency.

Ca: Wheat was the most efficient species. All species had higher efficiencies at L1. As the Mg level in solution was reduced efficiency of species, especially the weeds, decreased.

Mg: The effect of level of Mg on the utilization of Mg was significant. Summed over all treatments there was no effect of species and no significant interaction, but at the third harvest both were significant, wheat being more efficient than the weeds. The efficiency of wheat was little affected by reduced Mg, while the efficiency of both weeds increased with a decrease in Mg level (Figure 1.12d).

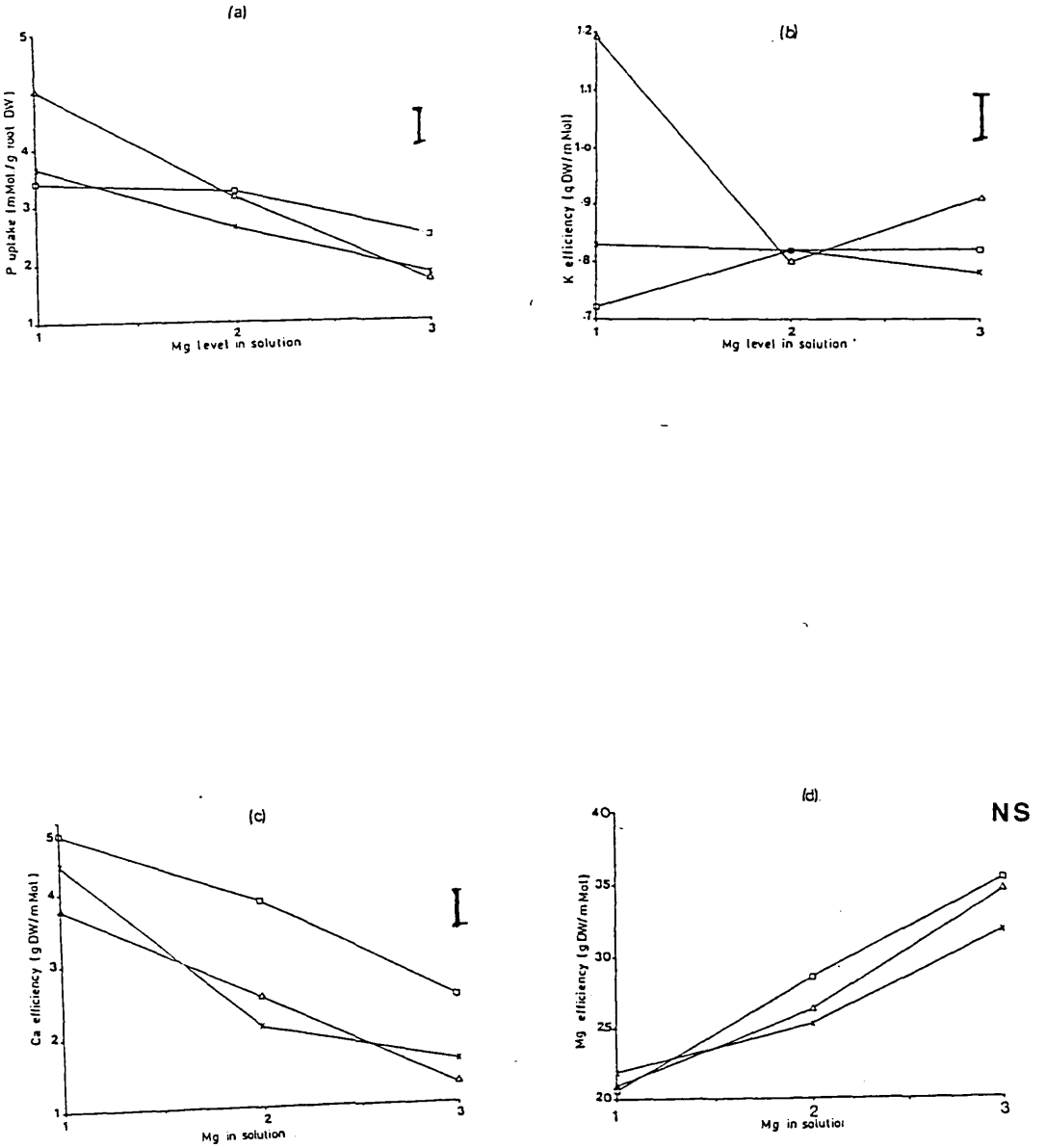


Figure 1.12 (a–d) Effects of magnesium level in solution on the efficiency of utilization ($\frac{g_{DW}}{mMol}$) of P, K, Ca and Mg in wheat (□), wild oat (X) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at 5% level of probability
NS = no significant differences

5.11. Discussion

Dry Matter Yield

The dry matter yield of wild oat was less affected than that of barren brome or the crop (Table 1.7) by level of Mg at all stages of harvest. Wheat and wild oat were similar in their dry matter yields at the highest level of Mg at the 2nd harvest. At the lowest level, the total dry matter yield of the crop and that of barren brome decreased by 45% and 55% respectively whilst that of wild oat was reduced by only 8.8%. In both weeds shoot dry matter was more reduced than root. The root dry matter in wild oat actually showed some increase down to the third level, whilst that of wheat and barren brome were reduced by 55% and 23% respectively. The effect of low Mg on barren brome was mainly on its shoots which showed a decrease of about 60% whilst the effect on the crop was reflected more on the roots.

The lack of sensitivity of wild oat to low Mg regimes may suggest ability to adapt to conditions where the element may be deficient. Russell (1973) reported that Mg can sometimes be limiting on heavy soils where the weed is frequent. Chancellor (1976) reported that wild oat grew on a number of soil types which included fen, sandy, loam and heavy marsh soils. Thurston (1962a) found soil pH to have no effect on the growth of wild oat and Jones (1976) reported that soil acidity affected barley more severely than A. fatua so that on acid areas wild oat were larger than on areas where the pH was higher. In agreement with the results of the present experiment (Pawlik, 1957, quoted by Chancellor, 1976) reported that Mg availability had no effect on wild oat, but that boron was essential for the growth of this weed. On acid soils, where Mg may be deficient, this weed might be expected to grow and reproduce normally due either to its low requirement for the element or its special ability to extract it from lower levels. Because of its ability to produce extensive root system in general and especially due to increased proliferation of roots noted in this experiment as a result of reduction in Mg, it is suggested that this weed may thrive in soils which are low in the element. The mechanism of adaptation by wild oat to low Mg appears to be production of more roots at the expense of the shoot. The

production of more roots and the simultaneous reduction in shoots is also reflected in the higher root/shoot ratio of the weed, particularly at the third harvest. Contrary to wild oat, the root system of the crop was more affected than its tops, and may become inefficient in taking up Mg from a low level, leading to generally reduced growth. The greater reduction in the shoots of barren brome also led to a general reduction in its total yield. In this respect it resembled wheat. At early stages of growth symptoms of Mg deficiency were visible on the leaves of the crop and barren brome.

Tarawali (1983) found serious Mg deficiency symptoms on wheat at the lowest concentration of the element, whilst A. myosuroides was healthy, as in the highest concentration. However, the concentrations of Mg used in the two experiments were different. The lowest concentration (0.033 mM Mg) used in Tarawali's experiment was much lower than that in the present experiment i.e. 0.25 mM Mg. Replenishments were made fortnightly in the present experiment, while he changed solutions once or twice a week.

Root Morphology

The finest roots were, as usual, produced by barren brome, which show no significant variation with variation in the level of Mg. Root thickness in wheat and wild oat was similar except at the lowest Mg level where roots of the latter were thicker. Wheat roots became slightly finer as Mg level was reduced (Table 1.7) whilst wild oat had its thickest roots at the lowest level.

The total root length and surface area per plant differed between and within species (Table 1.7). At the highest Mg level barren brome exceeded both species in root length, but this was more reduced by low Mg than in wheat or wild oat. The length of root and surface area increased in wild oat as the level of Mg was reduced. Wheat produced longer roots at the 2nd level (L2) of Mg, but had similar lengths at L1 and L3. The total surface area in wheat was greater than that of barren brome at all Mg levels. In both species this was significantly reduced at the lowest level whilst that of wild oat actually increased at this level. Both length and surface area were more reduced in barren brome than in wheat (Table 1.7).

The total root length per unit root dry weight was the largest in

barren brome. Wheat also exceeded wild oat except at the highest nutrient level. This ratio increased in wheat while it remained similar at all levels in wild oat. In barren brome it was reduced with Mg level. The species also showed differences for area per unit root weight, but not at a statistically significant level. Summed over all the species barren brome had the highest ratio and the crop the lowest. Summed over species, the ratio was significantly higher at the lowest Mg in the feeding solution.

The fact that wild oat is able to produce its potential yield at low Mg levels may be due partially to its ability to produce an extensive root system at such levels. This may have enabled the weed to enhance the absorption of Mg as well as the other essential elements leading to unaffected growth. The advantages of a large root system have been discussed in relation to earlier results. The fine roots in barren brome and its greater ratios for length and area per unit dry weight did not appear to be useful for the weed in water culture conditions, since its yield was the most reduced by low Mg.

The differences in total dry matter production and root growth and morphology may be genetic, and may reflect responses to habitat fertility conditions. The work of Bradshaw et al. (1958, 1964) on the response of plants to Ca, P and N as a function of their provenance has also been discussed earlier.

Clark (1974) studied the responses of two inbred lines of maize (Zea mays L.) B57 and OL40B to levels of Mg in nutrient solutions. He found that inbred B57 grew considerably better at low Mg levels and was more Mg efficient than the inbred OL40B. It was also noted that B57 produced maximum dry matter near 0.12 mM Mg whereas OL40B continued to increase dry matter up to 4.1 mM. Sayre (1955) also found varietal differences in response to Ca and Mg in maize. He reported the variety WF9 to be Mg efficient and OL40B to be Mg inefficient.

In the present experiment the species differed greatly in the total amount of dry matter produced at lower levels of Mg. Wild oat produced the highest dry matter i.e. the highest growth rate, at the lowest level. In order to produce similar quantities of dry matter wheat and barren brome would require about 1.6 and 4.5 times as much Mg in solution respectively.

Chemical analysis of barren brome tissues in the previous experiments revealed high concentrations of Mg suggesting a high requirement. However analysis in the present experiment did not show significantly higher concentration in barren brome, although it was slightly higher than the other species. The reasons for these differences are at present not clear.

Nutrient Uptake and Accumulation

The species did not differ in Mg concentration, although the effect of increasing its external concentration on dry matter accumulation was particularly evident in wheat and barren brome. Tissue concentrations of Mg in all species increased only slightly with increasing Mg concentration. This may imply that nutrient concentration may not be an indicator of the actual plant requirement and thus may have no correlation with growth. The species differed significantly in total Mg contents, which reflected differences in dry weight already discussed which in turn depended on the reaction of a species to external Mg concentration. An implication of the results is that of wheat and/or barren brome were grown in competition with wild oat, the latter would be expected to deprive both of Mg directly. It may indirectly also deprive them of other elements because of its size. There was about 4.24 and 2.52 times the P, 5.30 and 2.00 times the K and 3.77 and 3.00 times the Ca in wild oat as in barren brome and wheat respectively at the lowest level of Mg in solution.

Wheat and wild oat showed similar concentrations of P except at the lowest level where the weed exceeded the crop significantly (Figure 1.10a, b, c and d). At the same level barren brome had a higher P concentration than the crop and was similar to wild oat. Barren brome also had a similar concentration to the crop at L2, but was lower than wild oat. At L1, both species exceeded barren brome. In all three species the concentration of P increased as the level of Mg in external solution decreased. The higher concentration of P in both weeds at lower Mg levels is in agreement with the findings in the previous experiments and may suggest higher efficiency of the weeds under such conditions. The general trend of increase in P in all species as Mg in solution decreases may imply that uptake at higher levels was impeded, while at the lowest it was facilitated. One of the func tions ascribed to Mg in plant nutrition is that of a carrier of the P used by the plant. Under

the circumstances of the present experiment, some sort of positive correlation between Mg and P uptake might thus be expected.

Potassium concentration was lowest in barren brome and higher in wheat and wild oat, as in Experiment 3. This again shows the inefficiency of barren brome in K uptake and hence its susceptibility in competition with either or both species. In the crop, Mg increase in solution increased K uptake, whilst in barren brome it decreased it. In wild oat Mg did not appear to have any effect on the uptake of K. It may be suggested that high Mg further reduces the competitive ability of barren brome for K, but may not affect wild oat, and yet may enhance the crop in competition for K. The depressive effect of Mg on the uptake of K observed in barren brome may be interpreted as a result of competition for metabolically produced binding compounds (Fageria, 1973). Similar competitive effects between Mg and Ca may also be suggested for low Ca at the higher Mg levels in all three species. As reported elsewhere (Experiments 1, 2 and 3) barren brome had a higher tissue Ca concentration than the other two species. In the present experiment barren brome also had the highest Ca at L1 and L3, but at L2 it was lower than wild oat and higher than the crop. In all three species and particularly the weeds, Mg had a considerable effect on the uptake of Ca. The reduction of Mg in the external solution led to increase in the uptake of Ca (Figure 1.10a, b, c and d).

The interaction between the species and Mg levels for root efficiencies were not significant for P, K and Ca, but were for Mg (Figure 1.11a, b, c and d). At the highest Mg level barren brome was most efficient whilst wheat and wild oat were similar. At L2, wheat and barren brome had similar root efficiencies, but wild oat was less efficient. At L3 all species had similar uptake rate efficiencies for Mg. The rates of uptake of P and Ca increased with decrease in the level of Mg though those for K and Mg did not. The species which showed a higher concentration of a specific element also showed a higher efficiency for its uptake. For example, the weeds, especially barren brome, were not very efficient in taking up Mg, Ca and P. The crop showed higher efficiency than the weeds in taking up K.

The mechanisms which account for the observed differences in the uptake rate and transport of specific nutrients in species may be varied and root size and morphology may play a role. The ability of species in

absorbing nutrients may also depend on level of availability of other nutrient ions in the growing medium as demonstrated for P, K and Ca, by varying Mg in solution. There is adequate evidence of variation between and among species in uptake mechanisms. For example Epstein and Jefferies (1964) found that the barley variety Chevron had a K uptake mechanism subject to competition from Ca and Mg. They reported that good growth of this variety was restricted to soils of low Ca and Mg status. The observed differences in absorption of P, K, Ca and Mg at various levels of Mg may be attributed particularly to differences in the chemical and physiological properties of the roots. Drake et al. (1954) suggested that cation-exchange capacity of roots is important in determining selective absorption of cations. Roots in general are assumed to have a higher cation-exchange capacity than the soil and would selectively accumulate divalent cations such as Mg over monovalents such as K. The competitive effects between such ions for absorption sites on the roots and the cation-exchange capacity of individual roots of the species may have contributed towards the observed differences in uptake and accumulation of nutrients in the crop and the weeds. As opposed to the ionic interactions involving competitive inhibition of ion uptake, the rate of absorption of one nutrient may increase the concentration of others in a medium and in the plant. For example Thien and McFee (1972) and White (1972) showed that improved plant N status caused up to a 10-fold increase in root absorption capacity for P. Hills et al. (1970) and Williams (1948) also showed that increasing P supply improved N uptake. Haynes and Goh (1978) showed that many plant species including crops fail to absorb Ca and Mg in adequate amounts in the presence of NH_4^+.

The three species also differed in the utilization efficiencies for P, K and Ca, but showed similarities for Mg (Figure 16a, b, c and d). Except for Mg, efficiency in all species declined as Mg solution concentration was reduced. This suggests that the plants may have less capacity to use other elements which are available in large quantities if Mg is deficient in a medium. The observed higher concentrations of P, K and Ca in the species at low Mg levels may only indicate luxury consumption. Several authors, for example Christie and Moorby (1975, Clarkson (1967) and White (1972) found that when grown under similar conditions, slowly growing species from infertile habitats generally had higher tissue concentrations (low utilization efficiency) than do rapidly growing species. However, nutrient use efficiency is not considered by

some an important adaptation to nutrient stress (Clarkson, 1967), because this efficiency is simply the inverse of tissue concentration and could be affected by processes such as luxury consumption involving large vacuolar storage reserves (Chapin, 1980). The higher concentrations of P and Ca in the weeds, and their low use efficiencies may therefore be due in part to the obvious relationship between concentration and efficiency of dry matter production. A similar relationship was also noted for the crop. Although wild oat accumulated higher dry matter unaffected by the lowest Mg level, the dry matter produced per unit Mg at any level was not significantly higher than the other species. This emphasises the fact that the relationship between concentration and dry matter production may not reflect the actual efficiency of utilization of a given nutrient.

Experiment 1.5

5.12. Results

Calcium concentration decreased from L1 (control) to L4. For reasons discussed later the results highlighted below are those for the third harvest unless otherwise state.

Tops: Tef was the species most affected by reduction in Ca (Table 1.9). The reduction in dry weight in tef, wheat and barren brome in L2-L4 compared with its control was 50%, 12% and 33% respectively. At the first harvest tef and wheat were more affected than the weed.

Roots: The root dry matter yield was more affected than the shoots. Tef was the most reduced by decreasing Ca and wheat the least. At the first harvest the root weight in wheat was more reduced than in the third harvest, whilst the reverse was true for tef and barren brome.

Whole plant weight: Tef was the most affected and wheat the least (Table 1.9). The reduction in whole plant dry matter yield over the range of Ca levels used was 53%, 14% and 36% in tef, wheat and barren brome respectively. The species showed a consistent trend of reduction, except for tef which was more reduced at the 2nd level than the third. At the first harvest the weight fell consistently for all three species.

Root/shoot ratio: The interaction between species and Ca levels was

Table 1.9 Effects of Ca levels on some growth variates of wheat (W), tef (T) and barren brome (BB) grown in NFT at harvest II

Ca level		Shoot dry wt (g/plant)	Root dry wt (g/plant)	Whole plant wt (g/plant)	Root/Shoot ratio
L1	T	6.12	3.69	9.81	0.60
	W	2.76	2.60	5.36	0.50
	BB	0.77	2.09	2.86	2.71
L2	T	6.04	3.53	9.57	0.58
	W	3.41	2.89	6.30	0.85
	BB	0.78	2.19	2.97	2.81
L3	T	6.85	3.24	10.09	0.47
	W	2.96	2.56	5.52	0.86
	BB	0.88	2.13	3.01	2.42
L4	T	3.11	2.61	5.72	0.84
	W	2.50	2.70	5.20	1.08
	BB	0.71	2.08	2.80	2.93
Significance level					
	SP	***	***	***	***
	N	***	***	***	***
	SP*N	***	***	***	***
LSD ($P \leq 0.05$)					
	SP	0.26	0.16	0.33	0.33
	N	0.30	0.19	0.38	0.38
	SP*N	0.52	0.32	0.66	0.66

not significant for root/shoot ratios at harvests 1 and 3. However, summed over all treatment levels the species differed significantly. Wheat had the highest ratio and tef the lowest. Summed over all species, the first level gave the highest ratio, whilst the 2nd, 3rd and 4th levels were similar to each other.

Nutrient Concentration

N: The species differed at every level (Figure 1.13a). At the highest and lowest Ca levels the weed had the highest N concentration. At the 2nd level wheat had the highest concentration whilst tef was the highest at L3. The concentration of N in tef increased down to L3, but was reduced at the lowest level. Wheat N concentration remained similar at all levels except L2 where it had the highest. Barren brome had its highest concentration at L1. Its concentration declined with Ca level, finishing slightly higher than both crops at L4.

At the second harvest interactions were not significant; both main effects gave significant differences. Wheat and barren brome had similar concentrations, both being higher than tef. N uptake declined with reduction in Ca level.

P: Except at the lowest level the weed had the highest concentrations of P, which increased as the level of Ca decreased. Concentration of P in tef was higher at L1 and L4 than in wheat, whilst the latter had higher concentrations at L2 and L3. In both crops, P concentration increased with reduced levels of Ca (Figure 1.13b).

The species differed in P concentration at all levels, the weed having higher concentrations than the crops, which were similar to each other.

K: At L1 the weed had higher K concentrations than the crops but at the other three levels wheat exceeded both tef and barren brome (Figure 1.13c). In general the species showed a trend of increase in K concentration with decrease in Ca level. At the 2nd harvest wheat had the highest K except at the lowest Ca, where all three species were similar. Concentrations declined with reduction in Ca at this harvest, which contrasts with the third.

Ca: The species differed in Ca concentration (Figure 1.13d), tef had the highest Ca concentrations at all levels. In all three species

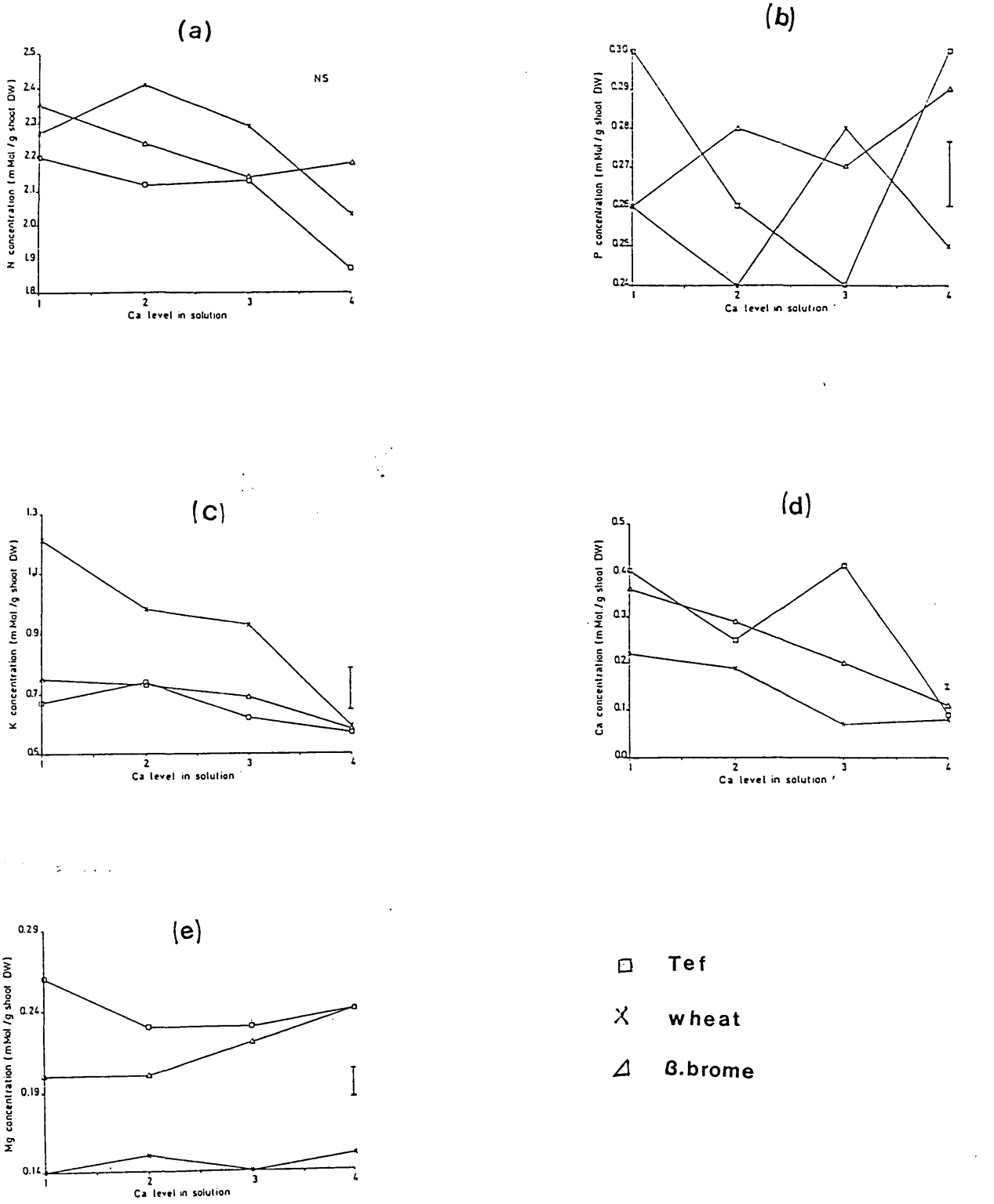


Figure 1.13 (a–e) Effects of calcium level on the concentration (mMol/g DW) of N, P, K, Ca and Mg in tef (□), wheat (X) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at the 5% level of probability
NS = no significant differences

concentration declined consistently with reduction in Ca level, with wheat showing the greatest effect which tef and barren brome were similar to each other.

Mg: The weed had high concentration than tef at L1, but was similar at L4. At L2 and L3 tef was higher than the weed. Wheat had the lowest concentration of Mg at all Ca levels (Figure 1.13e). In general Mg concentration increased as Ca level decreased. At the 2nd harvest tef had the highest Mg at L1 and L2. At L3 and L4 it was similar to barren brome. Wheat always contained lower concentrations than the other species.

Total nutrient contents

Totals naturally tended to reflect dry weights.

N: Tef contained by far the greatest quantity of N at all levels of Ca except the lowest, where it was similar to wheat. Barren brome always had the lowest (Table 1.10). The greatest amounts for tef occurred at L1 and L3 and those of wheat and barren brome were at L1. Total N declined in all species at the lowest Ca level. At the 2nd harvest N in barren brome did not significantly change as Ca level was reduced. N in tef was also constant down to the 3rd Ca level. Wheat had its greatest amount of N at L2.

P: Tef had the greatest and barren brome the least total P (Table 1.10). Reduction in Ca level down to L3 did not affect total P in barren brome significantly. In both crops total P was highest at L3 and their contents were lower at L2 than L1. The lowest for all species occurred at L4.

At the 2nd harvest main effects were significant, but not the interactions.

K: The species differed in total K content. Tef had the higher at L1 and L3; at L2 and L4 it was similar to wheat (Table 1.10). Barren brome always contained the lowest amount. K content in the weed consistently declined as Ca was reduced. In the crops significant reduction occurred at L2 and L4 only.

At the second harvest total K in the weed was not reduced significantly by Ca reduction.

Table 1.10 Effects of Ca levels on the total uptake of P, K, Ca and Mg (mMols/plant) of wheat (W), tef (T) and barren brome (BB) grown in NFT at Harvest II

	L1			L2			L3			L4			Significance level			LSD (P 0.05)		
	T	W	BB	T	W	BB	T	W	BB	T	W	BB	SP	N	SP*N	SP	N	SP*N
N	21.60	11.99	6.83	20.38	15.10	6.75	21.48	12.79	6.55	10.65	10.51	6.02	***	***	***	0.89	1.02	1.77
P	2.88	1.38	0.76	2.49	1.51	0.83	2.46	1.55	0.85	1.72	1.31	0.81	***	***	***	0.11	0.13	0.22
K	6.56	6.47	2.14	7.06	6.16	2.15	6.27	5.19	1.98	3.26	3.16	1.64	***	***	***	0.46	0.53	0.91
Ca	3.94	1.14	1.05	2.39	1.22	0.88	4.14	0.40	0.62	0.54	0.42	0.30	***	***	***	0.101	0.116	0.202
Mg	2.52	0.69	0.57	2.20	0.97	0.60	2.28	0.80	0.69	1.39	0.77	0.69	***	***	***	0.097	0.11	0.20

Ca: Values for tef were about 2.5 and 7.8 times larger than wheat and barren brome at L1 respectively, and at L4 about 1.90 and 5.83 times larger than these species respectively. However, reduction at L4 as % of the control was greatest in tef. Wheat appeared to be less affected than barren brome by reduction in Ca.

Mg: Wheat and barren brome had lower total Mg than tef. Wheat was significantly higher than barren brome at all Ca levels except the highest (Table 1.10). In all three species total Mg was reduced in parallel with Ca.

Nutrient uptake efficiency

N: Except at the 2nd level where wheat was similar to tef and barren brome, it was always the least efficient in the uptake of N per unit root weight (Figure 1.14a). Barren brome and tef had similar efficiencies at L1 and L4. Tef was the most efficient at L3. In general efficiency increased for tef as Ca level was reduced. Barren brome had the highest efficiency at L4 and that of wheat showed a slight increase at L2 and L4.

P: Barren brome showed higher efficiencies at L2 and L3 than the other species, being similar to tef but higher than wheat at L1. It was also higher than wheat at L4. Tef was more efficient than wheat at L1 and L4, but the two were similar at L2 and L3.

K: Barren brome was most efficient at the highest Ca level and it was similar to wheat at L2 and L4. It was also similar to tef at L3 and L4. Wheat was more efficient than tef at L2 and L3 but similar at L1 and L4. Efficiency of K uptake increased for tef and wheat as Ca level was reduced. Barren brome had its highest value at higher levels, whilst that of the crops showed increased efficiency as Ca was reduced.

Ca: Tef was the most efficient species at every level of Ca in solution. Wheat and barren brome had similar efficiencies, although the weed had a slightly higher value. At L4 the weed was more efficient than wheat. In general and in all three species Ca uptake efficiency decreased with decrease in Ca level (Figure 1.14d).

Mg: Except at the highest Ca level tef showed higher efficiencies than both wheat and the weed. The weed was more efficient than wheat at all levels of Ca. Mg uptake efficienceis at the lower levels were higher

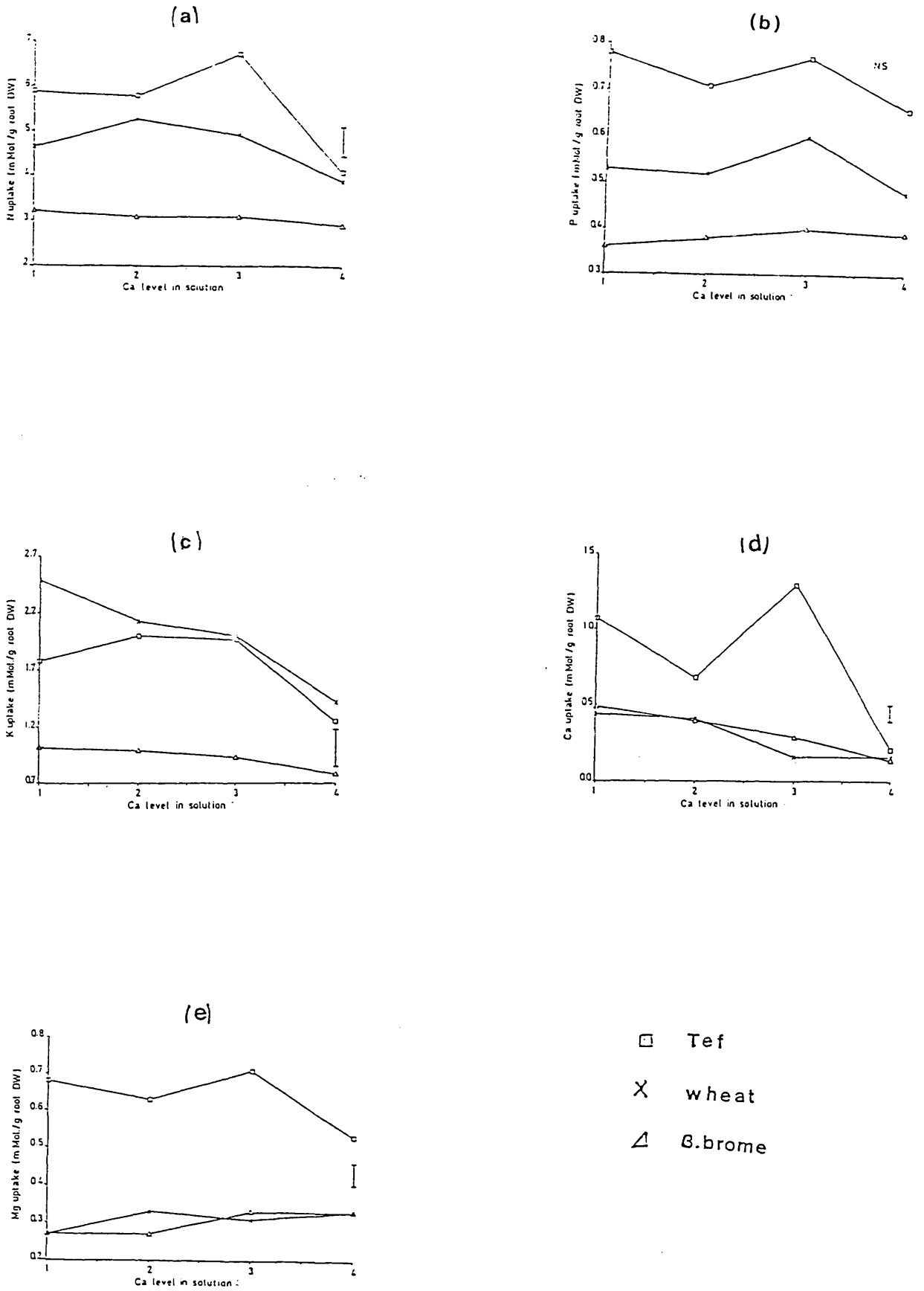


Figure 1.14 (a-e) Effects of calcium level on the efficiency of uptake (mMol /g root DW) of N, P, K, Ca and Mg in tef ( ), wheat ( ) and barren brome ( ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at the 5% level of probability
NS = no significant differences

for tef and barren brome but remained similar for wheat at all levels (Figure 1.14e).

Nutrient utilization efficiency (g mM^{-1} of nutrient)

N: Utilization efficiency of the species varied with level of Ca. At L1 wheat produced significantly the greatest dry matter per unit N absorbed. At L2, the weed was more efficient than both crops, and at this level rate of utilization was at its lowest for all three species. At L3, wheat and the weed were similar, but both were higher than tef. At the lowest level tef had higher efficiency than wheat and barren brome, which were similar to each other. Efficiency increased in tef and the weed as Ca was reduced, though wheat showed no clear trend (Figure 1.15a).

P: At the highest level of Ca wheat was more efficient than tef and barren brome was less so. Wheat remained more efficient than the weed at L2 and L3, but they were similar at L4. Tef showed a higher efficiency of utilization than the other species at L2 and L3, and was still higher than the weed at L4. In general P utilization efficiency in all three species decreased with a decline in Ca level in solution.

At the second harvest wheat had a higher efficiency than tef and the weed, which were comparable when summed over all Ca concentrations.

K: Tef was significantly more efficient than both species at all levels except L4 where it was similar to the weed. The weed was also more efficient than wheat at lower Ca levels, but at the highest level the reverse was true. They had similar efficiencies at L2. Except at the lowest level, where its efficiency was significantly lower, the efficiency of tef remained constant. That of wheat did not change significantly, but in barren brome efficiency increased significantly with decreases in Ca.

At the 2nd harvest, species did not differ in K utilization efficiency.

Ca: All species were similar at the highest level. At L2 wheat and barren brome were similar and tef was the least efficient. At L3 tef and barren brome were similar and wheat was more efficient. Wheat remained the most efficient but barren brome was more efficient than tef at L4. The efficiency of Ca utilization increased with decrease in its level.

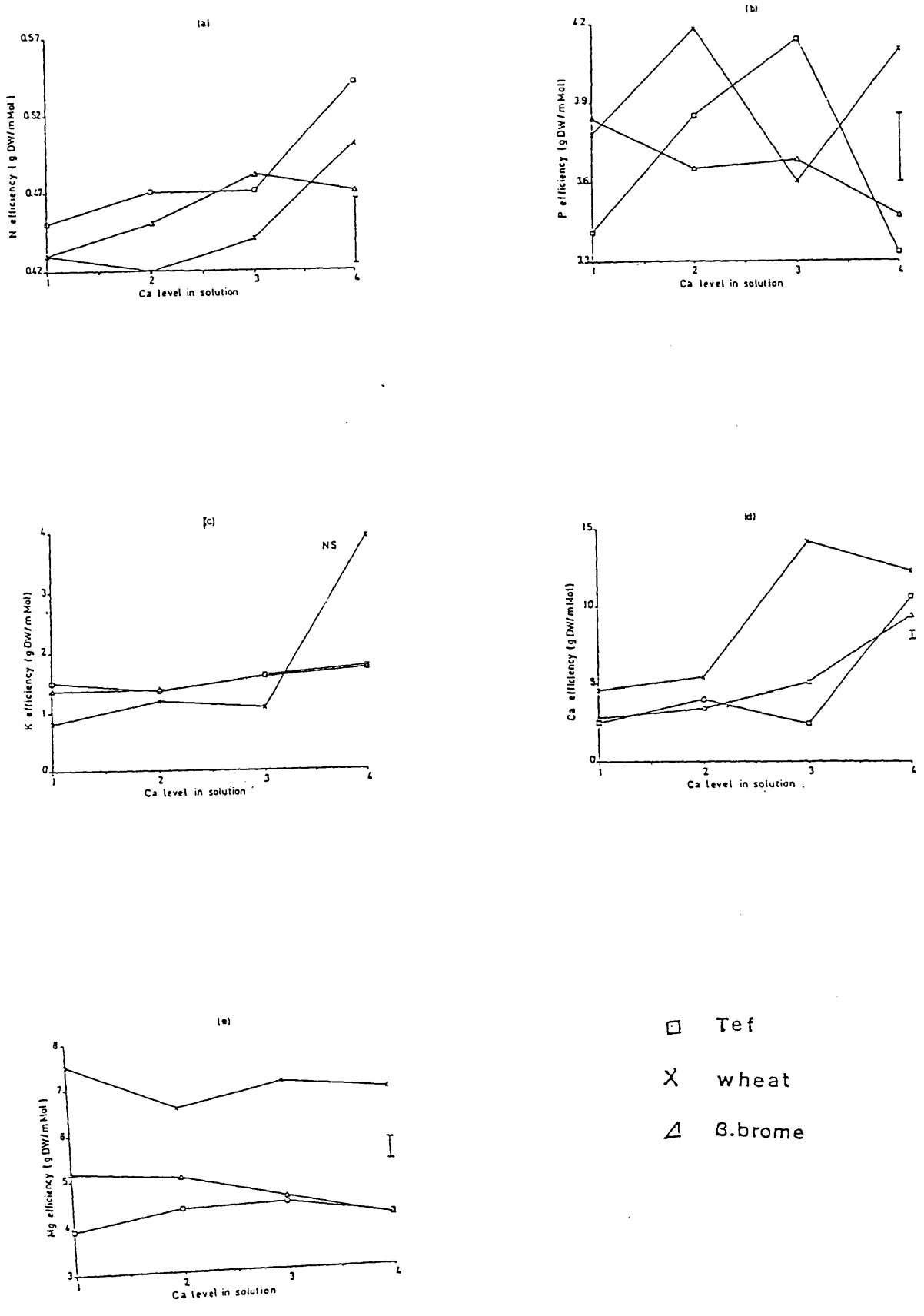


Figure 1.15 (a–e) Effects of calcium level on the efficiency of utilization (g/mMol) of N, P, K, Ca and Mg in tef (□), wheat (X) and barren brome (Δ) grown in N.F.T. (Harvest II)
Vertical bars represent LSD at the 5% level of probability
NS = no significant differences

In general wheat was more efficient than both tef and barren brome.

At the 2nd harvest the weed was more efficient than either crop and wheat was also more efficient than tef.

Mg: Wheat showed higher efficiencies at all Ca levels (Figure 1.15e). Tef and barren brome differed at the higher levels only. At the highest level, tef was more efficient than barren brome and at the 2nd level, the reverse was true. Generally Mg utilization efficiency showed a decreasing trend in all three species as Ca was reduced.

At the 2nd harvest wheat showed higher efficiency than both tef and barren brome.

5.13. Discusssion

The inclusion of the Ethiopian cereal tef in this experiment requires a brief explanation. Chronologically this was one of the earlier experiments of the study. Because of a general departmental interest in the cereal and because it is a relatively unimproved crop, certainly in comparison with wheat, it was considered useful to include it on a preliminary basis. Some features of its nutritional performance were of potential interest - for example it is rarely fertilised in Ethiopia, and is well known for its high content of Ca and Fe. Despite the results obtained in this particular experiment, some of which were of considerable interest, it was eventually decided on grounds of practical expediency, to omit study of this plant from later experiments.

Dry matter yield

The species differed in their responses to decreases in the levels of Ca. Dry matter was more reduced in tef than in wheat or barren brome (Table 1.9). Wheat was the least sensitive to changes in Ca concentration. In all three species the growth of the root system was more reduced than the shoot although the relative reduction was highest in tef and lowest in wheat. The relative reduction in shoot growth followed similar trends to the roots. At the lowest Ca level tef produced less than 50% of its yield in the control, whilst wheat and barren brome produced about 86% and 64% respectively. Individual tef plants were much larger than wheat or barren brome at all levels of Ca.

For example, at the highest Ca (L1) tef was about 2.3 and 6.8 times heavier than wheat and barren brome respectively and at the lowest level (L4) this was about 1.2 and 5.0 times. At the lowest level of Ca, deficiency symptoms were observed for roots and shoots of all the species, especially tef and barren brome, similar to those described by Islam et al. (1987) and Loneragan et al. (1968).

The discussion below relates to harvest 3. At the 2nd harvest there were anomalies in root/shoot ratios of barren brome which were clearly different from those observed at the first and 3rd harvests. At every level of Ca the ratio in barren brome was very much greater than in both crops. The recorded root dry weight invariably exceeded that of the shoot, resulting in root/shoot ratio several times greater than those of the crops. Although shoot production in barren brome was seriously affected at the lowest Ca level at that stage of growth, no explanation can be offered for the observed higher root/shoot ratios for barren brome at all levels, which were greater than those observed in any other experiment. The harvest 2 data for shoot and root dry weights and their ratios were not, therefore, used for comparisons.

Despite the significant differences in the species X level interactions for shoots, roots and total dry matter accumulation, such differences were not found for the root/shoot ratios. However, species and Ca effects were significant and the ratio was highest for wheat and lowest for tef, and the root/shoot ratios in tef decreased with decrease in Ca, whilst those of wheat and barren brome tended to remain similar. At the first harvest interactions for these ratios were significant, but the species only differed at L3 of Ca, where wheat had the lowest ratio. At other Ca levels differences were not significant.

The variation of nutrient response of plants with provenance has been discussed in relation to earlier experiments. Bradshaw et al. (1960b) studied the responses of six grass species to four levels of Ca in sand culture. They reported that L. perenne, Agrostis stolonifera and Cynosurus cristatus showed marked response to increase in Ca levels, whilst, Nardus stricta by contrast showed higher yields at 15 ppm than at 5, 10 and 200 ppm of Ca. Two ecotypes of A. tenuis (a normal and a lead-resistant) showed no significant response to increases in Ca levels. Another species A. canina did not show any trend of response. They also found no significant effects on the root/shoot ratio except in C.

cristatus and A. stolonifera. These authors also correlated the observed behaviour of the species with their original habitats. The three species which responded markedly are usually found in soils of high base status and may therefore, be expected to be more responsive to higher levels. The lack of ability to respond in the remaining species was attributed to ability to grow in soils where Ca may be low.

Ramakrishnan (1969) investigated the response of two populations of Hypericum perforatum collected from acid and calcareous soils to supply of Ca, P, Al and Mn. He found that the growth yield of the acidic populations was less affected by low Ca than that of the calcareous type. The root/shoot ratio values for the calcareous populations were significantly reduced at low Ca levels. He suggested that the differences point to the restriction of the two populations to their own habitats being due, at least in part, to available Ca in the medium.

Similarly Davies and Snaydon (1973b) studied the response to Ca in solution culture of populations of one perennial grass Anthoxanthum odoratum collected from contrasting plots of the Rothamsted Park Grass Experiment. They reported that at low levels of Ca the dry weight yields of the populations from limed plots were more affected than those from unlimed plots. The response of each population to Ca was closely correlated with soil pH and Ca status of its source plot. The concentrations of Ca and P in the shoots of the populations from unlimed plots were also found greater than those from limed plots. The concentration of K, Ca, Mg and Na were similar in both populations. They came to the conclusion that the observed differences between the two populations in response to Ca were large enough to account for their wide edaphic distributions.

It is therefore suggested that the differences in the dry matter accumulation and distribution between tef, wheat and barren brome seen in the present experiment may reflect the level of Ca in the plants' normal habitats. The greatest reduction in the dry matter yield of tef and the greater reduction in barren brome yield than wheat at the lowest Ca level may be attributed, among other factors, to higher Ca requirements in the first species. Wheat on the other hand may have developed tolerance to low Ca levels and hence show a wider adaptability to a range of Ca concentrations in soil solution.

The trends in the responses of the species to Ca levels were

similar, although there were significant differences between them in the yield level at which the response occurred. The dry matter of barren brome was the smallest at any treatment level and that of tef the largest. Differences in the dry matter yields were more pronounced at a higher Ca level than at low levels. The good growth condition during the experiment may have enabled the tropically adapted tef to accumulate storage materials in excess of its requirements for growth, providing a reserve in time of limiting conditions. Gebre Sellasie (1985) reported the best temperature for tef to be between 16-24°C, and a wide differential of day and night temperatures favoured rapid growth and development. According to Brown and Cocheme (1970) high temperatures do not limit the growth of tef in any part of Ethiopia and their report shows that the crop can thrive even at temperatures as high as 40°C provided that moisture is not limiting. However, tef does not show the same tolerance to low temperatures as wheat or barley. As a result, in the high altitudes of the country (i.e. above 2500 m) barley and wheat are the most widely grown cereals. Tef also shows a great power of adaptation to the extremes of soil conditions. According to farm practice in Ethiopia, tef is never fertilized and the farmers even believe that fertilization will injure the crop. Information on its nutrition and ability to compete with weeds is scanty, though weeds are one of the main limiting factors in attaining better yields of tef. Results from field trials by Ergstrom (1974), quoted by Mersie and Parker (1983) show that the crop has a poor capacity to compete with weeds and the variability of yields in weedy plots correlated with actual weed infestation. Very little information is available on the specific nutritional requirements of the crop. Alkamper (1973) reported that the figures he obtained for the uptake of the main elements by tef were relatively low. He also concluded that N produced more straw whilst P encouraged good grain production, whilst K appeared to be of minor importance. Mengesha (1966) found exceedingly high contents of Fe and Ca in the seeds of tef. This prompted the investigation into the response of the crop to levels of Ca in the present experiment.

The responses of tef and barren brome to higher Ca levels and the high Ca tissue concentration noted for the weed in experiments 1, 2, 3 and 4 may suggest a high requirement for the nutrient in both species. Wheat appeared to be unlikely to respond positively to higher levels of Ca, since its yield was similar at lower levels (L1 and L2) and at the

highest level it showed yield depression.

The reduction in root dry matter yield in all three species is in agreement with Russell (1973) who attributed the stunting of the root system to inadequate Ca. Similar conclusions were also drawn by Howard and Adams (1965) and Loneragan et al. (1968). Walker et al. The importance of Ca in maintaining the integrity of cell membrane is well established (Marinos, 1962). In the present experiment the lowest Ca level used was inadequate to support growth and development and prevent deficiency symptoms particularly in tef and barren brome. The agronomic implications which may be made from the results of the present experiment is that if barren brome or tef were grown with wheat, low levels of Ca would favour wheat, whilst the other two species would benefit from fertiliser Ca.

Nutrient Uptake and Accumulation

The species differed in absorption of Ca, but all three increase in the level of Ca increased Ca tissue concentration. Tef had the highest concentrations at all levels of Ca. At lower levels of Ca the weed exceeded wheat (Figure 1.13d). Summed over all Ca levels tef had the highest and wheat the lowest Ca concentrations. Differences in the tissue concentration of N, P, K and Mg were also noted (Figures 1.13a, b, c, d and e). N concentration between and within the species was different, although no single species had a regular pattern of increase or decrease with Ca level. The weed normally showed P concentration greater than or similar to the crops at all Ca levels. P concentrations in wheat exceeded those in tef at the two middle concentrations, but the reverse was true at L1 and L4. As a result, when summed over all levels, these two species did not differ in P concentrations.

Differences in K concentrations were obvious and wheat exceeded both the other species at lower Ca levels. At higher levels it also exceeded tef. At the highest level of Ca, barren brome was higher than wheat, but at the 2nd level, both were similar. Tef contained the lowest concentration at any level of Ca and its requirements for the element may be lower than either of the other species. The results of the present experiment support the conclusion reached by Alkamper who stated that K is of minor importance to tef. The high K concentration in wheat, perhaps reflecting a high requirement as reported in the previous experiments, is confirmed by the results of the present experiment. The

concentration of Mg in tef was higher than the other species at the 2nd and 3rd level. At the highest and lowest level tef and barren brome were similar in Mg and wheat was much lower than either. High concentration of Ca and Mg in tef may again point to the possibility that the preferred habitat of the introduced crop may be higher pH to neutral soils where these nutrients tend to be found in abundance. The same may be true for Mg in barren brome.

Clarkson (1956b) compared two closely related species of the grass A. stolonifera common in high Ca soils and A. setacea which occurs in acid, low Ca soils. When grown at pH 4.5 with increasing levels of Ca, A. stolonifera accumulated greater amounts of Ca and grew better, whilst A. setacea did not respond to increasing Ca above 0.25 mM. It was concluded that its adaptive mechanism appeared to be saturated at this level. In general tissue concentrations of N, P, K and Ca decreased with reduced level of Ca, whilst Mg was increased.

Differences in total accumulation were very clear. At harvests 2 and 3, and all levels of Ca, tef had the greatest amounts of N, P, K, Ca and Mg (Table 1.10), except at L2 and L4, where the two crops were similar in total K contents. The total nutrient contents of the three species obviously followed their dry matter yields. Therefore, since dry matter accumulation in all species in general was higher at higher Ca levels, total nutrient also was higher at higher levels for all the elements. The variability in tissue concentration does not appear to have any influence on total nutrient per plant in any species. Because of its characteristics of rapid and vigorous growth, tef clearly showed its capacity to exploit nutrient resources in much higher quantities than the other two species. Assuming that the observations made for tef in water culture would also hold true under appropriate field conditions this crop might be expected to compete favourably with wheat or barren brome for soil nutrients and moisture.

Efficiency of Uptake and Utilization

Tef was the most efficient species in Ca uptake at both harvests and all Ca levels, except at the highest where it was similar to barren brome. Wheat was less efficient than the weed. Summed over all levels of Ca the weed showed slsightly higher efficiency than wheat and tef for N and P uptake. Wheat had the highest efficiency for K at lower Ca levels, whilst barren brome was the most efficient at higher levels. Tef

was the least efficient for K uptake, again reflecting its apparent insensitivity to this element. Increasing solution Ca concentration increased K uptake per unit weight of root, whilst the reverse happened for Mg and P. The concentration of Ca in solution did not appear to influence the uptake rate of N and K (Figures 1.14a, b, c, d and e).

The species also differed in their efficiency of use of the nutrients (Figures 1.15a, b, c, d and e). Summed over Ca levels, tef showed the highest efficiency of utilization for N, P and K, and wheat for Ca and Mg. Wheat had the lowest K use efficiency. The weed was either similar to the crops or less efficient for these elements. This lack of efficiency in nutrient use may lead to tissue accumulation, which may be used at times of stress and thus ensure sustained growth. The efficiency of utilization for Ca and K increased in all species with decrease in the concentration in solution and those of P and Mg decreased. Nitrogen use efficiency did not show any clear trend with Ca level.

Species with a higher concentration of an element showed higher efficiency of uptake, but a correspondingly lower efficiency of utilization. Examples are given by the cases of tef for Ca and Mg and wheat for K. The low use efficiency for Ca and Mg in tef may indicate some luxury consumption leading to storage in the tissue. In this respect it resembles the weed more than the crop. It therefore seems that, high tissue concentrations and rates of uptake by roots may indicate a high requirement, as suggested in earlier discussions. However, since both lead to accumulation, they may play a role in that inter-relationships in the communities. If tef and barren brome, which showed some similarity in their uptake and concentrations of Ca and Mg, were made to compete for these elements, especially under limiting conditions, intensive competition might be expected because of these similarities and some similarities of root morphology. The crucial importance of root morphology has been previously discussed. Loneragan and Asher (1967) found that higher efficiency of nutrient use could be an important mechanism of adaptation and this characteristic may also thus have an important role.

5.14. Conclusion

The responses of wheat, tef, wild oat and barren brome to different levels of five major elements were studied in water culture. In a preliminary study, the responses of wheat, wild oat and barren brome were first compared in nutrient solutions containing deficient amounts of N, P and K.

A number of points emerged from these studies. Nitrogen deficiency more seriously retarded the growth of the three species than did P or K, although the latter also reduced this appreciably. Reduction in the growth of wild oat relative to wheat and barren brome was less in P and K limiting solutions. The fact that N deficiency greatly reduced the growth of the three species indicates that the element is a critically important nutrient in determining growth. Despite this, further investigations on the nitrogen nutrition of the three species were not made. The decision not to investigate this element was bsed on the fact that most nutritional studies on crop/weed interactions have been biased towards it and according to Zimdahl (1980) and Tarawali (1983) this is reflected in the availability of very little information for the other major elements.

The responses of wheat, wild oat and barren brome to various concentrations of P, K and Mg in solution were further investigated. The responses of tef, wheat and barren brome to different Ca levels were also studied in NFT under glasshouse conditions. The results from these experiments clearly suggested that there is a marked difference between and within the species in their responses to different levels of these nutrients. The general response of the species to dry matter accumulation was similar, although differential responses in root growth and morphology and in the uptake and utilization of the different nutrients were noted. At higher levels of N, P, K and Mg wheat was the most responsive, whilst tef was more responsive to high and low levels of Ca than wheat and barren brome. Again the reduction in the growth of wild oat as the result of the reduction in the levels of P, K and Mg was less than those of wheat and barren brome.

The weeds, particularly barren brome, showed higher root/shoot ratios, and longer roots and greater surface areas of roots per unit dry weight especially at lower levels of the nutrients. The total dry

weights of shoots and roots were usually higher for wheat. The main features of barren brome which may enhance its uptake of nutrients and thus its adaptation to low nutrient conditions in its habitat may be the production of finer and more numerous roots. The relatively smaller yield in this weed in relation to the crop and wild oat is a typical characteristic of weeds growing on soils of low nutrient potential. Crop plants are normally associated with soils of high fertility whilst it is one of the characteristics of weeds that they can grow and reproduce in a wide range of environmental conditions (Baker, 1974), including soils of very low fertility. The greater total dry matter yield in wheat and wild oat than barren brome may be expected to give these plants a competitive advantage over barren brome. This prediction was confirmed in other experiments (see Section III) where wheat and wild oat both depressed the dry matter yield of barren brome to a greater extent than the reverse. The fact that wild oat grew as large as the crop, especially at high nutrient levels, may reflect its long association as a serious weed of the crop in the relatively fertile soils where the crop is normally cultivated.

Other investigators have noted the differential ability of various plants in relation to levels of nutrients (see Rorison, 1968; Johnson, 1987; Qasem, 1987; Tarawali, 1983). Differences between various plants tended to reflect their natural habitats.

One of the main points which emerges from these studies is that the species differed in the concentration, content and efficiencies of uptake and utilization of N, P, K, Ca and Mg. The weeds, particularly barren brome, clearly showed higher concentrations of N, P, Ca and Mg and higher efficiencies of uptake (mMol/g dry weight of roots) for these nutrients, especially at lower levels. Wheat usually had higher or similar tissue concentrations to the weeds when these nutrients were provided at higher levels. The crop often showed higher concentrations of K than either weed. In general wheat required high levels of nutrients to grow larger than the weeds. This is characteristic of plants from nutrient-rich habitats. Hence, the potential competitive ability of the crop appeared to depend on the availability of higher amounts of nutrients, especially K in the soil. The total nutrient contents and efficiency of utilization were also often higher for the crop or similar to those of wild oat. If tissue concentration is any reflection of requirement for a nutrient then barren brome showed higher requirements for N, P, Ca and Mg and wheat for

K. Wild oat was less sensitive to variation of levels of P, K and Mg in solution. The fact that the growth of wild oat was not seriously affected by low levels of these nutrients may be a bonus in any competitive situation in the field where variation in soil nutrient level can be large.

The ability of the weeds to take up and concentrate nutrients at low levels better than the crop in the media is clearly influenced by the observed differences in root morphology. The results also showed that the supply of nutrients can induce changes in the morphology of roots which in turn may affect the efficiency of nutrient uptake. Silverbush and Barber (1984) reported that nutrient uptake is clearly influenced by root length and radius. In the K deficient solution the crop showed a higher root/shoot ratio, indicating the sensitivity of the crop to changes in K level. The deficiency of this nutrient tended to increase root/shoot ratio in all the species. In this study the ratio for wild oat was lower than the other species under limiting P and K reflecting the relatively low sensitivity of this species to low levels of these nutrients.

Experiments where Ca was varied in NFT showed that tef was more affected than wheat or barren brome. Tissue concentrations of the element were highest in this crop possibly indicating a higher requirement, though as in all such cases the possibility of luxury consumption cannot be excluded. Tef may thus be more competitive in soils where Ca is found at relatively high concentrations. Tef also showed the highest total contents of the five major nutrients and greater efficiency of uptake of N, Ca and Mg. Barren brome again showed the highest concentrations of N, P and Mg and wheat for K. Barren brome was more efficient in taking up P and K than either crop. The efficiency of use of P and K was highest in tef and wheat was the most efficient in utilizing Ca and Mg. Variations in the levels of Mg also showed the sensitivity of wheat to this element. Similar observation was also made by Tarawali (1983), who reported Mg deficiency symptoms of wheat plants at concentrations where the weed Alopecurus myosuroides was normal.

The pattern which emerged for these experiments, therefore, is one which does not allow broad generalization relating to nutrient requirements, uptake efficiency or efficience of use across the species or across the various nutrients examined. It does give results which are

interpretable in terms of the possible nutritional background of the species and which may be of some predictive value in relation to the performance of the plants in competition.

SECTION II

SECTION II

Some studies relating to the kinetics of phosphorus and potassium ion uptake using intact plants of *Avena fatua*, *Bromus sterilis* and wheat

6.1 ABSTRACT

The depletion of P and K concentrations from a continuously flowing nutrient solutions by plants of wheat, wild oat and barren brome following 24 h period of depriviation of the two elements was studied at three stages of growth.

Statistical analysis on the data for the concentration (mMol/l) remaining in the feeding solutions at different sampling intervals showed clear differences in the capacity of the species to remove P and K. The amount of P remaining in solution was lower for the crop and wild oat than for barren brome up to 15-17 hrs from the start of the depletion after which differences between the species were not consistent. Both differences and similarities reflecting balances between influx and efflux of ions appeared up to the end of the depletion period. P uptake rates (mMol/g FW of roots) were higher for barren brome than the other species.

Differences between species were also found in the amount of K remaining in the uptake solution at various times and in their ability to take up the element per unit root fresh weight. The crop always removed the greatest quantity of K and gave the highest values for its uptake rates at the three growth stages. The solution containing barren brome plants again showed higher K concentrations in the solution during the depletion than the other species. Wheat and wild oat plants depleted K more rapidly than barren brome and by about 6-7 hrs the two species lowered the initial K concentration to zero. Generally the weeds, especially barren brome, reduced P to a lower final concentration (C min) than did wheat.

The implications of these differences in relation to general responses of the species to variations in the levels of these nutrients in water culture and their ability to compete are discussed. Attempts to determine values for kinetic uptake parameters (Vmax and Km) were unsuccessful and reasons for failure to obtain these values are pointed out.

SECTION II

Some Studies Relating to the Kinetics of Phosphorus and Potassium Ion Uptake using Intact Plants of *Avena fatua*, *Bromus sterilis* and Wheat

6.2. Introduction

Although roots have other important functions, their unique ability to extract and selectively concentrate inorganic ions ranks as one the the most important. Plant species and even genotypes have been recognized to differ extensively in their efficiency of up-take and utilization of specific mineral elements. They tend to have a characteristic salt content which is relatively independent of the medium in which they are grown and they accumulate ions from low concentrations in the medium. For example *Laminaria digitata* accumulates iodine to a concentration of about 300 ppm from a concentration of less than 1 ppm in the sea. MacDonald *et al.* (1960) exposed discs of rutabaga, *Brassica napus*, to flowing water containing potassium at a concentration of 0.01mM. After several days, the accumulation ratio, i.e. concentration within the cell divided by the concentration of the same solute in the solution was over 10,000. The classical experiments of Hoagland (1944) with the fresh water alga *Nitella clavata* also showed a significant difference in the chemical composition of its sap from that of the surrounding pond water. The characteristic feature of plant species selectively to concentrate ions, particularly under stress conditions, has provided the basis for survival and adaptation. However, the physiological mechanisms by which plant roots selectively concentrate inorganic ions are not fully understood, although much progress has been made in recent years (Luttge and Pitman, 1976; Luttge and Higinbotham, 1979; Lauchli, 1984).

Inorganic ions in the soil solution are delivered to the cell wall space (apoplast) of epidermal and cortical cells of the root system by the processes of simple diffusion and mass flow (Nye and Tinker, 1977). Once in the cortical apoplast the ions must be transported through the plasma membrane of living cells to be utilized by the plant. The process requires the expenditure of metabolic energy in the form of ATP (Poole, 1978; Spanswick, 1981). The absorption of ions through the active transport increases as the external ion concentration increases until saturation occurs. This saturation, together with the selective nature

of ion absorption, served as the basis for the ion-carrier theory (Epstein and Hagen, 1952). The carriers were specific for different ions (Epstein and Hendricks, 1956) and appeared to be under genetic control (Epstein and Jefferies, 1964). The ion-carrier complex has been considered to be analogous to a substrate-enzyme complex (Epstein and Hagen, 1952), and Michaelis-Menten kinetics have been employed extensively to describe ion absorption data (Epstein, 1966; Laties, 1969; Nissen, 1971, 1973a; Claassen and Barber, 1974; Drew et al., 1984). Studies on the rate of ion uptake as a function of the external concentration were conducted on excised roots or leaf tissues using radioactive elements (Hoagland and Boyer, 1936; Epstein, 1966, 1972; Nissen, 1971; Tarawali, 1983; Johnson, 1987). The relationship between the rate of ion absorption and its external concentration has also been investigated using intact roots (Olsen, 1952; Fageria, 1973; Claassen and Barber, 1974; Nielson and Barber, 1978; Drew et al., 1984; Becerril-Roman, 1988).

Initially it was recognized that the absorption of ions could not be described by a simple Michaelis-Menten treatment, because ion absorption over a large concentration range did not saturate (Epstein and Hagen, 1952). In addition, when Lineweaver and Burk (1934), Eadie (1942) and Hofstee (1952) plots of ion absorption data were drawn, they resulted in curves rather than a single straight line as predicated by Michaelis-Menten kinetics (Hagen and Hopkins, 1955). These results were interpreted as indicating that two mechanisms for the transport of a single ion existed, one carrier having a high affinity for ions and being functional when the external concentration was low, and a second having a low affinity and being functional at higher external concentrations (Epstein, 1966). Epstein (1972) has demonstrated that the absorption in the low concentration range (0-1mM) does saturate and can be adequately described by Michaelis-Menten kinetics, but in the high concentration range (1-50mM) a true saturation does not occur. The systems of absorption in the low and high concentration ranges are referred to as Mechanism I and Mechanism II respectively and work in parallel, hence "the Parallel Model". Several conflicting models have been proposed to account kinetics of ion uptake which has led to considerable debate (Laties, 1969; Epstein, 1972; Nissen, 1974a; Borstlap, 1981a, b cited by Nissen, 1983). Various alternative explanations have also been suggested (e.g. Oertli, 1967; Baker and Hall, 1973; Leigh et al., 1973). Although

numerous investigators subscribe to the concept of two processes of ion uptake there is a disagreement as to the location of the mechanisms. Mechanism I has been generally placed at the plasmalemma. Epstein and his co-workers (see Epstein et al., 1963, 1972) also located Mechanism II at the plasmalemma, while Laties and his associates placed it at the tonoplast (see Torii and Laties, 1966; Laties, 1969). More recently, Nissen (1971) proposed a single multiphasic mechanism rather than two to explain the complex nature of ion uptake. He located the mechanism only in the plasmalemma. The multiphasic isotherms of Nissen consisted of a series of phases (hence "the Series Model") each of which obeys Michaelis-Menten kinetics. By reanalysis of uptake data of the experiments carried out by Epstein et al. (1963); Torii and Laties (1966) and Nissen (1971, 1973, 1974a-d, 1980, 1983) reaffirmed that the concept of single multiphasic mechanism differs fundamentally from that of the Dual Concept. In the present experiments the rate of uptake of P and K ions in the low concentration ranges where Mechanism I of the dual concept operates has been employed.

Since the relative abilities of species sharing a common medium to compete for nutrient ions depend on aspects of the physiological behaviour of the roots characterized by Km and Vmax (Jackman, 1965), attempts were made to determine ion uptake kinetics of wheat, wild oats and barren brome in order to explain observed differences in their responses to levels of P and K both in mixture and pure stands. In this laboratory, Tarawali (1983) and Johnson (1987) have used uptake kinetics to relate the relative abilities of wheat and blackgrass (A. myosuroides) in taking up P and K to competition and growth in pure stands. Numerous workers have also determined uptake parameters to study aspects of the nutrition of plants (Jefferies et al., 1969; Claassen and Barber, 1974; Nielson and Barber, 1978; Atwell et al., 1980; Drew et al., 1984; Becerril-Roman, 1988).

In the present work a method based on that of Claassen and Barber (1974) and similar to that of Drew et al. (1984) and Olsen (1952) was used. In this method only one plant or group of plants may be grown in a solution of a constant volume and it is assumed that the decrease in ion content of the solution is a measure of the net amount of uptake of the respective ion(s) into the root. The ion content of the solution is determined periodically at a series of intervals by mineral analyses and the resulting data used to draw the so-called "Depletion Curve" over a

period of several hours.

For many ions it is generally agreed that uptake over the low concentration range follows Michaelis-Menten kinetics (Claassen and Barber, 1974) and the rate of uptake is characterized by two parameters in the equation,

$$V = \frac{Vmax.Cs}{Km + Cs}$$

where V is the rate of uptake of ion across the cell membrane, Vmax is the maximum rate of uptake and is a measure of the total carrier capacity in the uptake system of the root, Km is the Michaelis-Menten constant which is analogous to Ks in ion uptake studies and Cs is the concentration of substrate in the medium. Ks measures the affinity of the carrier for the ion under investigation. It is defined as the concentration of the substrate ion giving half the maximal rate of absorption. Ion uptake exhibits specificity based on the differential affinity of the carrier in the transport system. It follows, therefore, that the higher the affinity a carrier possesses for the ion, the smaller is the value of the Ks and a species with a low Ks value for an ion signifies efficiency in taking up that ion. The absorption rates as related to external concentration have been expressed as mean uptake per unit surface, weight or length of the root (Brewster and Tinker, 1972; Claassen and Barber, 1974; Drew et al., 1984).

The specific feature of the present experiments is that the fluxes of phosphorus and potassium were measured in whole plants of the three species grown in continuously flowing solution culture. None of the earlier investigators measured uptake kinetics under such conditions and no depletion studies have been reported for wheat, wild oat and barren brome. There are a number of advantages in using Flowing Solution Culture:

(1) Using one population of plants the relationship between uptake of a nutrient by roots and its external concentration may be obtained.

(2) The system allows more plants to be compared simultaneously and reduces experimental error.

(3) It is possible to maintain pH and nutrient levels relatively constant by sampling and adjusting both.

(4) Whole plants may be removed, measured as necessary and returned without injury.

(5) It allows the use of a range of flow rates.

(6) There is no injury to the plant material on renewal or replenishment of the solution and the same plants may be used successively for different measurement.

(7) There is little risk of anaerobic conditions near the roots.

(8) The system is well suited to comparative studies in the nutrition of plant species.

The objectives of these experiments were:

(1) To determine and compare the quantity P and K remaining in solution after a period of depletion.

(2) To compare uptake rates (μMol/g FW/hr) of the species at various times during the period of depletion and at different stages of growth.

(3) To determine and compare the minimum concentration (C min) of these ions in the solutions reached at the end of the depletion period i.e. the concentration below which net influx ceases.

(4) If possible to compare the kinetics of P and K uptake in wheat, wild oat and barren brome.

(5) To look for differences in the kinetic parameters between the three species at different stages of growth.

6.3. Materials and Methods

(a) General

Studies on the rate at which P and K were depleted from a continuously flowing solution culture were undertaken with wheat, wild oats and barren brome plants at various stages of growth and development. The phosphorus depletion experiments were conducted in the spring to early summer of 1987, whilst potassium was investigated in the summer of 1988. Both experiments were carried out in an environmentally controlled



Plate 2.1 The equipment for sampling circulating solutions. The sampler (at the rear) carried test tubes and was connected to a programmable digital timer (front right) which allows sampling at intervals during the experimental period. About 5 ml of the solution from the individual buckets were pumped into the test tube in the sampler. Each bucket (only two of the three are visible in the plate) contained the circulating solution from channels in which one of the three species was grown

glasshouse under normal daylight throughout. Barren brome seeds were always sown 3-4 days before those of wheat and wild oat on nutrient-free soiless compost. Distilled water was used for watering. When the seedling reached the two leaf stage, they were transferred to a nutrient film culture installation. The seedlings were selected carefully for uniformity and 24 of each species were transferred to separate channels unless otherwise stated. The installation consisted of three channels; each was occupied by an individual species. A nutrient solution, Cooper (1979), which was in 10 l reservoirs, was circulated at a flow rate of 1 l per minute. The nutrient solutions were changed at regular intervals and the cF maintained between 2000-2500 micromhos by addition of small amounts of stock solution to ensure optimum nutrient concentrations throughout the experimental period. The pH was maintained at 6.0±0.2 following daily checks. When the stock nutrient solution or acid or alkali was added to correct cF or pH the reservoir was stirred briefly with a stick to complement the vigorous stirring it received constantly from the action of the pump. The plants were grown in the solution for up to three weeks before depletion rates of the two ions were determined because, for estimation of the rate of ion absorption, plants which have a rather large root system in proportion to the volume of the nutrient solution were found most suitable (Olsen, 1952). Before depletions were carried out the plants were deprived of the relevant ion for a time to reduce the concentration of that ion in the root free space (Nielson and Barber, 1978; Anghinoni *et al.*, 1981). Numerous workers (e.g. Lee, 1982; Tarawali, 1983; Drew *et al.*, 1984; Johnson, 1987; Becerril-Roman, 1988) have studied ion uptake by either intact or excised roots following various period of deprivation of a particular ion.

The uptake of P and K ions by wheat, wild oat and barren brome plants was monitored over a period ranging from 12 to 24 hours from flowing solution cultures. 5-10 ml of the circulating solution were sampled at regular intervals for mineral analysis. Sampling was done with an apparatus designed to withdraw 5-10 ml of the solution from the three separate reservoirs into sampling test tubes at the same time (see Plate 2.1). The sample was only 0.05-0.1% of the total volume of the cirulating solution and was thus considered negligible and ignored in calculations. The tubes containing samples were sealed with parafilm and stored in a fridge at 2-3°C until mineral analysis was carried out.

Attempts were made to maintain the total volume of the solution at

10 l throughout the depletion period of either ions. The pumps were stopped at regular intervals after samples were taken and rested for 5-10 min until all the circulating solution was returned to the containers, and the levels maintained by topping up with distilled water. The quantity added depended on the species, the size of the plants and the environmental factors.

The importance of maintaining other ions at more or less constant levels in the nutrient solutions during uptake rate studies of a specific ion has been emphasised (Wild, 1979; Becerril-Roman, 1988). The control of the concentration of nitrate ions in flowing solutions was described by Clement et al. (1974) who used a method in which automatic additions of $Ca(NO_3)_2$, H_2SO_4 or $Ca(OH)_2$ were made to maintain nitrate and pH constant. A method of controlling the concentration of potassium at constant levels has also been described by Woodhouse et al. (1978) and that of phosphate by Breeze et al. (1982). These methods were used to make automatic additions of K_2SO_4 and $Ca(H_2PO_4)_2$ to maintain K and P at optimum concentrations. In the present P and K uptake studies attempts were made to control the concentration of the levels of two major anions (nitrate and phosphate) and two major cations (potassium and magnesium), because numerous investigators have studied the uptake rates of these ions by different plant species and reported rapid depletion from solutions (Olsen, 1952; Claassen and Barber, 1974; Drew et al., 1984; Becerril-Roman, 1988). Details are given below in each case.

In order to determine the quantity of roots involved in the depletion of K from the culture solution, three plants of each species were harvested just before and at the end of the depletion period. The harvested plants were divided into shoots and roots and rinsed with distilled water twice. The free water on the surface of the roots were removed with paper towels and their fresh weights recorded. Because the depletion period was short (between 12 and 24 hours) it was assumed that a mean of the values of any root variate measured at the beginning and end of the period would give a suitable estimate of the amount of root involved in the depletion.

Chemical analyses of the collected samples were carried out. Phosphorus was determined using Vanadomolybdo-phosphoric yellow method and potassium by a Corning 410 flame photometer. The results from these analyses showed the amounts of P and K remaining in solution at different

intervals during the period of depletion. These data when plotted against time formed the 'depletion curve' - the initial stage for the determination of the uptake kinetic parameters. The curves were fitted to various functions and best fits produced predicted values. Data for the present experiments were fitted to exponential and simple linear regression models. Best fits for the observed P data were obtained using the exponential equation of the form $Y = A+b.e^{bx}$ whilst those of K fitted a simple linear ($Y = A+BX$) as well as exponential equations. In neither case, however, were very high correlations (R^2) between the observed and predicted values achieved. Uptake rates (μMol/gFW/hr) were determined from the fitted curve by taking the negative slope ($-dc/dt$) (Claassen and Barber, 1974; Becerril-Roman, 1988). The uptake rates were plotted against corresponding P or K concentrations remaining in solution and attempts to determine Vmax and Km values from the resultant curve were made.

Analyses of variance were carried out on the amounts of P or K remaining in solution at different intervals during the depletion period. The data for the rate of uptake were also similarly analysed and the three species compared. Values for Cmin were taken as the minimum P or K concentration measured in solution.

(b) Phosphorus depletion

Seeds of wheat and wild oats were sown on 31/3/87, and those of brome three days earlier. They were transferred to the NFT channels on 10/4/87. The maximum, minimum and mean daily air temperatures of the glasshouse cubicle were 33.5, 16.8 and 25.2°C respectively. Natural daylight was used throughout and daylength was up to 14½ h. The solution was completely changed at weekly intervals. For actual depletion determination, the solution was renewed, but contained no phosphorus for 24 h. At the end of this period the solution was once again renewed and phosphorus at half strength (9.68×10^{-4}M; 30 ppm P) included. The rate at which phosphorus was removed by each of the three species was followed during a period of 24 h. Samples were collected at hourly intervals. Throughout the depletion period, nitrogen, potassium and magnesium were added regularly to ensure that these nutrient elements are not depleted before the phosphorus. The approximate amount to be added was determined from a preliminary P depletion experiment with 4 week old wild oat plants. These were used because they were the largest plants

and were thus assumed to remove these nutrients from the solution rapidly. The results of analyses of samples collected 12 h after the commencement of the phosphate depletion indicated that 60-75% of these elements had been removed by this time. It was thus decided to add ¼ of the original amounts of N, K and Mg at 3-hourly intervals throughout the depletion period. The quantity of Ca removed was also determined, but was found to be very small and thus no additional Ca was given. No minor elements were added.

Phosphorus uptake studies were carried out on plants 5, 6 and 7 weeks after transplanting to the NFT system. The number of plants was kept constant at 24. Therefore, unlike the potassium depletion studies, harvests were not made before and at the end of the depletion period. Only one harvest was made at the end of the third depletion, i.e. when the seedlings were seven weeks old in the NFT system.

Hence at the last depletion, uptake rates (µmol/gFW/hr) were calculated using root fresh weight of plants harvested at the end of the period. The mean root fresh weight (g/plant) of wheat, wild oat and barren brome were approximately 29.99, 37.4 and 19.81 g respectively and the total amount of root per species was obtained by multiplying by the number of plants. It was assumed therefore that approximately 719 g of wheat, 833 g of wild oat and 475 g of barren brome root had been involved in the depletion of P from the solution. During the first and second periods of P depletion, uptake rates were calculated using root weight estimates based on an earlier experiment on the response of the spp to levels of P (Exp. 2, Section I). The plants in the present experiment and Section I, received similar amounts of P (0.968 mM) and the other elements. The age of the plants in the two experiments was also similar. For depletion 1, i.e. at 5 weeks, the roots of 5 week old plants of the three species were used. The root weight estimates were approx 451, 556 and 222 g for wheat, wild oat and barren brome respectively. The amounts at six weeks were 558, 703 and 276 g for the three species respectively.

(c) Potassium Depletion

These experiments were conducted in the summer of 1988 in a controlled environment glasshouse. The daylength was up to 17 h and the maximum, minimum and mean day and night air temperatures were 27.0, 17.2 and 22.1°C respectively. Barren brome seeds were sown on 30/5/88 and those of wheat and wild oat on 3/6/88. Seedlings were transferred to

the nutrient film culture installation on 13/6/88. 24 plants of barren brome and 23 of wheat and wild oats were transferred to separate channels.

Unlike the plants used for phosphorus depletion studies, these plants were raised in half strength Cooper's nutrient solution. In an earlier experiment where K levels were varied in the solution, full strength Cooper's solution was noted to cause some toxic effects on the roots of the plants, especially on barren brome. For K-depletion determination, the concentration of this nutrient was further reduced to 10^{-3}M (39 ppm K) in order to examine System I kinetics of nutrient uptake which operates at ion concentrations below about 1.0 mM (Epstein, 1966; Edwards, 1970). The pH of the solution was maintained at about 6.0 by frequent adjustments using dilute solutions of H_2PO_4 or NaOH. Potassium depletion studies were made 26, 36 and 44 days after transplanting to the NFT installation. Prior to the depletion determination the plants were deprived of potassium for a period of 48 hrs. When K was withheld from the plants, KNO_3 and KH_2PO_4 were excluded from the solution and NaH_2PO_4 and $NaNO_3$ were added to replace the phosphate and nitrate ions. These two ions plus the Mg^{2+} were maintained at near constant concentrations at the time of K-depletion studies. 75% of the original NO_3^{o-} and $Mg^{2;}$ concentrations in the solution was added in three applications during half the depletion period and 25% was replaced in two applications during the rest of the period. Phosphorus was also added at regular intervals and the quantity that needed to be replaced in order to maintain at constant levels was obtained from the P depletion rate studies carried out in 1987 (Table 2.1). 90-98% of the initial phosphorus concentration in solution had been absorbed in about 12 hrs of the depletion period at the three stages of growth, 60-80% of which was removed during the first 6 hrs. Although these plants were larger than those used for K uptake studies, the data were used to maintain P near optimum levels.

Table 2.1 % P removed after 6 and 12 hours at three stages of plant growth. The original P concentration (100% P) was 0.968mM (30 ppm P)

Growth stages (weeks)	5		6		7	
Time since start (hrs)	6	12	6	12	6	12
Species						
Wheat	75	97	75	98	82	98
Wild oat	67	96	79	98	81	98
Barren brome	60	88	61	89	71	92

The depletion rates of K were monitored over periods of 12, 14 and 12 h respectively in the three successive experiments carried out at 26, 36 and 44 days after transplanting. For the K depletion period of 12 hrs, 60-80% of the initial P concentration was added at regular intervals in three applications between 0-6 hrs and 20-30% during the remaining period. During the longer depletion periods P was replaced at the rate of its removal between 6 and 12 hrs, i.e. 20-30% at 2 hourly intervals throughout depending on the species. NO_3^- and Mg^{2+} were added at 25% of their original amounts together with the phosphorus additions.

To determine the quantity of roots of each species at the time of the depletion study, three plants were harvested just before and at the end of the K uptake period, except in the second trial where harvesting was done only at the end of the depletion period. The number of plants per species and the quantity of roots measured are given in Table 2.2.

Table 2.2 Number of plants/species and amount of root at the three stages of K-uptake studies

Depletion	1			2			3		
Species	W	WO	BB	W	WO	BB	W	WO	BB
No. of plants	20	20	21	17	17	18	11	11	12
Root fresh wt. (g/plant)	5.53	6.17	2.30	18.26	46.37	9.25	43.80	71.16	20.25
Total root fresh wt (g/species)	110.60	123.4	48.30	310.42	788.29	166.50	481.80	782.76	247.00
Root dry wt. (g/plant)	0.24	0.32	0.12	1.14	1.73	0.62	2.03	2.40	1.38
Total root dry wt (g/species)	4.80	6.40	2.52	19.38	29.41	11.16	22.33	26.4	16.56

6.4. Results

The initial phosphorus concentration in the nutrient solutions decreased exponentially with time at all stages of growth (Fig. 2.1a-c). Analyses of variance of the data on the amount of P remaining in solution at various times showed that the species removed different amounts. The initial rate of depletion following periods of deprivation was the highest for all species and also varied with species and plant age (Tables 2.3-2.5). The species did not in general differ significantly in the minimum P concentration remaining in solution, although the weeds, reduced the initial P to the lowest values.

Uptake rates were determined by visual estimation of the slope of

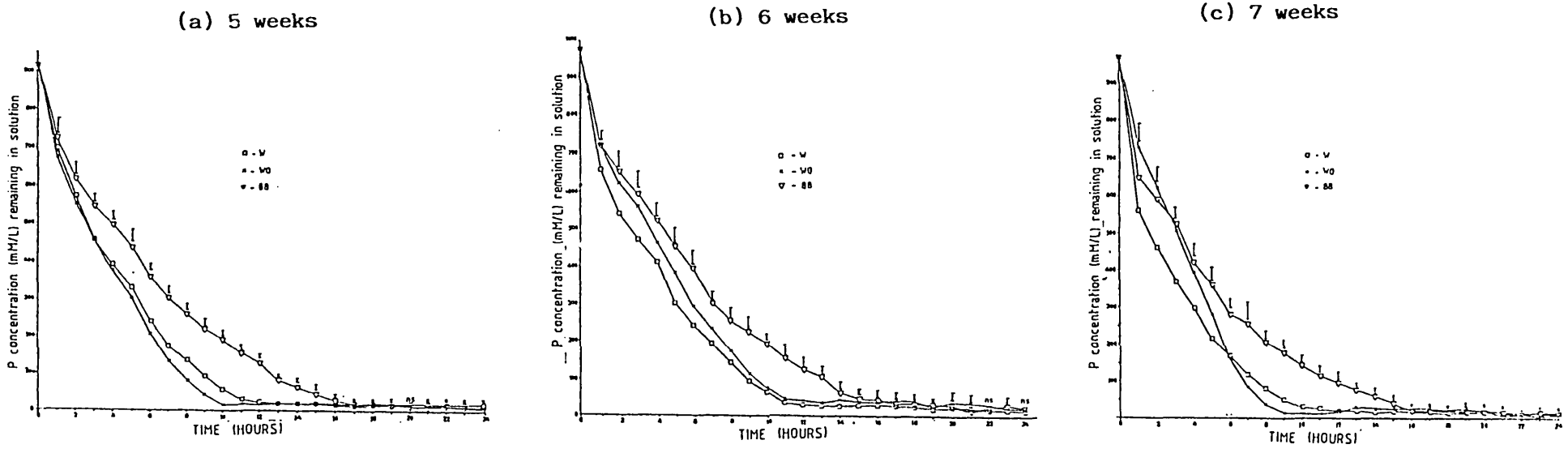


Figure 2.1 (a-c) The relationship between ion P concentration (C) remaining in uptake solution and time (T) during uptake by plants of wheat (W), wild oat (WO) and barren brome (BB) at three stages of growth
Vertical bars represent LSD at the 5% level of probability

Table 2.3 Mean phosphorus uptake rates (uMol/g FW of root/hr) after various times during the depletion period by 5 week old plants of the three species

	Time (hrs) after start of depletion						
Species	1	2	3	4	5	6	7
W	0.24a	0.19a	0.15a	0.13a	0.10a	0.09a	0.08a
WO	0.18a	0.15a	0.13a	0.11a	0.09a	0.08a	0.07b
BB	0.76b	0.63b	0.53b	0.44b	0.36b	0.30b	0.25c

	8	9	10	11	12	13	14
W	0.060a	0.050a	0.040a	0.040a	0.030a	0.020a	0.028a
WO	0.057a	0.047a	0.040a	0.033b	0.030a	0.023b	0.020a
BB	0.213b	0.173b	0.147b	0.120c	0.100b	0.087c	0.070b

	15	16	17	18	19	20	21
W	0.020a	0.017a	0.013a	0.010a	0.010a	0.010a	0.010a
WO	0.020a	0.013a	0.010a	0.010a	0.010a	0.010a	0.010a
BB	0.057b	0.050b	0.040b	0.037b	0.030b	0.027b	0.020b

	22	23
W	0.005a	0.003a
WO	0.005a	0.005a
BB	0.0153b	0.015b

Means followed by the same letter in columns are not significantly different at the 5% level of probability as determined by LSD

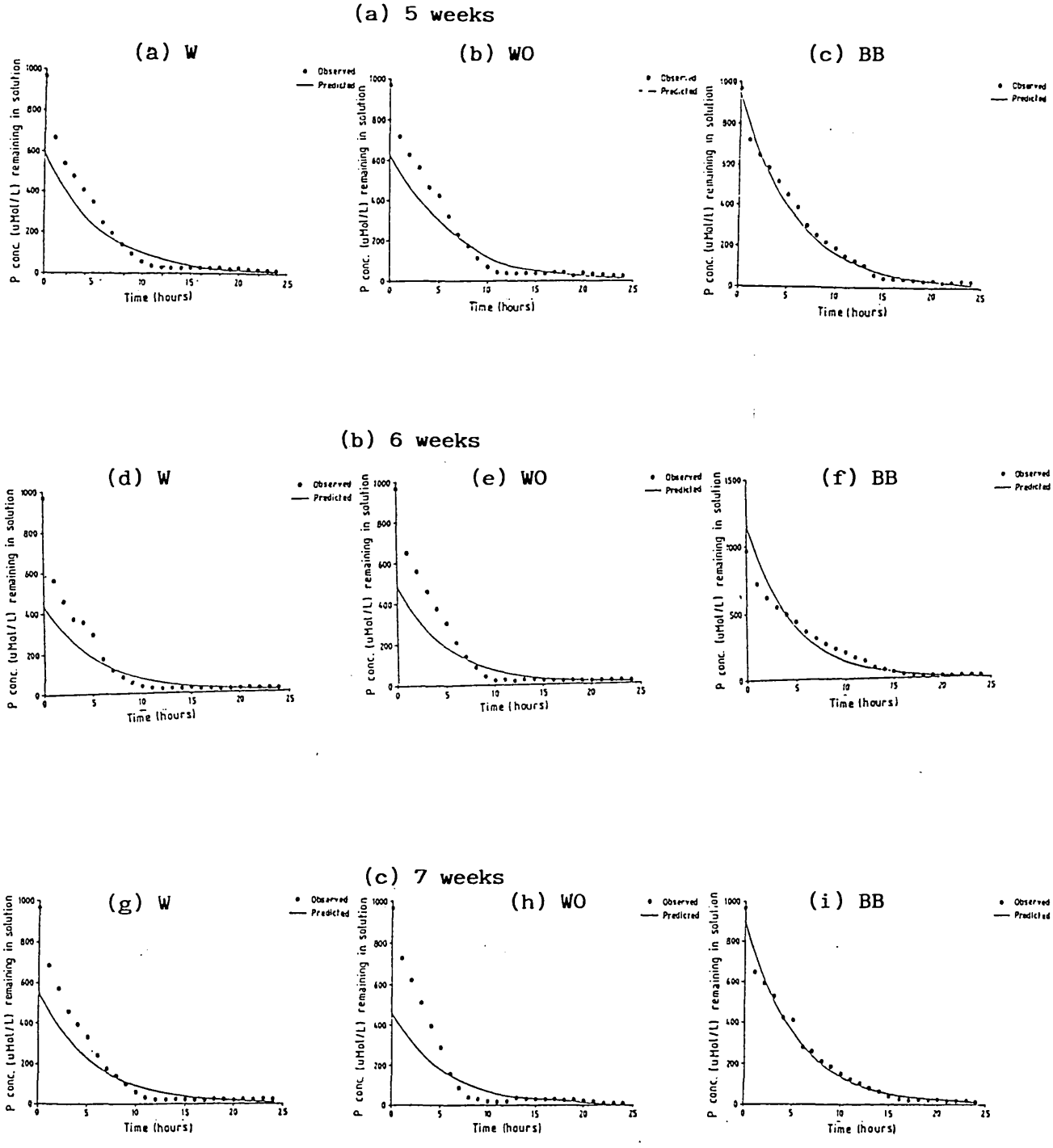


Figure 2.2 (a–i) Predicted P depletion curves for wheat (W), wild oat (WO) and barren brome (BB) plants grown in sol ion culture and at three stages of growth (5, 6 and 7 weeks) with plants deprived of P prior to depletion

(Note: on the Figures the word 'predicted' is used instead of 'fitted')

the tangent to the depletion curve fitted to the experimental points (see below) at a series of points over the length of the curve, because uptake at any point on the curve is equal to -dc/dt (Claassen and Barber, 1974; Becerril-Roman, 1988). The data obtained this way were expressed in umols/g FW of roots/hr and when plotted against the corresponding P concentration in solution, the resultant curve failed to show the point where uptake became saturated at the higher P levels, though uptake rates for all species increased with increase in P level at all three stages of growth. Hence attempts to determine Vmax and Km values for the three species graphically from the resulting curve proved unsatisfactory for this reason and because of problems of curve fitting also described later. Further attempts to determine these values following Line-Weaver Burk and/or the Eddie:Hoftsee transformations were not successful for similar reasons.

Phosphorus depletion from solution by plants of wheat (W), wild oat (WO) and barren brome (BB)

1. Five week old plants:

The species were compared statistically on the amount of P remaining in solution at hourly regular intervals during the depletion period. Initially the decrease in P concentration was rapid for all three species; at later stages the process was generally slow (Fig. 2.1a, b and c). Up to 16 hours the solution with wheat plants generally contained the lowest P, whilst the highest quantity was found in the solution containing barren brome plants. From 16 hrs onwards any differences were less clear cut. For any one solution after 16 hrs of depletion, small fluctuations in P concentration were common due partly to the greater influence of efflux processes at a stage where tissue concentration of P were, on the basis of tissue analysis carried out in other experiments (Section I), likely to be higher than the external solution concentration. Uptake continued up to the end of the period (24 hrs) although at a very slow and steady rate. For both wheat and wild oat P in solution reached minimum concentrations after 14-16 hrs (17 hrs for barren brome), beyond which time both uptake and release of P from tissues became apparent. At the end of the 24 hrs depletion period all three species had reduced P to similar concentrations.

Phosphorus uptake rates (µMols P/g FW/hr) calculated for the three species at this stage of growth showed that barren brome was the most

Table 2.4 Mean phosphorus uptake rates (uMol/g FW of roots/hr) after various times during the depletion period by 6 week old plants of the three species

	Time (hrs) after start of depletion						
Species	1	2	3	4	5	6	7
W	0.187a	0.155a	0.127a	0.107a	0.089a	0.072a	0.060a
WO	0.127b	0.010b	0.083b	0.068b	0.056b	0.043b	0.035b
BB	0.852c	0.68c	0.553c	0.444c	0.36 c	0.286c	0.232c

	8	9	10	11	12	13	14
W	0.049a	0.040a	0.033a	0.028a	0.023a	0.021a	0.016a
WO	0.029a	0.025a	0.021a	0.016b	0.014a	0.013b	0.009a
BB	0.174b	0.140b	0.113b	0.092c	0.064b	0.052c	0.041b

	15	16	17	18	19	20
W	0.013a	0.011a	0.009a	0.008a	0.005a	0.005a
WO	0.008a	0.006a	0.005a	0.004a	0.003a	0.002a
BB	0.029b	0.023b	0.019b	0.016b	0.012b	0.011b

	21	22	23
W	0.004a	0.004a	0.003a
WO	0.003a	0.002b	0.002a
BB	0.008b	0.007c	0.007b

Means followed by the same letter in columns are not significantly different at the 5% level of probability as determined by LSD

efficient species (Table 23).

2. Six week old plants:

Wild oat depleted the solution most rapidly at this age. The solution P concentration was again highest for barren brome (Fig. 2.1b) up to 16-20 hrs. From this time onwards results were similar to those after 5 weeks, although barren brome plants rediced P to the lowest value of about 9 µM. The values for wheat and wild oat were about 20 and 13 µM respectively at this time. The fact that the weeds, especially barren brome depleted P to a lower level than the crop suggests greater efficiency of the weed roots in the uptake of P from dilute solutions.

Mean phosphorus uptake rates (µmols P/g Fw/hr) at various times during the depletion period clearly showed that values were always higher for barren brome than either of the other species. During the early part of the depletion uptake rates for the crop were greater than for wild oat, but at later stage the two were similar.

3. Seven weeks:

During the initial periods of depletion wheat plants removed P from solution in larger quantities than either weed. As depletion proceeds up to 16 hrs P concentration remaining in solution was markedly lowest for wild oat plants, although at a few points this was similar to wheat, the solution containing barren brome plants being the highest. At 16 hrs concentrations were highest in solution containing wild oat and lowest containing the crop. In this case at the end of the 24 hours, wild oat plants had reduced P to 5.81 µM, whilst the value was 15.48 µM for wheat and 11.40 µM for barren brome.

Mean phosphorus uptake rates were again greater for barren brome than for the other species, although some exceptions were apparent (Table 2.5). Wheat and wild oat had similar uptake rates initially but as depletion continued wheat absorbed P at faster rates than the weed and at later stages of the depletion period both species again showed similar uptake rates.

Table 2.5 Mean phosphorus uptake rates (P uMol/g FW of roots/hr) after various times during the depletion period by 7 week old plants of the three species

	Time (hrs) after start of depletion						
Species	1	2	3	4	5	6	7
W	0.093a	0.093a	0.076a	0.064a	0.052a	0.045a	0.036a
WO	0.103a	0.085a	0.065b	0.054b	0.043b	0.035b	0.028b
BB	0.350b	0.288b	0.236c	0.194c	0.159c	0.131c	0.107c
	8	9	10	11	12	13	14
W	0.031a	0.025a	0.021a	0.018a	0.014a	0.012a	0.009a
WO	0.024b	0.020b	0.016b	0.012b	0.010a	0.008a	0.007a
BB	0.087c	0.073c	0.059c	0.049c	0.027b	0.031b	0.075b
	15	16	17	18	19	20	21
W	0.007a	0.006a	0.005a	0.004a	0.003a	0.002a	0.003a
WO	0.006a	0.005a	0.004a	0.003a	0.002a	0.002a	0.001b
BB	0.021b	0.018b	0.015b	0.012b	0.010b	0.007a	0.007c
	22	23					
W	0.001a	0.002ab					
WO	0.002a	0.001a					
	0.006b	0.003b					

Means followed by the same letter in columns are not significantly different at the 5% level of probability as determined by LSD

6.5. Discussion

As the initial P concentration in the feeding solution was depleted, the amount remaining in solution at hourly intervals was plotted against time. This resulted in the depletion curve which is the initial stage for the determination of the uptake parameters, Vmax - the maximum rate of uptake which measures the carrier potential and Km, the solution concentration occurring at half Vmax, which measures affinity of the carrier for an ion. To describe the relationship between these parameters the P contents of the solution are plotted against influx rates. Best fits are obtained for the depletion data using different regression equations and influx rates at various levels of P determined by visual estimation of the slope of the tangent to the depletion curve, at a series of points over the length of the curve. Influx rates, Vmax, Km, efflux (E) may also be determined using the integrated rate equation developed by Michaelis-Menten for enzyme kinetics (see Claassen and Barber, 1974; Drew et al., 1984; Becerril-Roman, 1988; Mullins and Edwards, 1989). Claassen and Barber (1974) developed the integrated rate equation to describe nutrient uptake rates by intact root systems of plants. The equation fitted to the data of the depletion curve describes the curve and from this predicted values of nutrient concentration remaining in solution and values of Vmax, Km and efflux (E) can be obtained. In the present study an exponential equation of the form $Y = A+B.e^{bx}$ and simple linear equations were fitted to produce predicted values of P concentration in solution.

Unfortunately this did not give high values of R^2 (correlation coefficient) between the observed and predicted values (Fig. 2.2a-i). Attempts to determine Vmax and Km values graphically from the rate versus concentration curve did not yield satisfactory results, owing partly to this poor correlation. As the concentration of P in nutrient solution increased uptake rate increased linearly at all stages of growth. This shows that the uptake mechanism was not saturated and hence maximum uptake rates were not reached with the amount of P used in these experiments. A very large amount of literature available shows that for many ions influx over the low concentration range (<1.0 mM P) follows Michaelis-Menten kinetics, although problems in curve fitting for depletion data have been reported for various ions (see Claassen and Barber, 1974 (for N uptake), Drew et al., 1984; Mullins and Edwards,

1988) for K uptake and Becerril-Roman, 1988 (for some major cations and anions). It follows that the kinetics of uptake of some ions did not fit the pattern appropriate to simple Michaelis-Menten kinetics as applied to enzymes.

Criticisms of the application of the procedure to determine kinetic curves for nutrient depletion by intact plants are not uncommon. For example Shock and Williams (1989) questioned the use of depletion curves to provide data base on variable concentrations and rates and instead used the initial uptake rate from any depletion to estimate the kinetic curve. This meets the criticism that orthodox Michaelis-Menten kinetics are based on the initial rate of enzyme reactions and not those operating after a period of exposure to the relevant substrate. If the rate of phosphate uptake is determined continuously as the P concentration declines with time the kinetic estimates would be different, since estimate for Vmax and Km might be expected to vary with the concentrations chosen as starting points.

Mullins and Edwards (1988) also attempted to calculate K uptake parameters for trimmed and untrimmed corn seedlings by fitting the integrated rate equation developed by Claassen and Barber (1974) to the depletion curve data. Their results were unsatisfactory as the predicted depletion curves did not correspond very well to the actual depletion curve. However, they were able to estimate the parameters graphically and Imax (Vmax) was calculated from the initial linear slope of the depletion curve, assuming that the plants were operating at Imax in this region, since the rate of K removal from solution was constant with time. In contrast to these approaches Mullins and Edwards (1989) did not agree with the idea that K uptake parameters should be determined with initial uptake rates only, because they found that these parameters for K are dependent on the concentration of K in the cell which is in turn dependent on the concentration of K in the external solution. They considered that, for an intact root system growing in soil, kinetic parameters measured using a depletion procedure give a realistic description of K uptake.

To get a reliable estimate of the parameters needed for calculating the relation of influx versus concentration Claassen and Barber (1974) suggested that it is necessary to have a good estimate of the near linear initial and near horizontal final parts of the depletion curve and a

reasonable number of observations joining these segments.

One of the main aims of the present study was to establish the relationship between P uptake rates and the external solution concentration and to look for differences between species in their uptake parameters, because such differences may contribute to the effectiveness of associated species in competition for limiting phosphorus. Differences in P uptake kinetics could have ecological consequences for plant survival and distribution. A higher efficiency of uptake of P by a species may be the result of a greater surface area exposed/unit weight of roots and/or a lower K_s. In this study although the uptake kinetics could not be determined for the three species higher influx rates (μMol/gFw/hr) for the weeds, especially barren brome, at all stages of growth suggested that the weeds were the most efficient in this respect. One explanation of this could be that barren brome roots have more carriers molecules which bind to the phosphate ion than the other species. If these carriers in barren brome roots have more affinity for the ion i.e. a lower Ks value than wheat or wild oat, this would affect the final concentration reached in the external solution. The quantity of P remaining in solution at later parts of the depletion curve showed that in general the weeds, especially barren brome, reduced the initial P in solution to a minimum value lower than those for wheat, although the total amount of root was much smaller for this weed than for the other species. This implies that the roots of barren brome have the ability to absorb P from low levels in solution even when its tissue concentrations are higher than the external concentation. At low external concentrations, net uptake of ions ceases before the ions are completely depleted and a minimum value is reached (Cmin). The Cmin describes the level of the ion in solution beyond which uptake ceases as the result of a limited affinity of carrier sites for the ion or an equilibrium being established between influx and efflux. The minimum concentration is, therefore, an important factor in ion uptake from the soil, because it is the lowest concentration at which roots can extract an ion in solution (Marschner, 1986). The lower values of Cmin found in the weeds, particularly barren brome for P in this dtudy may enable the species to grow at a lower soil-phosphorus concentration. In both responses and competition experiments (Sections I and III), tissue P concentrations of the weed were usually higher than those of wheat or wild oat. Wild oat removed greater total amounts of the element, especially at early stages

of the depletion period, because of the large amounts of root produced.

Differences in Cmin values among ions and species have been found. For example, in maize Barber (1979) reported values to be 2 uM for K and 0.2 uM for P and in barley corresponding values of 1 uM and 0.1 uM respectively were found by Drew et al. (1984). The values for the phosphate ion in the present experiments were much higher than those reported above and such differences may be partly attributed to limited affinity of carrier sites. The K ion, however, was reduced to zero or values not significantly different from this value (see below) by all species except with 26 day old plants. Fluctuations in the concentration of the phosphate ion at later stages of depletion also suggested efflux of P from the roots but no comparisons were made between the species in this regard. Efflux may be of significant importance in regulation of P supply to the root (see Bieleski, 1973).

Differences between the species in the relationship between external concentration and ion influx might also reflect the presence of a different number of carrier systems, operating at different external concentration levels as suggested by Nissen (1973a and 1980). Considerable further work would be needed to investigate this possibility.

Potassium depletion from solution by plants of wheat (W), wild oat (WO) and barren brome (BB)

6.6 Results

1. 26 day old plants:

During the first few hours of the depletion period, the three species did not differ in the amount of K they removed. Some differences appeared later as shown in Figure 2.3a. The amount of K remaining in solution after depletion by barren brome plants was always greater than for the other species. The depletion data were fitted to exponential equations (Figure 2.4a-c) and K uptake rates (μMol/g FW of roots/30 min) calculated for the three species at 30 min. The crop always showed higher rates than either weed (Table 2.6). At the beginning of the depletion period, wild oat removed K faster than barren brome, a situation which was reversed later in the period. Such differences may arise, because at any one time rate of removal is related to the K content of the solution and was higher for barren brome than for wild oat (see above).

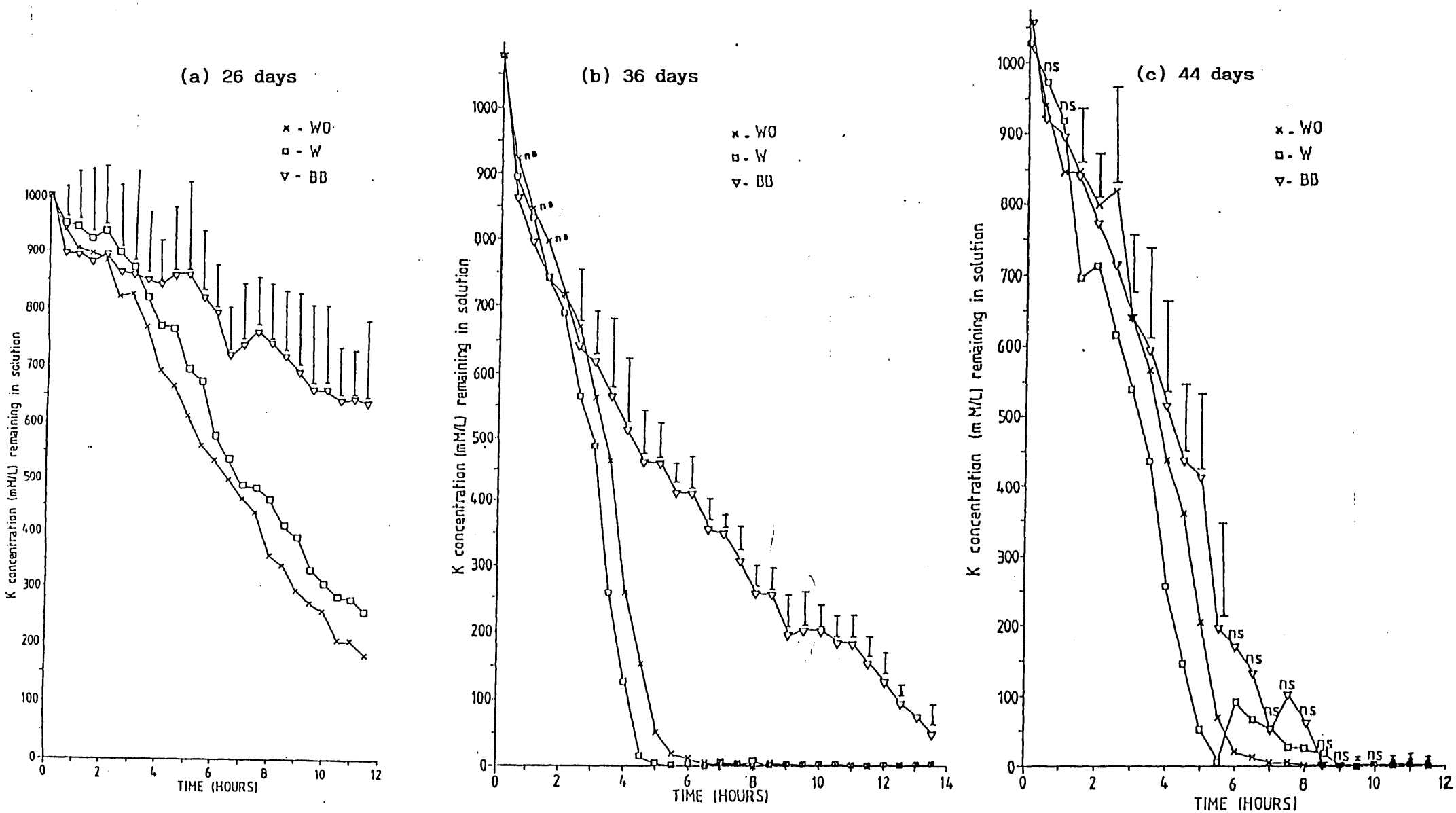


Figure 2.3 (a-c) The relationship between K ion concentration (C) remaining in uptake solution and time (T) during uptake by plants of wheat (W), wild oat (WO) and barren brome (BB) at three stages of growth
Vertical bars represent LSD at the 5% level of probability

Table 2.6 Mean K uptake rates (μMol/g FW of roots/30 min) after various times during the depletion period by 26 day old plants of the three species

Species	Time (hrs) after start of depletion ½	1	1½	2	2½	3	3½
W	0.48a	0.45a	0.41a	0.39a	0.37a	0.34a	0.32a
WO	0.25b	0.24b	0.25b	0.23b	0.22b	0.21b	0.20b
BB	0.21c	0.21c	0.21c	0.20b	0.21b	0.20b	0.20b

	4	4½	5	5½	6	6½	7
W	0.31a	0.28a	0.26a	0.24a	0.24a	0.22a	0.20a
WO	0.18b	0.17b	0.16b	0.15b	0.14b	0.14b	0.14b
BB	0.19b	0.19b	0.19c	0.18c	0.17c	0.17c	0.18c

	7½	8	8½	9	9½	10	10½
W	0.19a	0.18a	0.17a	0.16a	0.15a	0.13a	0.13a
WO	0.12b	0.11b	0.10b	0.10b	0.10b	0.09b	0.08b
BB	0.17c	0.17c	0.16c	0.15c	0.16c	0.16b	0.14c

	11	11½
W	0.12a	0.11a
WO	0.07b	0.07b
BB	0.15c	0.16c

Means followed by the same letter in columns are not significantly different at the 5% level of probability as determined by LSD

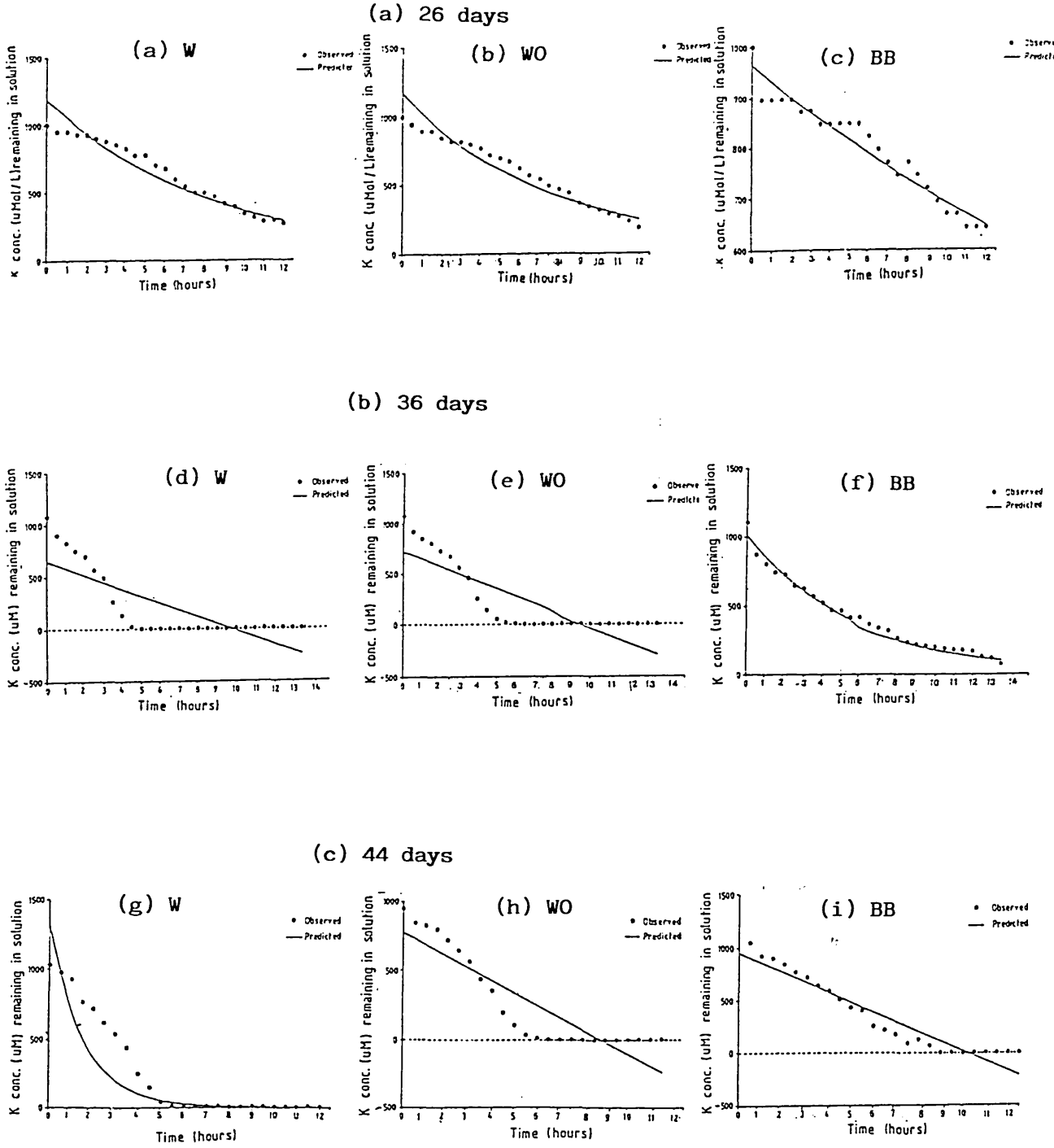


Figure 2.4 (a-i) Predicted K depletion curves for wheat (W), wild oat (WO) and barren brome (BB) plants grown in solution culture and at three stages of growth (26, 36 and 44 days) with plants deprived of K prior to depletion

(Note: on the Figures the word 'predicted' is used instead of 'fitted')

2. 36 day old plants:

K removed at early stages of the depletion was similar for all species but as the process continued the amount removed by barren brome was the lowest. Wheat and wild oat in general removed similar amounts. By about 6 hours after the commencement of depletion both species reduced the initial K concentration to amounts not significantly different from zero. At the end of the depletion period, i.e. 14 hrs after the commencement of the depletion process, barren brome plants had reduced the initial 1103 mM/L of K to only 50 mM/L.

Simple linear regression equations were fitted to the depletion data of wheat and wild oat and an exponential equation fitted those for barren brome (Figures 2.4d-f). Uptake rates calculated for the three species for the first 5½ hrs of the depletion period showed that wheat plants removed K at higher rates than either weed. The uptake for wild oat was the lowest at any point on the depletion curve (Table 2.7) and remained similar up to the end of 5½ hrs.

3. 44 day old plants:

The pattern was similar to the 36 day old plants. Wheat plants removed more K for most of the depletion period. After 5½ hrs of depletion wheat had removed all the K present (Figure 2.3c). Wild oat plants also reduced K to a level not significantly different from that of the crop, but this took 8½ hrs. Barren brome reduced K to zero level after 9½ hrs. Both influx and efflux continued until the experiment was terminated after 12 hrs.

The depletion data for the crop were fitted to an exponential equation of the form $Y=A+B.e^{bx}$, and those of the weeds to simple linear regression $Y=A+BX$ (Figures 2.4g-i). Uptake rates (μmols/g FW/30 min) were calculated for all three species. The crop again showed higher rates of uptake than either weed (Table 2.8). The weeds also differed and wild oat rates were higher than those of barren brome. For the weeds especially wild oat, uptake rates at different times during depletion remain similar, whilst those of the crop decline dramatically. The rates were calculated for the first 7½ hrs of the total period only, because by about this time, net uptake had ceased in wheat and wild oat. Both uptake rate and the quantity remaining in solution after depletion by wheat suggested that the crop has a high requirement for the element or

Table 2.7 Mean K uptake rates (uMol/g FW of roots/30 min) after various times during the depletion period by 36 day old plants of the three species

	Time (hrs) after start of depletion					
Species	½	1	1½	2	2½	
W	0.28a	0.29a	0.29a	0.29a	0.28a	
WO	0.09b	0.09b	0.09b	0.09b	0.09b	
BB	0.42c	0.38c	0.36c	0.33c	0.30c	
	3	3½	4	4½	5	5½
W	0.29a	0.29a	0.29a	0.28a	0.29a	0.28a
WO	0.09b	0.09b	0.09b	0.09b	0.09b	0.09b
BB	0.28c	0.25a	0.29c	0.22a	0.20c	0.18a

Means followed by the same letter in columns are not significantly different at the 5% level of probability as determined by LSD

Table 2.8 Mean K uptake rates (uMol/g FW of roots/30 min) after various times during the depletion period by 44 day old plants of the three species

	Time (hrs) after start of depletion				
Species	½	1	1½	2	2½
W	0.73a	0.54a	0.34a	0.29a	0.21a
WO	0.12b	0.12b	0.12b	0.12b	0.12b
BB	0.10c	0.09c	0.09c	0.10c	0.10b
	3	3½	4	4½	5
W	0.15a	0.12a	0.08a	0.06a	0.04a
WO	0.12b	0.12a	0.11b	0.12b	0.12b
BB	0.10c	0.09b	0.09c	0.10c	0.09c
	5½	6	6½	7	7½
W	0.33a	0.02a	0.02a	0.01a	0.01a
WO	0.12b	0.12b	0.12b	0.12b	0.12b
BB	0.09c	0.09c	0.09b	0.09c	0.09c

Means followed by the same letter in columns are not significantly different at the 5% level of probability as determined by LSD

shows luxury consumption of it, and may have efficient uptake mechanisms to meet these demands.

6.7. Discussion

Potassium (K) depletion following a period of deprivation was similar for wheat and wild oat at all stages of growth, although the crop reduced the initial concentration to a minimum value (C min) quicker than either weed. Barren brome depleted the element more slowly than the other species. However, the weed was capable of reducing K to levels similar to those of wheat and wild oat at the first stage of growth tested. Uptake rates (μ Mols/g FW of roots/30 min) were the highest for wheat and lowest for wild oat (Tables 2.6, 2.7 and 2.8).

The ability of the crop to reduce K to a minimum value quicker than the weeds may be significant for the crop in competitive situations under limiting K. Competitive ability of the three species at various levels of the element showed that the crop was more competitive than barren brome and slightly more so than wild oat (see Section III). In the response experiments (Section I), the crop was also more responsive to higher levels of K than either weed. Tissue concentrations determined for the three species in competitive and non-competitive situations also showed that the crop usually contained greater than or similar quantities of K to the weeds. The lower and steady uptake rates observed for wild oat at 36 and 44 days may explain the lower sensitivity of the weed to various levels of the nutrient (Section I) than the other species. The lower K tissue concentration noted for wild oat than the other species in the different sections of this report may well be due in part to the slower uptake rate of its roots. The lower uptake rate of the weed for this nutrient may imply less carrier sites/unit root fresh weight and also perhaps a higher Km value. However, the latter seems unlikely because the weed is less responsive to relatively high levels of the nutrient in competitive and non-competitive situations.

Attempts to determine kinetic parameters for K uptake were not successful and the reasons for the failure to estimate these values were similar to those described for the P depletion data. The relationship between absorption rates and ion concentration again does not exclude the

possibility that there may be several different carrier sites on the root active at different ion concentrations. Epstein suggested low and high concentrations of kinetics for K uptake (his system I and II). Nissen (1973a) has looked in detail at isotherms and suggested a single multiphasic uptake system already referred to in the discussion on the P uptake experiment.

Plant age may affect the relation between the demand of the plant for an ion and the rate of K uptake by the root. With increasing age up to 44 days there was a decrease in the average K uptake rate per unit root fresh weight in all three species, especially in wild oat (Tables 2.6, 2.7 and 2.8), although the depletion curves for all three species were steeper with older than young plants (Figures 2.3a-c). Reductions in the rate of P and K absorption with increasing age have been recorded for a number of species (Edwards and Barber, 1976; Fageria, 1973; Anghinoni et al., 1981). The P and K uptake rates calculated here were within the ranges previously calculated for wheat (see Anghinoni et al., 1981) and 18 to 39 day old corn (Zea mays) Warnicke and Barber, 1974). Both increases and decreases in Imax (Vmax) and Km values with plant age were reported in the studies of Anghinoni et al. (1981) and Fageria (1973). Anghi noni et al. also found a lower Km value for K uptake in wheat than in various other species. He stated that the crop usually shows little response to K fertilizer additions and suggested that this may be partly due to the low Km value. In this report the crop was less affected than the weeds by K deficiency both in competition and pure stands and thus may be related to a lower Km, since this indicates efficiency in the absorption of the element at low external concentrations.

It is clear from the results that no general rule can be applied relating to the nutrient uptake status of the crop and the two weeds, since the situation differs for the two nutrients studied. In addition the studies of Johnson (1987) and Tarawali (1983) in this laboratory have shown that the grass weed Alopecurus myosuroides (blackgrass) shows lower values than wheat in the low concentration range for both P and K when uptake of radioactive tracers by excised roots is followed.

6.8 Conclusion

There is little or no published information on the connection between P or K ion concentration in the external medium and the uptake isotherms and kinetics of wheat, wild oat and barren brome plants. It has been demonstrated (e.g. Lee, 1982) that the nutritional history of a plant can profoundly affect its subsequent capacity to absorb ions. For example, Cartright (1972) observed that plants absorb phosphate ions more rapidly when the supply is restored after a period of deprivation than do the control plants. It is suggested that the behaviour is due to an increased number of transport sites in the deficient plant. It is also possible that in deficient plants the same number of transport sites may operate more efficiently. The efficiency with which the three present species absorbed P or K from continuously flowing solution may differ due to the affinity of the carrier system for the ion and/or to the total capacity of the carrier system in the root cells.

Nutrient uptake by plants is an active process involving the movement of ions into and across the root. Claassen and Barber (1974) developed a procedure for measuring nutrient uptake kinetics of intact root systems that follow Michaelis-Menten kinetics and values for Vmax and Km were determined by following the rate of nutrient depletion from solution over time. Uptake parameters measured by the depletion procedure have been used successfully to predict uptake of P and K of intact plants growing in soil and nutrient solutions (e.g. Claassen and Barber, 1976; Drew et al., 1984; Becerril-Roman, 1988) and others have used short term experiments using excised roots (e.g. Johnson, 1987; Tarawali, 1983). In the present study attempts to determine these parameters for three species at different growth stages using intact plants growing in continuously slowing nutrient solutions were not successful. Although data from depletion experiments showed some flexibility (see Claassen and Barber, 1974) in that reasonable fits could be obtained using various different equations. They developed a procedure which takes account of both efflux and influx of ions and used this to produce a curve of net ion influx against solution concentration, from which they then derived values for Km and Vmax. In the present experiments, uptake rates at any given time is determined as the negative derivative of the ion concentration in solution (C) with respect to time (T), i.e. the slope of the fitted curve. One difficulty in the present

experiments was that the maximum rate of uptake (Vmax) was not reached. Since the depletion process was continuous under the continuous solution flow system and only one concentration was used only one initial rate could be estimated. In some studies where the starting point of the depletion was at different concentrations, the initial rates only were used to estimate uptake parameters (see Shock and Williams, 1984), because there is doubt that kinetic parameters remain constant as the level of the nutrient in solution declines. However, this approach was criticised (see Mullins and Edwards, 1989) expressly for this reason. Under natural conditions the concentration of an ion in soil solution does not remain constant and kinetic isotherms determined using depletion type procedure would appear to be more realistic in describing the uptake of P and K.

The main objectives of these experiments were to determine various uptake parameters for P and K uptake for the three species and relate these values to their performances in competition at various nutritional levels. Some aspects of the work did not achieve the hoped-for results for reasons explained above. In competition when any two species are competing for limiting P or K, a greater efficiency of uptake will be of a competitive advantage. Such efficiency of a species may be characterised by a low Km value and/or ability to produce greater area of root surface. P uptake rates calculated on a root fresh weight basis at various growth stages clearly indicated that the weeds, particularly barren brome, were more efficient than the crop. The total amount of P removed at any time during the depletion clearly reflected the size of the plants and direct comparisons can thus be misleading. Although the weed was smaller it was nevertheless capable of reducing the initial P concentration in solution to values lower than or similar to those produced by wheat or wild oat. In contrast, the crop showed greater efficiency in K uptake than either weed. Both in competition and pure stands, the crop also showed greater efficiency of K uptake and thus usually contained higher concentrations than either weed. The crop also reduced initial K concentration to zero more rapidly than the weeds which also reflects its apparently higher requirement for the element.

If the kinetic uptake parameters could be estimated from the depletion data they would probably indicate which aspect of the process was the one most important in determining efficiency in relation to a particular nutrient.

The determination of kinetic uptake parameters using the depletion method has been widely used (e.g. Drew et al., 1984) with 'static' nutrient systems. The determination of these parameters from continuously flowing nutrient solution have been successfully achieved for P uptake in rice plants (see Fageria, 1973). Although in the present study attempts to estimate P and K kinetic uptake parameters of the three species on a comparative basis were not successful, the method still has considerable potential. The present study is clearly of a preliminary kind and further improvements are obviously possible and desirable. For example, optimum quantities of circulating solution and roots needed for satisfactory depletion should be predetermined (see Drew et al., 1984; Claassen and Barber, 1974). Shorter periods of depletion (less than 6 hrs) seem to be needed for K with plants grown under low levels of this nutrient. There seems no reason why frequent sampling should not result in satisfactory estimates of the uptake parameters. Data from depletion experiments may be most usefully fitted to the integrated rate equation developed by Claassen and Barber (1974) for the purpose of determining Vmax and Km. In order to compare uptake parameters for various initial concentrations of an element, depletion experiments using the NFT system would have to be designed to include a considerable number of concentrations. The argument suggesting that, even though the orthodox Michaelis-Menten analysis is based on initial rates, an analogous type of reasoning may be applied to uptake rates other than initial rates has much to commend it. Further work to establish the validity of conclusions drawn for such experiments would be of great value.

SECTION III

SECTION III

Some studies on the competitive abil ity of *Avena fatua*, *Bromus sterilis* and wheat

7.1 ABSTRACT

Investigations conducted in this section relate to the competitive ability of the three species.

Differences in the responses of the species to increases in their densities and applied phosphorus were obvious. Barren brome was the most sensitive and wild oat the least to intra-specific competition especially at early stages of growth and this sensitivity was greater at lower than at higher P levels.

When the crop was surrounded by increasing number of plants of either weed its dry matter and nutrient concentrations and contents were generally affected linearly by both weeds. The dry matter yield of the crop was less reduced in the presence of barren brome plants than wild oat, whilst the opposite was true with its P, K, Ca and Mg concentrations, suggesting that the weeds compete for different resources.

Competitive relationships between the three species were also investigated using replacement series techniques with variations in the levels of P and K. Dry matter yields, P, K, Ca and Mg concentrations and their total contents, relative yields (RYs) and relative yield totals (RYTs), relative crowding coefficients and their products indicated that the competitive order of the species in general could be summarised as WO W BB when they compete for P. This order was W WO BB when the object of competition was potassium in the medium.

These differences in the competitive abilities of the species are discussed in relation to their observed differences in growth, root morphology and efficiencies of nutrient uptake and utilization noted in the various sections of the thesis.

SECTION III

7.1. Introduction

Competition arises when one individual is sufficiently close to another to modify its soil or atmospheric environment and thereby decrease its rate of growth (Milthorpe, 1961). The factors which affect plant growth are nutrients, light and soil moisture and intra- and interspecific competition occurs when one or more of these factors is limiting. The proximity of individuals also brings about changes in the environment as a result of the production of chemicals which may be released into the soil. Where these are toxic the resulting effect on nearby plants is known as allelopathy (Rice, 1984).

The competition between crops and weeds depends on their relative densities. The effects of different weed species on the crop depends on their competitive abilities. The magnitude of crop yield depression depends on the extent and duration of competition. Generally, as weed populations increase, crop yields are reduced proportionately, but low infestations may suppress yields (Kira et al., 1953; Staniforth and Weber, 1956; Nelson and Nylund, 1962; Wilson and Cole, 1966; Wells, 1979). The period during which weeds are most competitive depends partly on the growth habit of the weeds. Weed competition during the early growing season usually depresses crop growth more than competition at any other time (Dawson, 1964). Weeds which emerge with the crop are generally most competitive (Nelson and Nylund, 1962).

The competition of species for nutrients and moisture occurs in the root zone and therefore roots are important in determining the competitive ability of plants. Weed species that develop extensive root systems tend to be strong competitors. For example, Blackman and Templeman (1938) grew wheat (Triticum aestivum L. var. Marquis) and wild oat (Avena fatua L.) under dry farming conditions and found the weed had developed a more extensive root system than the crop 22 days after emergence. Earlier, Pavlychencko and Harrington (1934) listed wild oat as a serious competitive weed and wheat as a moderately competitive cereal. Under low N and P soil levels, Bell and Nalewaja (1968b) reported that wild oat densities of 70 and 160 seedlings/square yard caused wheat yield reductions of 23.3% and 47.6% respectively. The competitive

ability of wild oat was attributed to the more extensive root system of the weed. Friesen (1960) also reported that a wild oat density of 135 plants/square yard reduced wheat yields by 77.5% when compared to a density of 14/square yard. A number of investigators (e.g. Blackman and Templeman, 1938; Smith, 1967) reported that good crop stands and high levels of nitrogen tended to minimise competitive effects of weeds on crops. Evidence is also available that phosphate fertilization stimulated weed growth and increased competition (e.g. Vengris et al., 1955). Weeds are generally less sensitive to low soil potassium than crops, although they respond to amounts applied additionally (Qasem, 1987). Since weeds respond to added nutrients in general, there is some evidence that increasing levels of fertilizer supply to the crop may not provide a benefit except where weed densities are low. For example, studies with wild oat (A. fatua L.) in wheat have shown that both plants responded similarly to fertilizer application and no additional yield reduction took place where higher levels of fertilizer were used (Thurston, 1959). However, a number of experiments (e.g. some cited in Zimdahl, 1980 ch. 7) have emphasised that weeds usually absorb fertilizers faster and in relatively larger amounts than crops.

Many authors have studied competition in an attempt to determine the relative competitive abilities of species found in association. This has usually been done in two-component mixtures (e.g. Harper and McNaughton, 1962; de Wit et al., 1966; Hall, 1974a; Tarawali, 1983; Johnson, 1987; Qasem, 1987). Mixtures of three or more species are rarely investigated due partially to the difficulties in interpretation. Exceptions are Haizel and Harper (1973), Mack and Harper (1977), Chestnutt et al. (1980). Plant competition studies which involve multispecies mixtures reflect true field situations and may give results that can be extrapolated with less danger of erroneous conclusions than may be the case with two-species mixtures. Similarly, problems exist in extrapolating from pot glasshouse experiments to field conditions.

A limited number of experimental designs have been regulary used in studies of plant competition. The two principal types are substitutive and additive.

(1) Substitutive (Replacement Series) Design:

The replacement method compares the performance of species in mixtures with that in pure stands. It involves the planting of two

species in varying proportions at constant overall density. It assumes that yield is either independent of density (de Wit, 1960) or directly proportional to density (McGilchrist and Trenbath, 1971). A major disadvantage of this design is its artificiality since natural species mixtures are almost invariably additive (Johnson, 1987). Joliffe et al. (1984) argued that comparisons with expected yields as done in replacement series experiments are of limited usefulness since they do not assess the contributions of intraspecific interference to the determination of mixture yields. More recently Connolly (1986) pointed out one of the major difficulties with replacement series experiments. He stated that "the fundamental difficulty with replacement series method stems from ignoring the two-dimensional nature of mixtures, the density of both species being independently variable. A replacement series consists of points on a one-dimensional line in this two-dimensional mixed density plane. Selection of a particular replacement line carries the risk of confounding effects of the two densities. Any interaction between competition and density remains undetected and the results depend critically on the exact mixtures used". The other point about which Connolly was seriously critical was that the replacement method is particularly prone to difficulties in mixing species of different sizes. This usually tends to favour the larger species. Several studies have shown that the ranking of competitiveness is correlated with the ranking of average plant size or total abundance of the neighbour or competitor species (e.g. Obeid, 1965; Connolly, 1986; Miller and Werner, 1987; Goldenberg and Fleetwood, 1987). A number of other experimenters have also criticised the design on different grounds (e.g. Harper, 1977; Austin et al., 1988; Wright, 1981; Firbank and Watkinson, 1985).

In replacement series experiments aspects of the impact of interspecific competition relative to intraspecific competition are measured (de Wit, 1960). In his derivation of the theory of replacement series, de Wit first considered wide-spaced plants where neither intra- nor interspecific situations would occur and simple relationship exists between yield and species proportions or planting densities. However, at higher densities interactions may occur which create a more complex situation. In cases where two species have equal competitive ability, he concluded that yield would be linearly related to species proportions. Later Willey (1979) called these linear trends 'expected yields' and interpreted any deviation from the 'expected yields' as being the outcome

of unequal competitive ability of the two species. In the conventional interpretation of replacement series experiments the concept of 'expected yields' has been widely used as a reference.

The most significant aspect of de Wit's replacement series technique was that interactions between species were analysed graphically in replacement diagrams and mathematically through indices such as the Relative Yield Total (de Wit and van den Burgh, 1965), the Relative Crowding Coefficient (de Wit, 1960), Aggressivity (McGilchrist and Trenbath, 1971) and Competitive Ratio (Willey and Rao, 1980).

(i) The Relative Yield Total (RYT):

De Wit (1960) and De Wit and Van den Burgh (1965) introduced the concept to measure niche differentiation between component species. In calculating RYT, yields of respective component species were first converted to relative yields (RY) by dividing yield of the species in mixture by their yields in monoculture and then the relative yields added. Using wheat (w), wild oat (wo) and barren brome (bb), as examples, the relative yields of wheat (Rw), wild oat (Rwo) and barren brome (Rbb) and their relative yield totals when grown in any two species combinations can be expressed as follows:

(1) $RYW = \frac{Owwo}{MW}$; $RYWO = \frac{Owow}{mwo}$; $RYTa = RYW + RYWO$

(2) $RYW = \frac{Owbb}{MW}$; $RYbb = \frac{Obbw}{Mbb}$; $RYTb = RYW + RYbb$

(3) $RYWO = \frac{Owobb}{MWO}$; $RYbb = \frac{Obbwo}{Mbb}$; $RYTC = RYWO + RYbb$

where: Owwo, Owbb = the yields of wheat in mixture with wild oat and barren brome respectively; Owow and Owobb = yields of wild oat in mixture with wheat and barren brome respectively; Obbw and Obbwo = yields of barren brome in mixtures with wheat and wild oat respectively; Mw, Mwo and Mbb = the monoculture yield of wheat, wild oat and barren brome respectively. RYTa, RYTb, and RYTc = the relative yield totals of wheat and wild oat, wheat and barren brome and wild oat and barren brome respectively. The relative yield provides one of the simplest measures of competitive interference. In a mixture, the species with the higher RY tends to dominate. The use of RY overcomes the difficulty of comparing the performance of different species in absolute yields (Van den Burgh, 1968). If RYT = 1.0, this implies that the two species are

making demands on the same limiting resource of the environment i.e. crowding for the same space (de Wit, 1960) and they are mutually exclusive. RYT 1.0, suggests that the species make different demands on resources, and avoid competition with each other, or the gain by one exceeds the loss by the other, or both species are benefiting from the relationship i.e. non-competitive interference (Hall, 1974a). RYT 1.0, implies that there is some kind of mutual antagonism. This can occur in situations where a species produces a chemical that inhibits the growth of the other species e.g. allelopathy.

The competitive effects of component species in replacement series experiments can be examined from replacement diagrams (e.g. Harper, 1977; Willey, 1979; Willey and Rao, 1980; Tarawali, 1983; Johnson, 1987). These diagrams are drawn from the relative yields of the competing species and their relative frequencies.

In cases where two species have equal competitive ability, the yield is linearly related to species proportions i.e. the species are not affected by mixing. Under these circumstances, intra- and interspecific competition are of the same magnitude and yield of the mixtures equals that of the pure stand and the relative yield total approximates to 1.0. Any deviation from RYT=1.0, is interpreted as the outcome of unequal competitive ability of two species in the mixture.

Since the introduction of the replacement series designs numerous experimenters have used them because the interpretation of results is simple. For example, the methodology has been widely used in agronomy (e.g. Willey, 1979; Mead and Riley, 1981), plant competition studies (de Wit and van den Burgh, 1965; Hall, 1974a, b,; Harper, 1977; Joliffe et al., 1984; Tarawali, 1983; Johnson, 1987), in animal ecology (Ayala, 1971) and animal production (Nolan and Connolly, 1977).

(ii) The Relative Crowding Coefficient (K):

The relative crowding coefficient, like the relative yield total, is a mathematical derivative commonly used in the interpretation of results of competing species in the replacement series model. It was also proposed by de Wit (1960) to determine the competitive power of species and examined in detail by Hall (1974a and b). De Wit used the mean yield per plant of component species to determine relative crowding coefficient (K). Later Bakhuis and Kleter (1965) introduced another method of

estimating the relative crowding coefficient, based on the relative frequency of the species in the mixture rather than mean yield per plant. This method was more widely used by numerous investigators than that of de Wit e.g. Hall, 1974a and b; Gray, 1981; Tarawali, 1983; Firbank and Watkinson, 1985; Frankow-Lindberg, 1985; Bhaskar and Vyas, 1986.

According to this model, the relative crowding coefficients of wheat, wild oat and barren brome grown in two species combinations may be given by:

$$(1)\quad Kwwo = \frac{Owwo \cdot Zwo}{(Mw - Owwo)Zw},$$

$$(2)\quad Kwow = \frac{Owow \cdot Zw}{(Mwo - Owow)Zwo}$$

$$(3)\quad Kwbb = \frac{Owbb \cdot Zbb}{(Mw - Obb)Zw}$$

$$(4)\quad Kbbw = \frac{Obbw \cdot Zw}{(Mbb - Ow)Zbb}$$

$$(5)\quad Kwobb = \frac{Owobb \cdot Zbb}{(Mwo - Obb)Zwo}$$

$$(6)\quad Kbbwo = \frac{Obbwo \cdot Zwo}{(Mbb - Owo)Zbb}$$

where Zw, Zwo and Zbb are the relative frequencies of wheat, wild oat and barren brome.

The relative frequency (Zw, Zwo or Zbb)=

$$\frac{\text{density of species in mixture}}{\text{density of species in monoculture}}$$

The sum of relative frequencies is always equal to 1.0. The values of relative crowding coefficients (K) for each species and their products are used to describe the level and type of interference occurring between two species grown in association. If a species has a coefficient less than, equal to, or greater than 1.0, it means it has produced less yield, the same yield, or more yield than expected respectively. The component species with higher coefficient is the dominant one (Willey, 1979). De Wit (1960) stated that when two species compete for the same space (competitive interference) the product of their relative crowding coefficient for yield should equal 1.0, and the two species are mutually exclusive. If their product is greater than 1.0, although they may still

be competing for the same resource(s), they are also competing for different resources, i.e. non-competitive interference is taking place. When the product of the relative crowding coefficients of the two component species is less than 1.0 this suggests an inhibitory mechanism in operation (Hall, 1974a and b). Thomas (1970) published a computer programme for calculating relative crowding coefficients of component species based on the method of least squares.

The relative crowding coefficient of species I, with respect to J and also be simply calculated from:

$$\frac{\text{Mean yield per plant of I in mixture}}{\text{Mean yield per plant of J in mixture}} \Big/ \frac{\text{Mean yield per plant of I in pure stand}}{\text{Mean yield per plant of J in pure stand}}$$

A ratio diagram similar to the replacement series diagrams can also be used to examine and describe the competitive relationships of two competing species. The ratio of the yields of two species in a particular association in replacement series may be plotted against the ratio of their relative frequencies, both axes being on a logarithmic scale, i.e. to produce a ratio diagram, log Owwo/Owow is plotted against log Zw/Zwo.

5(iii) Aggressivity (A):

The relative competitive ability of species and populations in replacement series mixtures is also measured by 'aggressivity' (McGilchrist and Trenbath, 1971). Aggressivity gives a simple measure of how much the relative yield increase in one species (a) is greater than that for species (b). For any replacement series treatment, the general formula for aggressivity was given by Willey (1979) as:

$$Aab = \frac{\text{mixture yield of a}}{\text{expected yield of a}} - \frac{\text{mixture yield of b}}{\text{expected yield of a}}$$

If the value of (A) is equal to zero, this means that the component species are equally competitive; a positive numerical value of (A) indicates dominance of a species whereas, the dominated species will have an (A) value which is negative. A number of investigators have used this index to determine the competitive power of species (e.g. Martin and Field, 1987).

The main theme of the experiments reported here was to determine the competitive abilities of the species under consideration. The other specific objectives were:

(1) To determine the responses of wheat, wild oat and barren brome to increase in the densities of their own plant populations i.e. to measure intraspecific competition in these species.

(2) To determine their responses to increase in the density of one species on the yields of the other species (i.e. to measure the effects of interspecific competition).

(3) To determine the nature of competition among these species using de Wit's (1960) model i.e. to examine whether the species compete for limited resource(s) or escape competition due partly to niche differentiation (Hall, 1974a, b).

(4) To determine the effects of the competing species (i.e. wild oat and barren brome) on the yield of the indicator plant (wheat) and thereby determine which weed is the more vigorous competitor.

(5) To assess the contributions of P and K concentrations in determining the relative yields of the species and the outcome of competition of these species.

(2) Additive Experimental Design

In these designs the density of an indicator or target species is held constant and the density of an associate or neighbour species varied. The density of the plants in the mixtures is greater than in the monoculture. There is a problem of interpretation of results with these experiments, because the effects of total plant density (crop+weed) and of weed density on the weed or the crop are confounded. However, despite this major difficulty, additive experiments have the advantage that they can simulate accurately the real situation of a crop planted at fixed density, infested with weeds. The most significant aspect of the additive series experiments is that they are used to compare the relative aggressiveness of a group of species to the indicator. In its simplest form an additive experiment becomes a phytometer experiment (Clements and Goldsmith, 1924) in which a single indicator plant is placed in a stand of a second species. In the present experiments, wheat was used as an indicator (surrounded species) with wild oat, and barren brome as

competitors (i.e. the surrounding species). The magnitude of competition and the ability of the two weeds to compete were determined in terms of the ability of the crop to produce dry matter and nutrient yields. Such experiments have been widely used in studies relating to the competition of a group of species to compare their mutual aggressiveness (e.g. Obeid, 1965; Bell and Nalewaja, 1968; Chancellor and Peters, 1974; Cousens et al., 1988; Johnson, 1987).

Two types of additive designs can be recognised in the literature for two-species competition experiments.

(i) Additive, equal proportions (Austin and Austin, 1980), where the density of one species in the mixture is constant and equal to the density in monoculture.

(ii) Additive, unequal proportion (Harper, 1977), where the density of one species is kept constant and that of the other is varied (e.g. Johnson, 1987).

The ability to compete for a given resource might be expected to change according to its availability, i.e. some plants may be better competitors when a resource is plentiful, others when it is in short supply (Mahamoud and Grime, 1976). In competition studies soil nutrient levels have frequently been included to see if the competitive abilities of species would change significantly. A number of investigators added fertilizers in order to offset crop losses from weeds by increasing the competitive ability of the crop studied (Blackman and Templeman, 1938; Thurston, 1959a; Welbank, 1963; Bell and Nalewaja, 1968b; Barrett and Campbell, 1973; Wells, 1979). However, there is still some controversy over the effects of fertilizer application on crops and weeds since conflicting results were reported. In the experiments in this section the competitive abilities of wild oat and barren brome were studied in relation to the effect of weed density and three levels of phosphorus on biomass and nutrient yields of wheat. Biomass production was found to be approximately linearly related to the uptake of that resource which limits growth, so that the distribution of the limiting resource among the plants is reflected in their biomass (Spitters, 1983). The effect of density on dry matter yield in pure stands (intraspecific competition) was also studied at two levels of phosphorus. Several equations have been used to describe the relationship between plant density and dry matter production (e.g. de Wit, 1960; Willey and Heath, 1969; Wright,

1981; Johnson, 1987). A number of investigators used the linear regression model to estimate yield losses in crops due to weed infestation as well as to compare the competitive ability of weeds (e.g. Aspinal and Milthorpe, 1959; Dew, 1972; Spitters, 1983; Cousens, 1985; Firbank and Watkinson, 1985; Johnson, 1987).

The relationship between dry matter yield and density of a plant species grown in pure stand was described by Willey and Heath (1969) as $Y = N/(b0\ b1N)$, where y = yield in gm^{-2}, N = plant density in numbers m^{-2} and b0 and B1 = constants. The average weight per plant was described as $W = Y/N = \frac{1}{(b0+b1N)}$ where w = weight in g $plant^{-1}$. The relation between yield of a given crop and the population density of a competing weed may be expressed in the form of a simple basic regression equation: $Y = b0 + b1N$, where y is yield, N is a measure of the weed population, b0 is the Y intercept, a constant, and b1 is the regression coefficient of Y on N. Dew (1972) proposed the use of the square root transformed values for the independent variable, N in order to obtain linearity.

$$Y = bo + b1\ N$$

The relative goodness of fit of each equation is estimated by correlating Y with X (predicted yield). Spitters (1983) proposed the reciprocal form:

$1/Y = b0 + bN$ The regression coefficients b0 and b1 in this model have biological meanings. As N approaches zero, 1/Y approaches the y intercept b0 and thus 1/b0 is the reciprocal of the biomass of an isolated plant given by interpolation and is greater than the observed biomass. The slope b1 measures how 1/Y increases, and hence how the per-plant weight Y decreases with any plant added to the population. The ratio b1/b0 expresses this increase of 1/Y relative to its value without competition, so that it may be used as a measure of competitive stress.

The ratio b1/b0 was also proposed as an index of competition to estimate loss due to the weed (Dew, 1972) when weed and crop populations and the dates of emergence are known. This ratio also gives a numerical value to the competitive ability that is unique for each weed and crop combination.

Wright (1981) extended the use of the linear relationship of the reciprocal of plant weight to density of two species mixtures. He found

the following model provided an adequate fit to the data and accounted for the effects of intra- and interspecific competition in additive series experiments which include both pure and mixed stands of two species.

Ya = Pa/(Aa+BaaPa+BabPb), where Pa and Pb are the densities of the two species A and B; the coefficients Baa and Bab represent the intra- and interspecific effects of increasing density, respectively; Ya is the yield of species A and 1/Aa is the extrapolated expected yield at low density. Spitters (1983) also proposed a multiple linear regression model for estimating both intra- and interspecific competition in crop-weed mixtures. The reciprocal of the per-plant weight was also used, and to estimate the regression coefficients and their standard errors he recommended the weighted multiple regression.

The results of the experiments in this section were analyzed by the simple linear regression model to establish the relationship between the reciprocal per plant weight of wheat and wild oat or barren brome and the resulting values of the regression coefficients were used to estimate competitive abilities of the two weeds. The data for dry matter production of species both in pure and mixed stands were also subjected to analysis of variance.

Orthogonal contrasts were also used to compare different treatments of weed-crop density interactions, as was done by Johnson (1987).

7.3. Materials and Methods

Competition experiments were carried out in 15 cm (6") pots in the College glasshouses. The growth medium was free of nutrients and consisted of medium grade peat (70%), coarse grit (20%) and river sand (10%) (all percentages are by volume). Because of the low pH of the peat the mixture contains lime to raise it to values between 5.8-6.2. The germination of all three species was carried out in a medium comprising only peat and grit (3:1). Before sowing, wild oat seeds were treated with 50% H_2SO_4 as in Section I. Preliminary germination tests and observations on subsequent stages of growth of wheat, wild oat and barren brome suggested that although all appeared at about the same time, wheat and wild oat grew faster up to the transplanting stage. Therefore,

barren brome seeds were sown up to five days earlier than the other two species in all these experiments. Transplanting was carried out when all species reached the 1-2 leaf stage. The plants did not receive any nutrients prior to transplanting and were watered with distilled water only.

Two substitutive and three additive experiments are reported in this section and details of the plant nutrients used are given later for each experiment. Phosphorus and potassium were chosen as factors to examine in competition. The Long Ashton nutrient recipe, based on nitrate nitrogen (Hewitt et al., 1975) was used. The different phosphorus and potassium concentrations were obtained by reducing the amounts on $NaH_2PO_4 \cdot 2H_2O$ and KNO_3 respectively. The reduced nitrate was replaced using $NaNO_3$. Treatments were applied weekly beginning two weeks after transplanting. The application of other elements started one week after transplanting and individual pots received 100 ml of nutrient solutions weekly. Distilled water was used for watering the pots as required between nutrient applications. The plants were sprayed when necessary with Milgo E (Ethirimol) at 5 ml/l against mildew and with Pirimol (Pirimicarb) at 0.5mg/l against aphids.

All experiments had a factorial complete block design. Three blocks were used in experiment 1 and four in the remainder. All experiments except 4 had two harvests and there were thus two pots per plot at the start, one being used for the first harvest. At each harvest, plants were clipped at soil level and shoots of each species separated. The number of tillers was recorded and shoots were then rinsed twice with distilled water. The plants were dried in an oven at 70°C for up to three days. Dry weights were recorded and the dry plant material was ground in a small ball mill to pass through a 0.5 mm sieve. Subsamples of between 150 and 200 mg were put in glass vials and ashed in a muffle furnace at 450-480°C for 4-6 hours. The ashed sample was dissolved in a few drops of concentrated hydrochloric acid and transferred, after dissolution was complete (approx. 10 min.), into a volumetric flask and then topped up to the mark with deionized water. Samples were taken from each solution to determine phosphorus, potassium, calcium and magnesium. Phosphorus was determined colorimetrically by the Vanado-Molybdate method and potassium by flame photometry. Calcium and magnesium were determined by atomic absorption spectrometry. The replacement series data so collected for the different plant attributes were used to

calculate relative yields (RY), relative yield totals (RYT) (de Wit, 1960) and the crowding coefficient (K) (de Wit, 1960; Bakhuis and Kleter, 1965). The data obtained from the additive experiments were used to calculate the relative aggressivity index (McGilchrist and Trenbath, 1971) and regression coefficients (Spitters, 1983). Details of these methods of estimating competitiveness of species in mixtures also were given by Johnson (1987).

Additive Experiments:

Experiment 3.1 The Effect of population density and phosphorus level on the vegetative growth of wheat, wild oat and barren brome

Seeds of the three species were sown simultaneously on 28/6/88. Ten days later seedlings were thinned to give densities of 1 (D1), 4 (D4), 8 (D8) and 16 (D16) plants/pot. Two phosphorus levels (L1 = 20.5 and 2.0 ppm P) were prepared and applied at 100 ml/pot/week. The Long Ashton nutrient solution based on nitrate nitrogen was used with appropriate modifications to obtain the two phosphorus levels. Two harvests were made two weeks apart starting 6 weeks after direct sowing to the pots. The overall mean temperatures of the cubicle up to the last harvest were 27.3, 15.2 and 2.12°C for maximum, minimum and mean respectively.

Experiments 3.2 and 3.3 The effects of weed density and P level on the yields of the crop and the weeds

The effects of phosphorus and the density of the weeds on the performance of the crop were studied in two pot experiments in the glasshouse. The first was conducted during the period 17/6/87-30/7/87. Barren brome seeds were sown on 2/6/87 and those of wheat and wild oats on 6/6/87. All species were transplanted on 17/6/87. At the time of transplanting a single wheat seedling was planted at the centre of each pot and was surrounded by increasing numbers of either wild oats or barren brome. A wheat plant by itself was also included as a treatment. Seven planting densities were thus produced:

(D1) - 1 wheat per pot
(D2) - 1 wheat and 1 wild oat per pot
(D3) - 1 wheat and 3 wild oat per pot
(D4) - 1 wheat and 5 wild oat per pot
(D5) - 1 wheat and 1 barren brome per pot

(D6) - 1 wheat and 3 barren brome per pot

(D7) - 1 wheat and 5 barren brome per pot

Three levels of phosphorus were used:

(L1) 0.645 mM (10 ppm P)

(L2) 0.258 mM (8 ppm P)

(L3) 0.0645 mM (2 ppm P)

Harvests were taken four and six weeks after transplanting. The maximum, minimum and mean overall temperatures were 26.7, 16.9 and 21.8°C respectively.

The second experiment (Experiment 3) was begun on 28/10/87. Barren brome seeds were sown five days earlier than wheat and wild oats. The same planting densities and phosphorus levels were applied as in experiment 2. The only difference between experiment 2 and 3 lies in the medium used to grow the species. In experiment 3 plants were grown in a natural soil of the 'Winchester Series' collected from open hilltop grazing land near the College. Between 2 and 4 cm of soil was gathered after about 4-5 cm turf had been removed. The soil was spread on the glasshouse floor and left to dry with the help of a hot air fan. The dry soil was crushed and sieved twice to pass through 9.5 and 5.0 mm wide meshes. Samples were taken from the sieved soil and sent to the Agricultural Development and Advisory Service for analysis of some soil properties, particularly pH and phosphorus status. The results of the analysis showed that the soil had a pH of 5.5, phosphorus at 4 ppm (0.129 mM) and potassium 51 ppm (1.308 mM) (soil dry weight basis). The concentration of calcium was given in terms of lime requirement and this was 3 tonnes/ha of ground chalk. However, no lime was added to the soil in this experiment. The sample was rich in magnesium (174 ppm or 7.250 mM). The soil was mixed 3:1 with river sand and the final pH of the mixture was 5.37. A few plants of all species, but especially wheat, failed to thrive or died just after transplanting and were replaced. Any death of plants occurring more than two weeks after transplanting was not replaced and plots thus affected were treated as 'missing values', estimates of which were obtained from the statistical analysis. All pots were sprayed with Filex (propamocarb hydrochloride, 1.5 ml/l) against damping-off disease on the 13th November 1987. Initially it was not intended to use artificial light in this experiment due to the difficulty of maintaining an even distribution over the pots spread over a large

area. However, plants showed such slow growth that additional light was introduced five weeks after transplanting for ten hours every day. This was provided by suspending 400 watt high pressure mercury fluorescent lamps approximately 145 cm above the level of the pots. A total of approximately 16 hrs light was maintained and the average daily maximum, minimum and mean air temperatures of the cubicle up to the last harvest were 21.6, 13.4 and 17.5°C. Two harvests were taken at 11 and 14 weeks after transplanting and all pots were harvested for tiller number, dry matter and nutrient yields.

Substitutive Experiments:

Experiment 3.4: Replacement series at different P levels

Wild oats, barren brome and wheat were transplanted on 17-18/3/87. The three species were grown both in pure stands and mixtures at a constant overall density of six plants per pot in a replacement series. Two species at a time were combined in different planting proportions to give twelve treatments in all:

(1) $\frac{\text{Wheat (W)}}{\text{Wild oat (WO)}} = \frac{6}{0} ; \frac{4}{2} ; \frac{3}{3} ; \frac{2}{4} ; \frac{0}{6}$

(2) $\frac{\text{Wheat (W)}}{\text{Barren brome (BB)}} = \frac{4}{2} ; \frac{3}{3} ; \frac{2}{4} ; \frac{0}{6}$

(3) $\frac{\text{Wild oat (WO)}}{\text{Barren brome (BB)}} = \frac{4}{2} ; \frac{3}{3} ; \frac{2}{4}$

Two phosphorus treatments were applied.

(L1) 0.645 mM (20 ppm P)

(L2) 0.0645 mM (2 ppm P)

The two harvests were taken at five and seven weeks from transplanting.

The cubicle air temperatures were recorded hourly during the entire period of the experiment. The daily overall maximum, minimum and mean temperatures were 26.7, 14.5 and 20.6°C respectively.

Experiment 3.5: Replacement series at different K levels

Barren brome seeds were sown on 5/4/87 and those of wheat and wild oats on 9/4/87. All species were transplanted on 19-20/4/87. The number of plants per pot were six as in Experiment 2. The combination of two species in various proportions produced nine replacement series mixtures.

(1) $\frac{\text{Wheat (W)}}{\text{Wild oat (WO)}} = \frac{6}{0} ; \frac{4}{2} ; \frac{2}{4} ; \frac{0}{6}$

(2) $\frac{\text{Wheat (W)}}{\text{Barren brome (BB)}} = \frac{4}{2} ; \frac{2}{4} ; \frac{0}{6}$

(3) $\frac{\text{Wild oat (WO)}}{\text{Barren brome (BB)}} = \frac{4}{2} ; \frac{2}{4}$

Three different potassium treatments were applied.

(L1) 4.0 mM (156 ppm K)
(L2) 1.0 mM (39 ppm K)
(L3) 0.5 mM (18.5 ppm K)

Harvests were made at four and six weeks after transplanting.

The cubicle air temperatures were recorded hourly during the entire period of the experiment. The daily overall maximum, minimum and mean temperatures were 27.8, 17.8 and 22.8°C respectively.

7.4. Additive Experiments

7.4.1 Results

Experiment 3.1: The effects of population density and phosphorus level on the vegetative growth of wheat, wild oat and barren brome

Tiller number/pot

The level of phosphorus and plant population density significantly affected mean tiller number in the three species at both harvests (Tables

In the case of interactions the value of the LSD is only given where effects are significant at P 0.05

Table 3.1 Tiller production (total tillers/pot) of wheat, wild oat and barren brome in response to plant density and phosphorus levels (harvest 1)

Population density (plants/pot)	Wheat P level L2	L1	Mean
1	7.0	21.3	14.15
4	14.7	51.0	32.85
8	16.8	60.3	38.55
16	25.3	84.1	54.70
Mean	15.95	54.18	

	LSD P < 0.05	P < 0.01
Density	6.86	9.62
Phos level	4.86	6.82
Interaction	9.72	13.64

Population density (plants/pot)	Wild oat P level L2	L1	Mean
1	3.33	7.00	5.17
4	7.00	21.67	14.14
8	12.03	28.03	20.03
16	17.33	37.33	27.33
Mean	9.92	23.51	

	LSD P < 0.05	P < 0.01
Density	4.42	6.20
Phos level	3.13	4.38
Interaction	6.25	8.77

Population density (plants/pot)	Barren brome P level L2	L1	Mean
1	4.33	13.33	8.83
4	16.00	39.67	27.84
8	23.71	71.01	47.36
16	39.04	86.72	62.88
Mean	20.77	52.68	

	LSD P < 0.05	P < 0.01
Density	5.93	8.30
Phos level	4.19	5.88
Interaction	8.38	11.76

3.1 and 3.5). For each species and density the effect of phosphorus was markedly different, and at the higher P level all densities of a given species differed from each other, but at the lower level this was not true.

The mean tiller number between densities differed significantly except for wheat between D4 and D8 at both harvests and for wild oat at the 2nd harvest between these two densities. Similarly tiller number/pot in barren brome did not differ for D8 and D16 at the 2nd harvest, and at the lower P level fewer tillers were actually produced at D16 than D8, though the difference between the two densities did not reach statistical significance. This may indicate higher intraspecific competition amongst plants of this weed.

Dry matter yield

Analysis of variance performed on the data for dry matter showed that effects of both P and density were significant for the three species at both harvests (Tables 3.2 and 3.6). For a given density, the amount of dry matter differed significantly with P level. The differences among densities within a P level differed with species, harvest and the level of P. In the crop intra-specific competition was more intense at the lower P level than at the higher. At the first harvest differences between means of all the densities were significant. At the higher P level all densities were also different from each other, whilst those at the lower were not. At the 2nd harvest the means for D1 and D4 also were not different at the higher P and at the lower level none of the densities were significantly different from each other, although the means for P and densities were. Similar results were noted for wild oat, except that the means for D4 and D8 were not different for dry matter accumulation at either harvest, indicating higher tolerance to intraspecific competition than wheat.

In barren brome, dry matter accumulation at the lower P did not differ between densities at either harvest. At the higher level differences were observed at the first harvest, but by the 2nd harvest these also disappeared, emphasising intensive competition amongst plants of the weed.

The dry matter data for each species were also subjected to analysis by linear regression of the reciprocal per plant weight on plant density

Table 3.2 Shoot dry matter production (g/pot) of wheat, wild oat and barren brome in response to plant density and P levels (Harvest 1)

Population density (plants/pot)	Wheat P level L2	L1	Mean
1	4.22	8.33	6.28
4	5.11	10.45	7.78
8	6.08	13.04	9.56
16	6.72	16.53	11.63
Mean	5.53	12.09	

	LSD P < 0.05	P < 0.01
Density	0.86	1.20
Phos level	0.60	0.85
Interaction	1.21	1.70

Population density (plants/pot)	Wild oat P level L2	L1	Mean
1	4.41	7.41	5.91
4	4.89	11.69	8.29
8	5.89	12.00	8.95
16	7.04	17.92	12.48
Mean	5.56	12.26	

	LSD P < 0.05	P < 0.01
Density	2.22	3.12
Phos level	1.57	2.21
Interaction	3.14	4.41

Population density (plants/pot)	Barren brome P level L2	L1	Mean
1	3.98	5.71	4.85
4	4.60	8.51	6.56
8	4.80	10.51	7.66
16	5.12	12.27	8.70
Mean	4.63	9.25	

	LSD P < 0.05	P < 0.01
Density	1.18	1.65
Phos level	0.83	1.17
Interaction	1.67	2.34

Table 3.3 Regression equations describing the relationship between reciprocal per plant weight and plant density in wheat, wild oat and barren brome (harvest 1)

			r^2	df
L1 (0.645 mM)	wheat (1/Wh)	= 0.127 (±0.0173) + 0.05468 Wh (±0.00189)	0.96	10
	wild oat (1/WO)	= 0.1569 (±0.0301) + 0.05123 WO (±0.00326)	0.75	10
	barren brome (1/BB)	= 0.1426 (±0.018) + 0.07518 BB (±0.00197)	0.94	10
L2 (0.0645 mM)	wheat (1/Wh)	= 0.1594 (±0.0419) + 0.14116 Wh (±0.00456)	0.96	10
	wild oat (1/WO)	= 0.2049 (±0.0729) + 0.13323 WO (±0.00794)	0.98	10
	barren brome (1/BB)	= 0.0937 (±0.0435) + 0.19104 BB (±0.0047)	0.99	10

Values in brackets are the 95% confidence intervals for the intercept and regression coefficients respectively

Table 3.4a Test of significance between regression coefficients

	L1 v L2
Wheat (wh)	17.65***
Wild oat (wo)	10.04***
Barren brome (bb)	19.43***

L1 wh v L1 wo	L1 wh v L1 bb	L1 wo v L1 bb
0.92 NS	7.51***	6.14***
L2 wh v L2 wo	L2 wh v L2 bb	L2 wo v L2 bb
0.87 NS	7.62***	6.26***

Table 3.4b Ratio of regression coefficient to intercept

P level (mM)	wh	wo	bb
L2 (0.0645)	0.886	0.650	2.039
L1 (0.645)	0.431	0.327	0.527

Table 3.5 Tiller production (total tillers/pot) of wheat, wild oat and barren brome in response to plant density and phosphorus levels (harvest 2)

Population density (plants/pot)	Wheat P level L_2	L_1	Mean
1	4.7	32.0	18.35
4	10.8	53.7	32.25
8	12.5	61.1	36.80
16	17.6	69.3	43.45
Mean	11.40	54.03	

	LSD $P < 0.05$	$P < 0.01$
Density	6.51	6.46
Phos level	4.60	9.14
Interaction	9.20	12.91

Population density (plants/pot)	Wild oat P level L_2	L_1	Mean
1	3.0	11.33	7.17
4	11.47	24.13	17.80
8	9.01	28.27	18.64
16	16.00	34.13	25.07
Mean	9.87	24.47	

	LSD $P < 0.05$	$P < 0.01$
Density	3.43	4.81
Phos level	2.42	3.40
Interaction	4.85	6.80

Population density (plants/pot)	Barren brome P level L_2	L_1	Mean
1	24.7	10.7	17.70
4	52.4	17.7	35.05
8	66.7	32.5	49.60
16	72.7	28.8	50.75
Mean	22.43	54.13	

	LSD $P < 0.05$	$P < 0.01$
Density	8.75	12.18
Phos level	6.19	8.69
Interaction	12.36	17.35

Table 3.6 Dry matter production (g/pot) of wheat, wild oat and barren brome in response to plant density and P levels (Harvest 2)

Population density (plants/pot)	Wheat P level L2	L1	Mean
1	4.68	12.04	8.36
4	5.12	11.73	8.43
8	5.92	16.40	11.16
16	6.99	19.79	13.39
Mean	5.68	14.99	

	LSD $P < 0.05$	$P < 0.01$
Phos level	1.28	1.80
Density	1.82	2.55
Interaction	2.56	3.60

Population density (plants/pot)	Wild oat P level L2	L1	Mean
1	4.48	15.64	10.06
4	7.03	19.21	13.12
8	7.07	22.19	14.63
16	9.97	24.32	17.15
Mean	7.14	20.35	

	LSD $P < 0.05$	$P < 0.01$
Phos level	1.44	2.03
Density	2.04	2.87
Interaction	2.89	4.06

Population density (plants/pot)	Barren brome P level L2	L1	Mean
1	3.58	10.55	7.07
4	5.31	12.05	8.68
8	5.28	13.97	9.63
16	6.40	11.57	8.99
Mean	5.14	12.04	

	LSD $P < 0.05$	$P < 0.01$
Phos level	1.78	2.51
Density	2.53	3.55
Interaction	3.58	5.02

Table 3.7 Regression equations describing the relationship between reciprocal per plant weight and plant density in wheat, wild oat and barren brome (harvest 2)

				r^2	df
L2 (0.0645 mM P)	wheat (1/Wh)	= 3.440 (±1.160)	- 0.229 (±0.126) Wh	0.57	10
	wild oat (1/WO)	= 3.52 (±1.42)	- 0.218 (±0.155) WO	0.63	10
	barren brome (1/BB)	= 2.790 (±0.972)	- 0.179 (±0.106) BB	0.57	10
L1 (0.645 mM P)	wheat (1/Wh)	= 8.70 (±1.395)	+ 0.571 (±0.152) Wh	0.54	10
	wild oat (1/WO)	= 11.79 (±1.715)	+ 0.773 (±0.187) WO	0.57	10
	barren brome (1/BB)	= 7.91 (±1.171)	+ 0.537 (±0.128) BB	0.59	10

Values in brackets are the 95% confidence intervals for the intercept and regression coefficients respectively

Table 3.8a Test of significance between regression coefficients

	L1 v L2
Wheat (wh)	4.05***
Wild oat (wo)	4.08***
Barren brome (bb)	4.31***

L2 wh v L2 wo	L2 wh v L2 bb	L2 wo v L2 bb
-0.55 NS	-0.304 NS	1.11 NS
L1 wh v L1 wo	L1 wh v L1 bb	L1 wo v L1 bb
0.90 NS	0.174 NS	1.04 NS

Table 3.8b Ratio of regression coefficient to intercept

P level	wh	wo	bb
L2	0.067	0.062	0.064
L1	0.066	0.066	0.068

following the methods of Johnson (1987) and Spitters (1983). Regression equations describing the relationship between the reciprocal per plant weight, and density for the species are presented in Tables 3.2 and 3.7.

At both harvest and both P levels, the regression coefficients for barren brome were the highest. The coefficient for wheat was also higher than that of wild oat, indicating that intraspecific competition amongst barren brome plants is more intensive than in the other species. Wild oat is the least sensitive to higher densities whilst the crop is intermediate.

Test of significance between regression coefficients within and between species (Tables 3.4a and 3.8a) showed differences and similarities. In all three species, differences in regression coefficients between P levels were highly significant at both harvests. The differences between the regression coefficients of wheat and barren brome, and wild oat and barren brome, were highly significant at both levels of P at the first harvest. The differences between whe)t and wild oat however, did not reach significance at this stage. At the 2nd harvest the regression coefficients did not differ significantly. The ratio between the regression coefficient and the intercept calculated for the species (Tables 3.3b and 3.6b) was highest for barren brome at both P levels. At the 2nd harvest the ratios for the three species were similar at both P levels.

7.4.2. Discussion

In wheat, the mean tiller number/pot diminished at population densities above 4 plants/pot at both stages of growth. In wild oat, however, tiller number significantly increased up to 16 plants/pot at the first harvest. At the second, the number diminished at densities between 4 and 8 plants/pot, but also increased beyond 8 plants/pot up to the highest density. The response of barren brome was different from these two species. At the first harvest the mean tiller number/pot increased linearly up to the highest density. At the second harvest this was true up to 8 plants/pot and increases in the number of plants beyond this level diminished tiller number/pot, and at the lower P level the actual number of tillers/pot at 8 plants/pot was higher than at 16.

The results indicate that density affects the species differently. In the crop, the effect of density stress was shown at earlier stages of growth and at lower density (4 plants/pot) than in the weeds. The results for dry matter yield also suggested that interference amongst wheat plants was more intense at the lower P level than at the higher. This may be because wheat, like other cultivated crops, responds to high levels of nutrients and becomes more competitive with itself than with other plants. When nutrients are limiting, the crop may be expected to suffer from interspecific competition. Johnson (1987) studied the responses of wheat and blackgrass (Alopecurus myosuroides) to P and population density in pot experiments. He reported no increase in dry matter accumulation of the crop above 0.45 mM P at densities of more than 8 plants/pot, whilst the weed showed significant increases above this level. The lack of response in the crop at higher P levels is contrary to the results of the present experiment where the response of the crop to P was an increased dry matter at all densities, especially at earlier stages of growth. At planting the relationship between population density and yield may be assumed to be linear. However, as plants grow, competition begins early in dense populations and more gradually at lower densities.

In barren brome intraspecific competition also began earlier than in wild oat at lower densities and at the lower P level. By the second harvest intraspecific competition in the weed was also operative at the higher P level and the plant showed virtually no increases in dry matter yield with density, or in the number of tillers produced at 16 plants/pot compared with the single plant.

In wild oat intraspecific competition was not as strong as in the other species. At both harvests and P levels differences among densities for dry weight per pot were noted except for D4 and D8. The lack of sensitivity of the weed to increases in density is in agreement with the findings of Haizel and Harper (1971) who reported insensitivity to increases in density in monoculture whilst barley and white mustard (Sinapis alba L.), with which it was compared, were extremely sensitive to density stress. In competition with either of these species, they found wild oat the most sensitive. Unlike wild oat, barren brome might be predicted to be the least sensitive to competition with either of the other two species. In pure stand, the absence of significant effects of density of barren brome plants at the lower level of P at harvests 1 and

2, and at the higher P at the 2nd harvest, shows greater intraspecific competition in the weed than in the other species. For densities higher than 1 plant/pot dry matter yield of the weed did not increase significantly and the yield of 16 plants/pot was similar to the yield of an individual plant per pot. This emphasises the extent of intraspecific competition in the weed and may illustrate the generalisation that, because of similar requirements, members of some species interfere more strongly with themselves than with other species in mixtures.

The sensitivity of barren brome to the presence of plants of its own species may, as suggested earlier, be attributed to its root competition. It has already been noted that barren brome is characterised by finer and denser roots than wheat or wild oat, and may thus explore a given volume of soil more intensively than both these species. It has also been shown that barren brome requires slightly higher P levels for normal growth and may therefore, show higher intraspecific competition for the element, particularly when it is deficient in the growing medium.

In wheat, the weight of a single plant/pot was similar to 8 plants/pot whilst in wild oat, weight of the dry matter yield of 4 plants/pot was similar to 8 plants/pot. The fact that this weed accumulated greater dry matter/pot at higher densities than the other species at similar densities shows its insensitivity to intraspecific competition. It has also been noted that wild oat is unresponsive to P levels in water culture. In the present experiments the response of wild oat to density occurred at both P levels. In competitive situations therefore, wild oat plants may be expected to outcompete the crop or barren brome, especially at earlier growth stages, irrespective of P levels. On the other hand, barren brome may be expected to compete better for limited resources such as P than either species because of its higher requirement for the element and features of its root system. The literature on the interaction of wheat and barren brome is limited whilst that of wild oat and the crop is extensive and is referred to later.

The regression of 1/W on density measures how the per plant weight (w) decreases with each plant added to the populations. The higher the value of the regression coefficient, the greater the reduction in the weight per plant as its density increases. The greater coefficients noted for barren brome than the other species again indicate greater magnitude of intraspecific competition amongst plants of the weed.

The ratios between regression coefficients and the intercepts also showed that values were much higher for barren brome at both P levels. According to Spitters (1983), this ratio expresses the increase in the reciprocal per plant weight relative to its value without competition so that it may be used as a measure of intraspecific stress. Because these values were again higher for barren brome at least at the first harvest, intraspecific competition is greater in the weed than in the other species. Values for wild oat were smaller than for wheat at both P levels and hence suggest insensitivity to intraspecific density stress.

Competition between these species is further investigated in the next experiments where it is shown that barren brome reduced the yield of wheat more than that of wild oat.

3.2 The effects of weed density and P level on the yields of the crop and the weeds

7.4.3. Results

Tiller number/plant

Orthogonal comparisons on the mean tiller number per plant of wheat showed that the two weeds did not differ in their effects on the crop (Table 3.9). Both significantly reduced shoot production in the crop and their effects were linear with increases in density of the weeds.

There was a clear effect of P level on tiller number in the crop. Analysis of variance performed on the data on tiller number per plant of the crop as affected by the density of either weed and P levels showed that effects were significant for both main effects and their interactions (Tables 3.10 and 3.11) At the lower P levels (L2 and L3), tiller number per wheat plant was not significantly reduced by the increase in population density of wild oat, but was significantly reduced by barren brome plants. The significant effect of barren brome on wheat at lower P levels, suggests a greater competitive ability of the weed than wild oat at such levels. The introduction of a single plant of wild oat and barren brome reduced tillering ability of the crop by about 18 and 24% respectively, summed over all P levels.

In tables 3.9, 3.12, 3.15, 3.18, 3.21, 3.24, 3.27, 3.29, 3.31, 3.33 and 3.35

* significant at $P < 0.05$
** significant at $P < 0.001$
*** significant at $P < 0.001$
NS not significant

Table 3.9 Analysis of the effects of weed density and phosphorus level on the yield of wheat (tiller number/plant). Mean of two harvests

	df	SS	MS	VR
Blocks	3	35.041	11.680	-
Treatment (contrasts)				
C v rest	1	291.825	291.825	220.664***
WO v BB	1	1.140	1.140	0.862 NS
WO Linear	1	47.389	47.389	35.833***
WO Quadratic	1	0.149	0.149	0.133 NS
BB Linear	1	79.467	79.467	60.089***
BB Quadratic		1.179	1.179	0.892 NS
L1 v L2, L3	1	61.941	61.941	46.837***
L2 v L3	1	98.971	98.971	74.837***
Deviations	12	147.689	12.307	9.309**
Residuals	57	75.689	1.322	
Total	80	915.552		

Table 3.19. The effects of phosphorus and density on mean no. of tillers/plant of wheat and wild oat. (Mean of two harvests)

Treatments	Phosphorus level L1 W	L1 WO	L2 W	L2 WO	L3 W	L3 WO	Mean W	Mean WO
(D0) W1+WO0	17.25	-	11.75	-	11.12	-	13.37	-
(D1) W1+WO1	13.12	5.00	10.25	3.10	9.23	2.43	10.87	3.49
(D3) W1+WO3	10.00	3.38	6.88	1.88	7.00	2.08	7.96	2.44
(D5) W1+WO5	7.13	3.15	6.50	2.65	4.50	1.44	6.04	2.42
Mean	11.87	3.84	8.84	2.54	7.95	1.98		

	LSD (5%) W	LSD (5%) WO
Phosphorus level	0.866	0.406
Density	0.999	0.406
Interaction	1.731	0.704

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 wild oat plants/pot
D3 = 1 wheat + 3 wild oat plants/pot
D5 = 1 wheat + 5 wild oat plants/pot

Table 3.11. The effects of phosphorus lev l and weed density on mean no. of tillers/plant of wheat and barren brom . (Mean of two harvests)

Treatments	Phosphorus level L1 W	L1 BB	L2 W	L2	L3 W	L3 BB	Mean W	Mean BB
(D0) W1+BB0	17.25	-	11.75		11.12	-	13.37	-
(D1) W1+BB1	13.37	12.37	9.12	8 17	7.75	6.82	10.08	9.12
(D3) W1+BB3	9.75	10.50	7.37	.77	6.90	6.32	8.01	7.87
(D5) W1+BB5	6.38	9.62	6.75	.47	4.37	4.12	5.83	6.41
Mean	11.69	10.83	8.75	5.80	7.54	5.75		

	LSD (5%) W	LSD (5%) BB
Phosphorus level	0.885	0.657
Density	1.021	0.657
Interaction	1.770	NS

D0 = 1 wheat plant alone/pot
D1 = 1 wheat + 1 barren brome plar :s/pot
D3 = 1 wheat + 3 barren brome pla: ts/pot
D5 = 1 wheat + 5 barren brome pla ts/pot

Table 3.12 Analysis of the effects of weed density and phosphorus level on the yield of wheat (shoot dry weight g/plant - mean of two harvests)

	df	SS	MS	VR
Blocks	3	0.7482	0.2494	-
Contrasts (Treatments)				
C v rest	1	7.06794	7.06794	176.225***
WO v BB	1	0.13513	0.13513	3.369 NS
WO Linear	1	2.90002	2.90002	72.306***
WO Quadratic	1	0.00675	0.00675	0.168 NS
BB Linear	1	2.49397	2.49397	62.182***
BB Quadratic	1	0.03286	0.03286	0.819 NS
L1 v L2, L3	1	1.41066	1.41066	35.172***
L2 v L3	1	1.21951	1.21951	30.406***
Deviations	12	14.3209	1.1934	29.753***
Residuals	57	2.28612	0.04011	
Total	80	32.62206		

Table 3.13· The effects of phosphorus level and weed density on mean dry weight of shoots (g/plant) of wheat and wild oat. (Mean of two harvests)

Treatments	Phosphorus level L1 W	L1 WO	L2 W	L2 WO	L3 W	L3 WO	Mean W	Mean WO
(D0) W1+WO0	3.375	-	2.580	-	2.065	-	2.673	-
(D1) W1+WO1	2.110	2.310	1.842	1.145	1.385	1.042	1.779	1.500
(D3) W1+WO3	1.432	1.417	1.337	0.842	1.298	0.805	1.356	1.022
(D5) W1+WO5	1.210	1.522	1.100	1.110	0.867	0.490	1.059	1.041
Mean	2.032	1.750	1.715	1.032	1.405	0.779		

	LSD (5%) W	LSD (5%) WO
Phosphorus level	0.158	0.158
Density	0.182	0.158
Interaction	0.315	0.273

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 wild oat plants/pot
D3 = 1 wheat + 3 wild oat plants/pot
D5 = 1 wheat + 5 wild oat plants/pot

Table 3.14 The effects of phosphorus level and weed density on mean dry weight of shoots (g/plant) of wheat and barren brome (Mean of two harvests)

	Phosphorus level							
	L1		L2		L3		Mean	
Treatments	W	BB	W	BB	W	BB	W	BB
(D0) W1+BB0	3.375	-	2.580	-	2.065	-	2.673	-
(D1) W1+BB1	2.202	0.962	1.700	0.610	1.240	0.500	1.714	0.691
(D3) W1+BB3	1.730	0.820	1.365	0.425	1.255	0.377	1.450	0.541
(D5) W1+BB5	1.275	0.657	1.107	0.305	0.915	0.265	1.099	0.409
Mean	2.146	0.814	1.688	0.447	1.369	0.381		

	LSD (5%)	
	W	BB
Phosphorus level	0.151	0.061
Density	0.174	0.061
Interaction	0.301	0.108

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 barren brome plants/pot
D3 = 1 wheat + 3 barren brome plants/pot
D5 = 1 wheat + 5 barren brome plants/pot

The number of tillers produced by the weeds was also significantly reduced by density and P levels. Interactions were significant in the case of wild oat but not for barren brome (Tables 3.10 and 3.11).

Shoot dry matter yield (g/plant)

Orthogonal comparisons on mean shoot dry matter yield of the crop generally showed that the effects of densities of both weeds were similar (Table 3.12) Data for the effects of the weeds were separately analysed by analysis of variance and showed that the yield of the crop was significantly reduced (Tables 3.13 and 3.14). The introduction of a single plant of either weed reduced the yield of the crop significantly. The effects of both weeds in reducing wheat yield were significantly higher at the highest P level. At lowest P, yield of the crop was more reduced by barren brome than wild oat, again indicating the ability of the first weed to compete for limited P in the medium. In the presence of either weed the crop appeared to be no better a competitor at higher than at lower P.

In both weeds intraspecific competition reduced shoot dry weight significantly and the intensity of competition was higher at lower than at higher P.

Nutrient concentrations (mMol/g dry shoot)

P: Orthogonal contrasts on mean P concentration of the crop indicated no differences between the effects of the weed species or L2 and L3, although L1 was significantly different from the other two P levels (Table 3.15 . Both weed density and P level reduced P concentration of the crop linearly and significantly (Tables 3.16 and 3.17). The effect of barren brome was greater than that of wild oat and in the presence of the former, P concentration in the crop was much lower than when grown with wild oat at similar densities and P levels. The lower concentration in the crop was reflected by a corresponding higher concentration in barren brome at all P levels and densities of the weed.

P concentration in the weeds was also reduced by intraspecific competition and P levels. In both weeds, P tissue concentration did not differ between L2 and L3. In competition with either weed, P concentration of the crop did not differ at L2 and L3.

K: Orthogonal comparisons of the means for K concentration in the crop

Table 3.15. Analysis of the effects of weed density and phosphorus level on nutrient concentration (mMol P/g dry weight) in wheat

	df	SS	MS	VR
Blocks	3	0.1768	0.0059	-
Treat (contrasts)				
C v rest	1	0.1006	0.1006	136.943***
WO v BB**	1	0.01398	0.01398	19.029***
WO Linear	1	0.01444	0.01444	19.659***
WO Quadratic	1	0.00013	0.00013	0.179 NS
BB Linear	1	0.02374	0.02374	32.319***
BB Quadratic	1	0.001176	0.001176	1.601 NS
L1 v L2, L3	1	0.0246	0.0246	33.479***
L2 v L3	1	0.00011	0.00011	0.151 NS
Deviations	12	0.0549356	0.004578	6.2319*
Residuals	57	0.0418748	0.0007346	
Total	80	0.29426		

Table 3.16 · The effects of phosphorus level and weed density on P concentration in wheat and wild oat (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 WO	L2 W	L2 WO	L3 W	L3 WO	Mean W	Mean WO
(D0) W1+WO0	0.232	-	0.130	-	0.057	-	0.139	-
(D1) W1+WO1	0.142	0.180	0.159	0.154	0.089	0.150	0.130	0.161
(D3) W1+WO3	0.172	0.090	0.177	0.085	0.081	0.083	0.143	0.085
(D5) W1+WO5	0.088	0.066	0.058	0.046	0.061	0.039	0.069	0.050
Mean	0.1586	0.122	0.1307	0.095	0.0717	0.091		

	LSD (5%) W	LSD (5%) WO
Phosphorus level	0.017	0.010
Density	0.020	0.010
Interaction	0.034	NS

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 wild oat plants/pot
D3 = 1 wheat + 3 wild oat plants/pot
D5 = 1 wheat + 5 wild oat plants/pot

Table 3.17. The effects of phosphorus level and weed density on P concentration in wheat and barren brome (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 BB	L2 W	L2 BB	L3 W	L3 BB	Mean W	Mean BB
(D0) W1+BB0	0.232	-	0.130	-	0.057	-	0.139	-
(D1) W1+BB1	0.154	0.261	0.079	0.181	0.051	0.203	0.095	0.215
(D3) W1+BB3	0.096	0.086	0.063	0.121	0.043	0.103	0.067	0.103
(D5) W1+BB5	0.075	0.075	0.046	0.077	0.041	0.074	0.054	0.075
Mean	0.139	0.141	0.080	0.126	0.048	0.127		

	LSD (5%) W	LSD (5%) BB
Phosphorus level	0.008	0.015
Density	0.009	0.015
Interaction	0.016	NS

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 barren brome plants/pot
D3 = 1 wheat + 3 barren brome plants/pot
D5 = 1 wheat + 5 barren brome plants/pot

Table 3.18. Analysis of the effects of weed density and phosphorus level on the concentration of K (mMol K/g dry weight) in wheat

	df	SS	MS	VR
Blocks	3	0.99374	0.33125	-
Treat (contrasts)				
C v rest	1	0.00008	0.00008	0.004 NS
WO v BB	1	0.05742	0.05742	2.914 NS
WO Linear	1	0.04442	0.04442	2.254 NS
WO Quadratic	1	0.00745	0.00745	0.378 NS
BB Linear	1	0.01165	0.01165	0.592 NS
BB Quadratic	1	0.00589	0.00589	0.299 NS
L1 v L2, L3	1	0.06354	0.06354	3.225 NS
L2 v L3	1	0.04450	0.04450	2.259 NS
Deviations	12	0.68371	0.05697	2.892 NS
Residuals	57	1.12310	0.01970	
Totals	80	3.03527		

Table 3.19 · The effects of phosphorus level and weed density on K concentration in wheat and wild oat (mMol/g dry weight of shoots)

	Phosphorus level							
	L1		L2		L3		Mean	
Treatments	W	WO	W	WO	W	WO	W	WO
(D0) W1+WO0	1.290	-	1.394	-	1.346	-	1.344	-
(D1) W1+WO1	1.241	0.858	1.372	0.750	1.347	0.761	1.320	0.790
(D3) W1+WO3	1.239	0.986	1.370	0.976	1.052	0.772	1.220	0.911
(D5) W1+WO5	1.193	1.193	1.206	0.983	1.281	0.898	1.227	1.025
Mean	1.241	1.012	1.336	0.903	1.257	0.811		

	LSD (5%)	
	W	WO
Phosphorus level	NS	0.09
Weed density	0.107	0.09
Interaction	NS	NS

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 wild oat plants/pot
D3 = 1 wheat + 3 wild oat plants/pot
D5 = 1 wheat + 5 wild oat plants/pot

Table 3.20. The effects of weed density and phosphorus level on K concentration in wheat and barren brome (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 BB	L2 W	L2 BB	L3 W	L3 BB	Mean W	Mean BB
(D0) W1+BB0	1.290	-	1.394	-	1.346	-	1.344	-
(D1) W1+BB1	1.242	1.264	1.312	1.200	1.328	1.014	1.294	1.159
(D3) W1+BB3	1.294	1.465	1.248	1.303	1.394	1.298	1.312	1.355
(D5) W1+BB5	1.097	1.537	1.078	1.435	1.063	1.580	1.080	1.517
Mean	1.231	1.422	1.258	1.312	1.283	1.297		

	LSD (5%) W	LSD (5%) BB
Phosphorus level	NS	NS
Density	0.112	0.124
Interaction	NS	NS

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 barren brome plants/pot
D3 = 1 wheat + 3 barren brome plants/pot
D5 = 1 wheat + 5 barren brome plants/pot

indicated that the effects of the weeds were similar and showed no evidence of quadratic or linear effects of the weed species on the crop. Varying P levels also showed no differences on the concentration of K in wheat (Tables 3.18, 3.19 and 3.20). Separate analysis on the effects of the weeds, however, showed that K concentration of the crop was reduced by increasing density of the weeds. In the presence of wild oat the crop had higher concentrations of K than when it was surrounded by similar population densities of barren brome. The lower K in the crop corresponded to the higher K in this weed (Table 3.20).

In wild oat, population density of the weed and P level significantly affected K concentration. In barren brome only the effect of population density significantly affected K concentration of the weed. In both weeds increasing population density increased K concentration, but this decreased with decrease in P level. In both weeds interactions of density and P levels were not significant (Tables 3.19 and 3.20).

Ca: Orthogonal comparisons between the two weeds on their effects on Ca concentration in the crop showed significant differences. There was no evidence of differences between P levels (Table 3.21).

In the crop neither density nor P levels significantly affected Ca concentration, but interactions were significant (Tables 3.22 and 3.23). When the crop was surrounded by increasing number of wild oat it contained higher Ca and the reverse happened with barren brome. Ca concentrations in barren brome were higher than in both the species and were not affected by either intraspecific competition or P level; wild oat was affected by these factors. The higher tissue Ca concentration found in barren brome in competition is in agreement with the earlier finding in water culture experiments (Section I).

Mg: The effects of the weeds on Mg concentration of the crop were different, but P levels did not affect this variete (Table 3.24). Analysis of variance on Mg concentrations in wheat showed that density of wild oat or P levels had no effect, whilst that of barren brome had (Tables 3.25 and 3.26). The interactions between weed densities and P levels, however, were significant. Both weeds, particularly barren brome, had higher Mg concentrations than the crop at all densities and P levels. In both weeds Mg concentration was reduced significantly by intraspecific competition. In wild oat, Mg decreases with increase in P, whilst in barren brome the trend was not clear.

Table 3.21 Analysis of the effects of weed density and P levels on the concentration of Ca (mMol/g dry weight) in wheat

	df	SS	MS	VR
Blocks	3	0.098669	0.03289	-
Treat (contrasts)				
C v rest	1	0.017681	0.017681	9.385**
WO v BB	1	0.241556	0.241556	128.225***
WO Linear	1	0.000005	0.000005	0.027 NS
WO Quadratic	1	0.005179	0.005179	2.749 NS
BB Linear	1	0.000409	0.000409	0.217 NS
BB Quadratic	1	0.001878	0.001878	0.997 NS
L1 v L2, L3	1	0.000317	0.000317	0.168 NS
L2 v L3	1	0.002834	0.002834	1.504 NS
Deviations	12	0.049972	0.0004164	2.2104 NS
Residuals	57	0.107379	0.001884	
Total	80	0.525925		

Table 3.22· The effects of phosphorus level and weed density on Ca concentration in wheat and wild oat (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 WO	L2 W	L2 WO	L3 W	L3 WO	Mean W	Mean WO
(D0) W1+WO0	0.222	-	0.198	-	0.198	-	0.206	-
(D1) W1+WO1	0.218	0.189	0.216	0.183	0.184	0.216	0.206	0.196
(D3) W1+WO3	0.209	0.178	0.252	0.180	0.199	0.202	0.220	0.187
(D5) W1+WO5	0.169	0.231	0.206	0.200	0.205	0.214	0.193	0.213
Mean	0.204	0.199	0.218	0.188	0.196	0.211		

	LSD (5%) W	LSD (5%) WO
Phosphorus level	NS	0.015
Weed density	N	0.015
Interaction	0.0367	NS

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 wild oat plants/pot
D3 = 1 wheat + 3 wild oat plants/pot
D5 = 1 wheat + 5 wild oat plants/pot

Table 3.23. Effects of weed density and phosphorus level on Ca concentration in wheat and barren brome (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 BB	L2 W	L2 BB	L3 W	L3 BB	Mean W	Mean BB
(D0) W1+BB0	0.222	-	0.198	-	0.204	-	0.208	-
(D1) W1+BB1	0.367	0.393	0.304	0.399	0.290	0.385	0.320	0.396
(D3) W1+BB3	0.287	0.393	0.328	0.397	0.380	0.395	0.332	0.395
(D5) W1+BB5	0.323	0.400	0.284	0.332	0.294	0.374	0.300	0.369
Mean	0.300	0.396	0.289	0.376	0.292	0.385		

	LSD (5%) W	LSD (5%) BB
Phosphorus level	NS	NS
Density	NS	NS
Interaction	0.063	NS

D0 = 1 wheat plant grown alone/pot
D1 = 1 wheat + 1 barren brome plants/pot
D3 = 1 wheat + 3 barren brome plants/pot
D5 = 1 wheat + 5 barren brome plants/pot

Table 3.24 · Analysis of the effects of weed density and phosphorus level on the concentration of Mg (mMol/g dry weight) in wheat

	df	SS	MS	VR
Blocks	3	0.0022603	0.0001534	-
Treat (contrasts)				
C v rest	1	0.0004833	0.0004833	4.654*
WO v BB	1	0.00048863	0.00048863	8.535**
WO Linear	1	0.0000292	0.0000292	0.281 NS
WO Quadratic	1	0.0000492	0.0000492	0.474 NS
BB Linear	1	0.0010335	0.0010335	9.952**
BB Quadratic	1	0.000005	0.000005	0.049 NS
L1 v L2, L3	1	0.0000004	0.0000004	0.004 NS
L2 v L3	1	0.001032	0.0001032	0.994 NS
Deviations	12	0.00276557	0.000230464	2.219 NS
Residuals	57	0.0059191	0.00010384	
Total	80	0.0131373		

Table 3.25 Effects of weed density and phosphorus level on Mg concentration in wheat and wild oat (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 WO	L2 W	L2 WO	L3 W	L3 WO	Mean W	Mean WO
(D0) W1+WO0	0.065	-	0.058	-	0.058	-	0.060	-
(D1) W1+WO1	0.064	0.091	0.065	0.079	0.053	0.096	0.060	0.089
(D3) W1+WO3	0.064	0.053	0.062	0.078	0.059	0.089	0.062	0.073
(D5) W1+WO5	0.064	0.077	0.057	0.083	0.072	0.078	0.064	0.079
Mean	0.064	0.074	0.060	0.080	0.060	0.088		

	LSD (5%) W	LSD (5%) WO
Phosphorus level	NS	0.0096
Weed density	NS	0.0096
Interaction	0.0099	0.0165

D0 = 1 wheat plant/pot
D1 = 1 wheat + 1 wild oat plant/pot
D3 = 1 wheat + 3 wild oat plants/pot
D5 = 1 wheat + 5 wild oat plants/pot

Table 3.26 Effects of weed density and phosphorus level on Mg concentration in wheat and barren brome (mMol/g dry weight of shoots)

Treatments	Phosphorus level L1 W	L1 BB	L2 W	L2 BB	L3 W	L3 BB	Mean W	Mean BB
(D0) W1+BB0	0.065	-	0.058	-	0.058	-	0.060	-
(D1) W1+BB1	0.059	0.117	0.054	0.110	0.050	0.113	0.054	0.113
(D3) W1+BB3	0.072	0.112	0.060	0.108	0.043	0.110	0.058	0.110
(D5) W1+BB5	0.047	0.105	0.048	0.079	0.047	0.092	0.047	0.092
Mean	0.061	0.111	0.055	0.099	0.049	0.105		

	LSD (P 0.05) W	LSD (P 0.05) BB
Phosphorus level	0.0051	0.0076
Density	0.0059	0.0076
Interaction	0.0102	NS

D0 = 1 wheat plant alone/pot
D1 = 1 wheat + 1 barren brome plants/pot
D3 = 1 wheat + 3 barren brome plants/pot
D5 = 1 wheat + 5 barren brome plants/pot

7.4.4. Discussion

The effect of density stress of the weeds on the growth and nutrient concentrations in the crop was used as a measure of their competitive abilities. Since the effects of the weeds were reflected on the general performance of the crop, the latter is referred to as an 'indicator species' and the former as 'competitors'. The effects of the competitor species on the indicator measures the magnitude of effects of interspecific competition, whilst the effects of density amongst plants of any one competitor measures the intensity of intraspecific competition within that species. The importance of experiments of this nature in investigating crop-weed competition has already been demonstrated by a number of authors (Obeid, 1965; Welbank, 1963; Bell and Nalewaja, 1968a; Blackshaw et al., 1981; Johnson, 1987). A classical example of such experiments is given by Welbank who compared the competitive abilities of several weed species by growing single pl+nts of kale, sugar beet or wheat alone and with 16 plants of any one of the weeds at two levels of N. The effects of different weeds on dry weight of the crop plants were used as a measure of their respective competitive abilities.

In the present experiments, the data for the indicator species were first investigated by orthogonal contrasts, and provided primary answers to some of the basic objectives of these experiments. For example, the effects of the two weeds for some measured variates of the crop were similar and for others they were different. In most cases, the effects of the weeds in reducing both shoot and nutrient yields were linear. Orthogonal contrasts also showed whether P levels were different or similar in affecting the various variates considered.

The data were further investigated separately by analysis of variance. The data for each competitor species were also analysed in the same manner to show the intensity of intraspecific competition.

Orthogonal comparisons on mean tiller number, shoot dry weight yield per plant and K tissue concentration of the indicator showed that density effects of the competitors were not different. Both weeds reduced tiller production and shoot dry matter of the crop linearly. There was no evidence of an effect on its K tissue concentration. There was no difference between P levels on the K concentration of the crop,

indicating that K was not an important factor in competition with the weeds. The absence of differences between the control (i.e. a single plant of wheat/pot) and the rest of the treatments in K concentration may also indicate that there was no competition for this nutrient whether weed densities were increased and/or P levels varied. Although both weeds similarly reduced the growth of the crop, they may not have competed for the same resources. For example, wild oat may have had a greater effect on shading, because it grew faster and upright, whilst barren brome may have competed for limiting P.

These comparisons also showed that competitors differed in their effects on P, Ca and Mg concentrations of the indicator. The general effect of the weeds in reducing P concentration in the crop was linear with increase in the population density of either weed. In general the effects of weeds on P uptake differed with the level of P. L1 was different from L2 and L3; whilst the latter did not differ. P levels, however, did not usually affect Ca and Mg concentrations, there being no evidence of linear or quadratic effects of the competitors on the two elements except for Mg in barren brome. The fact that the weeds differed in their effects on P, Ca and Mg concentration of wheat may suggest differences in requirements and efficiency of uptake between them. These differences have been reported earlier (Section I) where barren brome had shown higher efficiencies of uptake than wild oat for these nutrients. Wild oat was unresponsive to levels of P and Mg in water culture experiments. The higher Mg requirement of barren brome than wild oat is shown by the fact that this weed reduced the concentration in the crop linearly with density. The absence of effects of either weed for Ca and wild oat for Mg uptake may suggest that these nutrients were not important factors in competition. Similarly, the fact that P levels did not differ in their effects on the uptake and concentrations of these two elements, may suggest that P level did not matter in the uptake of Ca and Mg in competition. It may also support the suggestion that the species did not compete for these elements. The analysis of variance of data on the effects of densities of individual weeds and of P levels also showed that Ca and Mg concentration of wheat was not significantly reduced by these factors (Tables 3.22, 3.23 and 3.25), although this was not true for Mg in barren brome (Table 3.24).

The magnitude of competitive effects of competitor species and the ability of the indicator to continue to perform relatively well in the

presence of increasing number of plants of the competitors were investigated by analysis of variance. Tiller number and shoot dry weight/plant of the indicator species were both reduced by density, P levels and their interactions. The effects of both weeds were significantly higher at higher levels of P than at the lowest. The addition of a single plant of wild oat or barren brome to 1 plant per pot of wheat reduced its yield by 33 and 36% respectively. Intraspecific competition amongst plants of the competitors also significantly reduced tillering and shoot dry weight per plant.

The competitive effects of the weeds might be expected to be less with a high than with a low supply of P in the medium. The results of the present experiments however, showed that these effects actually increased with increase in the levels of added P. This may be because the weeds, as well as the crop, were stimulated by higher P, so that they exerted a more vigorous competitive effect. The effect of wild oat in reducing both tiller production and shoot dry matter yield of wheat at higher P may be due to the fact that the extra P promoted top growth of the weed and this resulted in shading of the crop. The growth of this weed was usually greater than or similar to that of the crop. The depressive effect of shading on tillering has been well documented in physiological studies (Aspinal and Mithorpe, 1959). The production of shoot dry matter per plant in barren brome however, was smaller than that of wheat and the weed may not have interfered so much with the light available to the crop. The reducing effect of this weed on the growth of wheat may have been exerted through its larger surface area of roots it usually produced. This may enable the weed to compete better for limited P, resulting in more reduced vegetative growth and nutrient concentration in the indicator than that caused by wild oat.

The results also indicate that the density of the weeds, P levels and the interactions between the two factors significantly reduced P uptake of the indicator. K concentration, however, was significantly reduced only by weed density. When the indicator species was surrounded by increasing densities of wild oat, it contained higher concentrations of both elements than in the presence of barren brome at similar densities and P level. Neither weed density nor P level affected the concentration of Ca and Mg in the indicator. The concentration of these elements in the crop was also higher in the presence of wild oat plants than those of barren brome. The higher concentrations in barren brome

and the corresponding lower concentrations in the indicator species confirm that the two weeds differ in affecting the common indicator. It also reaffirms that in competition barren brome is an efficient weed in taking up P, K, Ca and Mg. This may also support the earlier suggestion that the weed has a higher requirement for these elements. It may also be suggested that barren brome competes for underground soil resources, while in wild oat above ground competition for light may be more important.

Both intraspecific competition amongst plants of individual weeds and P levels affected P and Mg concentrations in both weeds. Both density and P also affected K and Ca concentrations in wild oat. In barren brome these factors did not have any influence on Ca, although population density affected K concentration. In both weed species the concentration of K tended to increase with density and to decrease with decrease in the level of P. The increase in K with increase in the density of the population of the weeds cannot be explained. Since Ca concentration in barren brome was not so affected as the growth of its shoots by density, P level and their interactions, it suggests that the elements may not have been a limiting factor in competition. In wild oat both density and levels of P affected Ca concentration.

Information on the relative importance of barren brome and wild oat as competitor species is not available. The most obvious and direct method for finding which of these two weed species is the stronger competitor is to measure their effects on a common indicator. The population of the indicator is held constant and remains lower than those of the weeds to be tested so that there is very little effect of the crop on the weeds. The density of the weeds however, is increased additively. A number of investigators have used additive experiments to compare competitive abilities of various crop and weed species. For example, Johnson (1987) used these experiments to compare the mutual aggressiveness of wheat and blackgrass. He used each species as an indicator of the competitive ability of the other. He grew a single plant of either species and surrounded it by 2, 4 and 6 plants of the other. Three P levels were also included in the study and single plants of each species/pot served as controls. He found that when blackgrass was the indicator species its shoot dry weight was much more reduced by surrounding wheat plants than was that of the crop by surrounding blackgrass plants. The addition of a single plant of wheat to a pot

containing one blackgrass plant reduced the shoot dry weight of blackgrass by 55%, whilst in wheat this was reduced by 20%. He also found greater reductions in per plant weight of wheat at the lowest level of P than at the highest and suggested that surrounding blackgrass plants had a greater effect on the weight/plant of wheat when the level of P was lower than when it was higher. This however, was not true for the dry weight of wheat, which was more reduced at higher P than at the lower level when it was surrounded by increasing number of either weed in the present study. The addition of a single plant of either weed to a pot containing one wheat plant reduced its yeild significantly and the reduction at that density was higher at higher than at lower P. This implies that the application of fertilizers to wheat infested by either/or both weeds may benefit the weed(s) even when they are at low densities. The relative competitiveness of crops and weeds is known to be changed with the application of fertilizers and it seems that a poor competitor becomes poorer when nutrients are added and a stronger competitor benefits from such practices. The effects of fertilizers on the competitive abilities of weeds and crops remain controversial and the available reports differ on the issue. For example, fertilizer did not alter the competitive balance between wild oat and wheat or barley (Thurston, 1959a; McBeath et al., 1970). Others found that the effects of weeds could be partly overcome by the application of some fertilizers at higher levels (Molberg and Leggett, 1955, cited by Jones, 1976; Koch, 1967). There are other reports where fertilizer favoured wild oats in wheat, flax and peas (Bell and Nalewaja, 1968a). The effects of weeds on the performance of crops may be due more to increase in the density of the weeds than low fertility conditions of the soil. Bell and Nalewaja (1968a) investigated the effects of wild oat densities and fertilizer levels on flax. The densities included 12, 48 and 192 wild oat plants/m^2 and two fertilizer levels. When fertilizer was applied, 12 and 48 wild oat/m^2 reduced yields on average by 23% and 57% respectively. When no fertilizer was added the comparable figures were 24% and 53%. At a wild oat density of 192/m^2 yields were reduced by 86% when fertilizer was applied and by 83% without fertilizer. Naylor (1972) showed that interference by blackgrass, sown at different densities, on the growth of winter wheat was reduced at high N levels.

Mahmoud and Grime (1976) studied competitive interactions of the perennial grasses of contrasted ecology, Festuca ovina, Agrostis tenuis

and Arrenatherum elatius under high and low N conditions. Under high N soil conditions F. ovina was totally eliminated by the other grasses and there was no survivals of A. tenuis when this species was grown with A. elatius. In low N treatments, all 3 species survived but suffered a reduction in growth. Leaf canopy was so sparse that it was inconceivable that competitive interactions occurred between shoots. In rice, phosphate fertilization stimulated weed growth and increased competition (Vengris et al., 1955; Smith and Shaw, 1966). Bhaskar and Vyas (1988) also studied interspecific competition between wheat and C. album, and noted competitive interference for P and to some extent for N. They concluded that wheat growth was limited by competition for P by C. album. In contrast there did not appear to be competition for K, because wheat showed higher competitive ability for the element.

Experiment 3.3 Effects of weed density and P levels on dry matter yield and nutrient concentrations of wheat

7.4.5. Results

Only data for shoot dry matter yield and nutrient concentrations of the crop were analysed unlike in the previous additive series experiment (Expt. 2) where those of the weeds were analysed to show intraspecific competition in these species. As stated earlier, the effects of the weeds were compared by measuring yields of the crop i.e. indirectly.

Shoot dry matter yield (g/plant) of wheat

Orthogonal contrasts on the overall effects of the weeds in reducing shoot dry matter of the crop showed non-significant differences (Table 3.27). Both weeds linearly affected yield of the crop as their density was increased and analysis of variance of the data also showed reduction with increases in the density of the weeds and decreases in P levels (Table 3.28).

Nutrient concentrations (mMol/g DW) in wheat

Comparisons of the overall effects of the two weeds on P and Mg concentrations of the crop showed non-significant differences. Both linear and quadratic regressions for barren brome were significant (Table 3.29) for P. Only the linear effect of this weed was significant for Mg

Table 3.27 Analysis of the effects of weed density and P levels on mean yield per plant (g) in wheat

Treatments	df	SS	MS	VR
Blocks	3	0.08915	0.02984	-
Control v rest	1	5.10600	5.10600	492.110***
WO v BB	1	0.00062	0.00062	0.060 NS
WO Linear	1	1.61720	1.61720	155.864***
WO Quadratic	1	0.00031	0.00031	0.030 NS
BB Linear	1	1.26087	1.26087	121.521***
BB Quadratic	1	0.00126	0.00126	0.121 NS
P1 v P2, P3	1	0.24602	0.24602	23.711***
P2 v P3	1	0.18183	0.18183	17.524***
Deviations	12	5.85975	0.4883	47.044***
Residual	59	0.61217	0.01038	
Total	82	15.06468		

Table 3.28. Effects of weed density and P level on shoot yield of wheat (g) (means of harvests 1 and 2)

Wild oat density	P level P1	P2	P3	Mean
W1 + WO (d0)	1.93	1.30	0.81	1.35
W1 + WO1 (d1)	0.52	1.44	0.71	0.89
W1 + WO3 (d3)	0.54	0.37	0.99	0.63
W1 + WO5 (d5)	0.44	0.42	0.29	0.38
Mean	0.86	0.88	0.70	

LSD ($P < 0.05$)

Phosphorus level	0.08
Density	0.09
Interaction	0.16

Barren brome density	P1	P2	P3	Mean
W1 + BB0 (d0)	1.93	1.30	0.81	1.35
W1 + BB1 (d1)	0.57	1.44	0.79	0.93
W1 + BB3 (d3)	0.44	0.67	0.99	0.70
W1 + BB5 (d5)	0.35	0.42	0.49	0.42
Mean	0.82	0.96	0.77	

LSD ($P < 0.05$)

Phosphorus level	0.07
Density	0.08
Interaction	0.14

Table 3.29. Analysis of the effects of weed density and P level on mean P concentration (mMol/g) in wheat

Treatments	df	SS	MS	VR
Blocks	3	0.005675	0.001892	-
Control v rest	1	0.041614	0.041614	11.007**
WO v BB	1	0.012449	0.012449	3.293 NS
WO Linear	1	0.01436	0.01436	3.798 NS
WO Quadratic	1	0.012213	0.012213	3.231 NS
BB Linear	1	0.024376	0.024376	6.448*
BB Quadratic	1	0.029105	0.029105	7.699**
P1 v P2, P3	1	0.003334	0.003334	0.882 NS
P2 v P3	1	0.000134	0.000134	0.035 NS
Deviations	12	0.456966	0.03808	10.0715**
Residual	58	0.219270	0.003781	
Total	81	0.825170		

Table 3.30. Effects of weed density and P level on P uptake in wheat (P concentration mMol/g DW)

Wild oat density	P level L1	L2	L3	Mean
W1 + WO (d0)	0.52	0.48	0.56	0.52
W1 + WO1 (d1)	0.32	0.64	0.49	0.48
W1 + WO3 (d3)	0.58	0.36	0.56	0.49
W1 + WO5 (d5)	0.38	0.46	0.45	0.43
Mean	0.45	0.48	0.51	

LSD ($P < 0.05$)

Phosphorus level	0.04
Wild oat density	0.04
Interaction	0.07

Barren brome density	P level L1	L2	L3	Mean
W1 + BB0 (d0)	0.52	0.48	0.56	0.50
W1 + BB1 (d1)	0.35	0.64	0.51	0.50
W1 + BB3 (d3)	0.47	0.47	0.54	0.49
W1 + BB5 (d5)	0.48	0.33	0.36	0.39
Mean	0.45	0.49	0.48	

LSD ($P < 0.05$)

Phosphorus level	NS
Density	0.06
Interaction	0.10

Table 3.31. Analysis of the effects of weed density and P level on mean K concentration (mMol/g) in wheat

Treatments	df	SS	MS	VR
Blocks	3	1.65315	0.55105	-
Control v rest	1	0.07264	0.06264	1.248 NS
WO v BB	1	0.01291	0.01291	0.222 NS
WO Linear	1	0.00009	0.00009	0.002 NS
WO Quadratic	1	0.00274	0.00274	0.047 NS
BB Linear	1	0.00657	0.00657	0.113 NS
BB Quadratic	1	0.02264	0.02264	0.389 NS
P1 v P2, P3	1	0.05184	0.05184	0.891 NS
P2 v P3	1	0.00088	0.00088	0.015 NS
Deviations	12	0.088891	0.007408	0.1273 NS
Residuals	59	3.43446	0.05821	
Total	82	5.90180		

Table 3.32. Effects of weed density and P level on K uptake in wheat (K concentration mMol/g DW)

Wild oat density	P level L1	L2	L3	Mean
W1 + WO (d0)	1.61	1.58	1.65	1.61
W1 + WO1 (d1)	1.40	1.71	1.44	1.52
W1 + WO3 (d3)	1.15	1.56	1.66	1.46
W1 + WO5 (d5)	1.46	1.53	1.54	1.51
Mean	1.40	1.60	1.57	

LSD ($P < 0.05$)

Phosphorus level	NS
Density	NS
Interaction	NS

Barren brome density	P level L1	L2	L3	Mean
W1 + BB0 (d0)	1.61	1.58	1.65	1.61
W1 + BB1 (d1)	1.54	1.71	1.64	1.63
W1 + BB3 (d3)	1.61	1.52	1.65	1.59
W1 + BB5 (d5)	1.60	1.51	1.51	1.54
Mean	1.59	1.58	1.61	

LSD ($P < 0.05$)

Phosphorus level	NS
Barren brome density	NS
Interaction	NS

Table 3.33. Analysis of the effects of weed density and P level on mean Ca concentration (mMol/gDW) in wheat

Treatments	df	SS	MS	VR
Blocks	3	0.015768	0.005256	-
Control v rest	1	0.000534	0.000534	0.382 NS
WO v BB	1	0.001615	0.001615	1.157 NS
WO Linear	1	0.014731	0.014731	10.549**
WO Quadratic	1	0.008508	0.008508	6.092*
BB Linear	1	0.005520	0.005520	3.953 NS
BB Quadratic	1	0.001773	0.001773	1.270 NS
P1 v P2, P3	1	0.004334	0.004334	3.103 NS
P2 v P3	1	0.002146	0.002146	1.537 NS
Deviation	12	0.043961	0.0036633	2.624 NS
Residual	56	0.078202	0.001396	
Total	79			

Table 3.34 Effects of weed density and P level on Ca uptake in wheat (Ca concentration mMol/g DW)

Wild oat density	P level L1	L2	L3	Mean
W1 + WO (d0)	0.29	0.23	0.28	0.27
W1 + WO1 (d1)	0.23	0.24	0.25	0.24
W1 + WO3 (d3)	0.21	0.23	0.26	0.23
W1 + WO5 (d5)	0.27	0.26	0.35	0.29
Mean	0.25	0.24	0.28	

LSD ($P < 0.05$)

Phosphorus level	0.02
Density	0.03
Interaction	0.05

Barren brome density	P level L1	L2	L3	Mean
W1 + BB0 (d0)	0.29	0.23	0.28	0.27
W1 + BB1 (d1)	0.24	0.24	0.24	0.24
W1 + BB3 (d3)	0.31	0.27	0.26	0.28
W1 + BB5 (d5)	0.28	0.28	0.25	0.27
Mean	0.28	0.25	0.26	

LSD ($P < 0.05$)

Phosphorus level	NS
Density	NS
Interaction	NS

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Table 3.35. Analysis of the effects of weed density and P level on mean Mg concentration (mM/g) in wheat

Treatments	df	SS	MS	VR
Blocks	3	0.00046904	0.00015365	-
Control v rest	1	0.0002859	0.00002859	0.362 NS
WO v BB	1	0.00002843	0.00002843	0.360 NS
WO Linear	1	0.00006877	0.0000677	0.872 NS
WO Quadratic	1	0.00000233	0.00000233	0.030 NS
BB Linear	1	0.00052053	0.00052053	6.598*
BB Quadratic	1	0.00019827	0.00019827	2.513 NS
P1 v P2, P3	1	0.00018899	0.00018899	2.395 NS
P2 v P3	1	0.0004626	0.00004626	0.586 NS
Deviations	12	0.00106428	0.00008869	1.1241 NS
Residual	58	0.00457608	0.00007890	
Total	81	0.00759981		

Table 3.36 Effects of weed density and P level on Mg uptake in wheat (Mg concentration mMol/g DW)

Wild oat density	P level L1	L2	L3	Mean
W1 + WO (d0)	0.07	0.06	0.07	0.07
W1 + WO1 (d1)	0.06	0.07	0.07	0.07
W1 + WO3 (d3)	0.07	0.07	0.07	0.07
W1 + WO5 (d5)	0.07	0.07	0.08	0.07
Mean	0.07	0.07	0.07	

LSD ($P < 0.05$)

Phosphorus level	NS
Density	NS
Interaction	NS

Barren brome density	P level L1	L2	L3	Mean
W1 + WO0 (d0)	0.07	0.06	0.07	0.07
W1 + WO1 (d1)	0.07	0.06	0.07	0.07
W1 + WO3 (d3)	0.08	0.08	0.06	0.07
W1 + WO5 (d5)	0.06	0.07	0.07	0.07
Mean				

LSD ($P < 0.05$)

Phosphorus level	NS
Density	NS
Interaction	NS

concentration (Table 3.35). Analysis of variance on the data for P concentration of the crop showed significant interactions (Table 3.30), whilst these were not significant for Mg (Table 3.36).

The weeds again did not differ in affecting the K concentration of the crop and neither weed density nor P levels affected K uptake in wheat (Tables 3.31 and 3.32).

Orthogonal comparisons on the overall effects of the weeds on Ca concentration of the crop also showed non-significant differences between them, although both linear and quadratic regressions for wild oat were significant (Table 3.33). Interactions were significant for the effects of wild oat on the crop whilst those for barren brome were not (Table 3.34).

7.4.6. Discussion

This additive series experiment was carried out in natural field soil containing low levels of phosphorus for purposes of comparison with experiment 1 which was carried out in a soilless medium. Orthogonal contrasts on the mean yield (g/plant) of the crop and its nutrient concentrations showed both differences and similarities in the effects of densities of the weeds and soil P levels.

In both experiments the monoculture yield of the crop was clearly different from its yield in mixtures with either weed species (Tables 3.27 and 3.28). The effects of the two weeds were similar and increases in their densities linearly affected shoot dry matter yield of the crop. Although the weeds affected the yield of the crop linearly and similarly, their mode(s) of competition could have been different. Since wild oat usually (and in this experiment) grew larger than or equal to the crop, its effects may have been due partially to shading, whilst barren brome, with its dense root system, may have competed strongly for limited P. When the root and shoot effects of the weeds on the crop were separated and quantified (see Section IV) the results suggested that competition for soil resources (i.e. root competition) was slightly greater in barren brome whilst wild oat appeared to compete through ability to compete for both root and shoot resosurces. In Experiment 1, comparisons between weed effects on P concentration in the crop showed that both reduced this

nutrient linearly. In the present experiment, barren brome affected the concentration of the element, both linear and quadratic regressions being significant, whilst wild oat did not have significant effects. Under P deficient conditions barren brome thus seems to compete better for the element than wild oat.

Orthogonal contrasts on the effects of the weeds on the K concentration of the crop at the two experiments were similar and analysis on the data for K concentration of the crop also showed that increase in the population of either weed did not reduce its concentration significantly. This clearly indicates the greater competitive ability of the crop in taking up K - a conclusion reached earlier in this section and in water culture experiments (Section I). In Section I, the crop showed relatively higher K concentrations and responded strongly to higher levels of the element. Later in this Section where the effects of the densities of the weeds were studies in replacement series with varying levels of K, the crop had also shown greater competitive ability for the element than either weed. All the above evidence, therefore, suggests that the crop may, during domestication, have developed special mechanisms which enables it effectively to take up this nutrient from soils both rich and poor in it. Such mechanisms are clearly not due to the ability to produce greater amounts of root per unit volume of soil, and thus may involve a difference in ion uptake kinetics, that is, the crop may have a higher Vmax and/or a lower Km than either weed. When intact plants of the three species were allowed to deplete similar concentration of the element from a continuously flowing nutrient solution the crop removed K ions faster than the weed species (see Section II).

Unlike the previous experiment the effects of the two weeds on Ca concentration of the crop were not significantly different, although both linear and quadratic regressions for wild oat alone showed significant effects. In most of the responses and competition experiments reported throughout this report, both weeds and especially barren brome, showed high concentrations of Ca and Mg suggesting a higher requirement for these nutrients. In competition both weeds, and particularly barren brome, would be expected to reduce the availability of these elements to the crop. However, because total requirements depend on the total growth of the species, wild oat would be expected to reduce Ca in the crop more than the smaller barren brome. Barren brome, however, affected Mg

concentration of the crop linearly in both experiments, although the overall effect of the weeds in the present experiment did not differ significantly.

Though the two experiments showed sosme differences between results in natural soils and in soilless compost, they may be criticised on the grounds of artificiality, since they were both carried out in pots. Pot culture certainly forces the species to use the same limited root space and soil resources whereas in the field the species may penetrate different zones of the soil and thus escape some measure of both interspecific and intraspecific competition. This matter has also been investigated (see Section IV) and the results suggested that whilst wheat and barren brome tended to occupy more or less the same layer of the soil profile (mostly the upper 0-20 cm) wild oat showed an ability to produce denser roots in deeper layers (40-50 cm). The possible advantages of this characteristic in relation to competition with the other two species are discussed in Section IV.

7.5. Substitutive Experiments

7.5.1. Results

Experiment 3.4: Replacement series at different P levels

1. Effects of plant ratio and P level on the competitive relationships between wheat (W) and wild oat (WO)

(a) Dry matter yield

The shoot dry matter yields of the two species whether in pure stands or mixtures were significantly reduced by a low level of phosphorus (Table 3.37). The mean pure stand yield (g/plant) of wheat was only different from the other treatments where population of the weed was greater than that of the crop. The per plant yield of the crop increased with increase in the density of the weed in the mixture, but not

Table 3.37 Effects of plant ratio and P level on the mean dry matter yields of wheat (W) and wild oat (WO)

(Means of 2 harvests)

A. Wheat yield (g/plant)

Plant ratio	P level L1	L2	Mean
W6 + WO0 (pure wheat)	1.17	0.78	0.98
W4 + WO2	1.05	0.71	0.88
W3 + WO3	1.19	0.71	0.95
W2 + WO4	1.34	1.01	1.18
Mean	1.19	0.80	

LSD ($P < 0.05$)

Plant ratio	0.13
Phosphorus level	0.09
Interaction	NS

B. Wild oat yield (g/plant)

	P level L1	L2	Mean
WO + W0 (pure wild oat)	1.35	0.92	1.14
WO4 + W2	1.53	0.86	1.19
WO3 + W3	1.50	0.95	1.22
WO2 + W4	1.27	0.91	1.09
Mean	1.41	0.91	

LSD ($P < 0.05$)

Plant ratio	NS
Phosphorus level	0.18
Interaction	NS

Table 3.38. Effects of plant ratio and P level on the mean relative yields (RY) and relative yield totals (RYT) calculated for dry matter yield of wheat (W) and wild oat (WO)

A. Effects of P levels
(Mean of three plant ratios)

	RYW	RYWO	RYT
L1	0.49	0.54	1.03
L2	0.50	0.49	0.99
LSD (P 0.05)	NS	NS	NS

B. Effects of plant ratios
(Mean of two P levels)

	RYW	RYWO	RYT
W4 + WO2	0.60	0.32	0.92
W3 + WO3	0.48	0.54	1.02
W2 + WO4	0.41	0.69	1.10
LSD (P 0.05)	0.09	0.10	0.10

C. Effects of plant ratio x P level (interaction)

	L1			L2		
	RYW	RYWO	RYT	RYW	RYWO	RYT
W4 + WO2	0.59	0.32	0.91	0.60	0.31	0.91
W3 + WO3	0.51	0.56	1.07	0.46	0.51	0.97
W2 + WO4	0.38	0.76	1.14	0.41	0.62	1.03

LSD (P< 0.05, interaction)

RYW	NS
RYWO	NS
RYT	NS

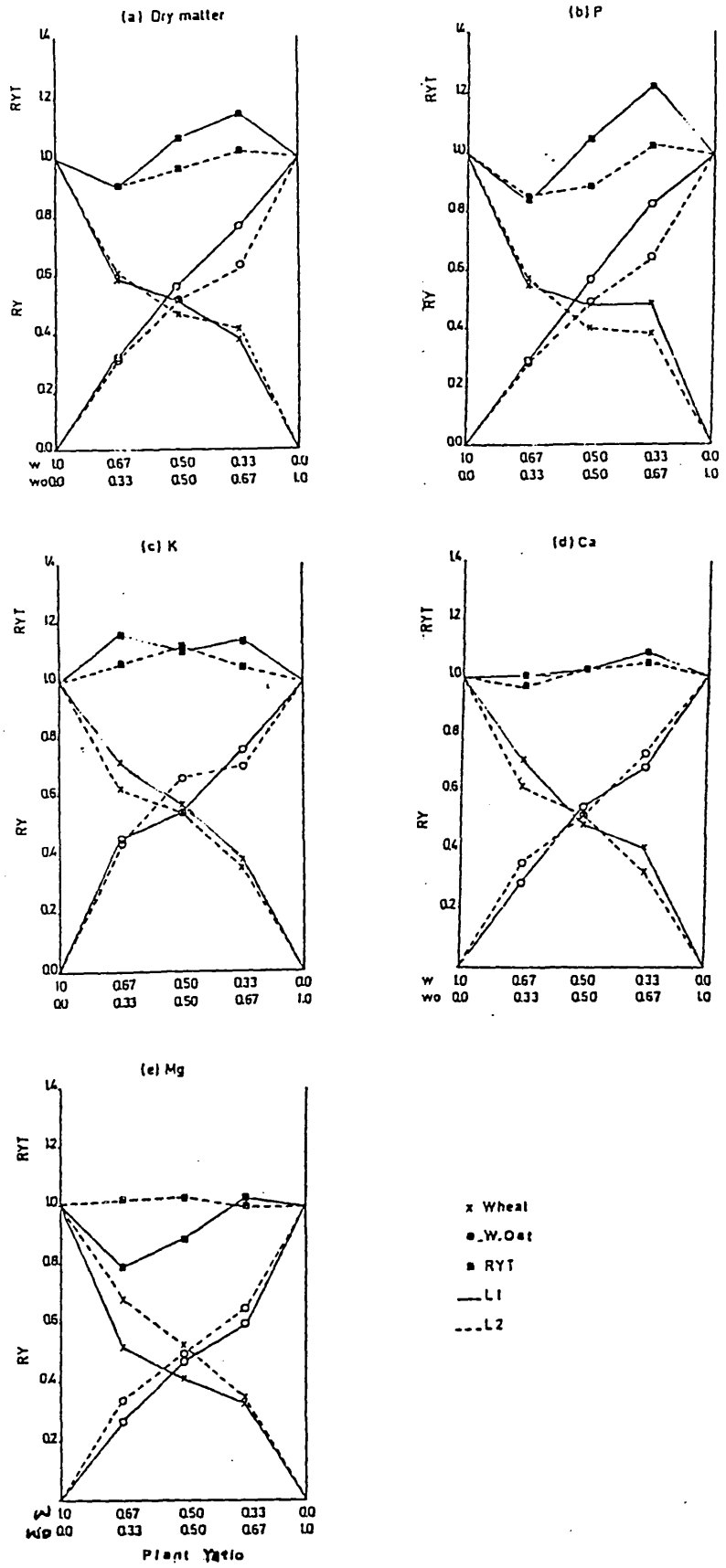


Figure 3.1 (a–e) Replacement series diagrams for wheat (W) and wild oat (WO) in response to levels of phosphorus

significantly. The yield of the weed, however, tended to decrease with increase in the number of wheat plants. In general, for all mixtures the dry matter accumulated by wild oat was greater than the crop.

(b) Relative yields (RY) and relative yield totals fRYT) for yields of dry matter

The effects of P level on the mean relative yields and relative yield totals of the species was not significant. Variation in plant proportion resulted in significant differences in both relative yields and relative yield totals (Table 3.3[illegible] and Fig. 3.1a). The relative yield of the crop decreased with increase in the number of plants of the weed, and the decrease in the relative yield of the latter with increase in the population of crop plants in the mixture was even greater. Higher ratios of wild oat in the mixture, however, produced greater values of relative yield of the weed than the crop. This shows that the effect of intraspecific competition in wild oat is less than interspecific competition with wheat. These relationships were clearly indicated by the significantly lower RYT of the two species when the proportion of the crop was higher than the weed and vice versa. When equal proportions were grown, the relative yield of the weed was higher by about 6%, and at that ratio RYT approximated to unity.

(c) Relative crowding coefficients of wheat (KWWO) and wild oat (KWOW) for yields of dry matter

Relative crowding coefficients (RCCs) also measure the competitive ability or aggressiveness of two competing species. At the higher P levels, the RCC of the weed was higher than that of the crop and at the lower level, the reverse was true, when the coefficients were summed over all plant ratios(Table 3.58a). The overall RCC for the weed, however, was higher than for the crop, indicating greater competitive ability on the crop. The products of the two RCCs varied with P and plant ratio. At the higher P level the product did not deviate from unity. At similar ratios of planting the ratios of the RCCs of the weed to the crop showed values greater than 1.0 at both levels of P. For example, these ratios were 0.83:1.20 and 0.86:1.16 at L1 and L2 and for wheat and wild oat respectively, indicating higher competitive power of the weed when equal proportions were mixed. The higher RCC of wild oat at the highest frequency of wheat may indicate greater competitiveness of the weed. At the highest ratio of the weed with wheat (i.e. W2 + WO4), relative CCs

Table 3.39. Effects of plant ratio and P levels on the nutrient concentration(s) (mMol./g shoot DW) in wheat (W) and wild oat (WO) in competition

A. Effects of plant ratio
(Mean over all P levels)

Nutrient	Species	Pure stand	W4+WO2	W3+WO3	W2+WO4	LSD(P 0.05)
P	W	0.24	0.22	0.22	0.24	NS
	WO	0.26	0.24	0.26	0.28	NS
K	W	0.65	0.68	0.71	0.60	0.05
	WO	0.60	0.87	0.71	0.65	0.08
Ca	W	0.33	0.36	0.34	0.31	0.05
	WO	0.43	0.44	0.42	0.44	NS
Mg	W	0.09	0.09	0.08	0.09	NS
	WO	0.15	0.14	0.14	0.14	NS

B. Effects of P levels
(Mean of plant ratio)

Nutrient	Species	L1	L2	LSD (P 0.05)
P	W	0.25	0.21	0.02
	WO	0.26	0.25	NS
K	W	0.56	0.76	0.04
	WO	0.52	0.89	0.06
Ca	W	0.36	0.31	0.04
	WO	0.52	0.89	0.06
Mg	W	0.09	0.09	NS
	WO	0.14	0.15	0.01

C. Effects of P levels x plant ratio

Nutrient	Species Frequency	L1 W	L1 WO	L2 W	L2 WO	LSD (P<0.05, interaction) W	LSD (P<0.05, interaction) WO
P	Pure stand	0.25	0.26	0.23	0.26		
	W4 + WO2	0.23	0.24	0.21	0.24	0.03	0.03
	W3 + WO3	0.24	0.26	0.20	0.25		
	W2 + WO4	0.27	0.28	0.21	0.27		
K	Pure stand	0.52	0.47	0.79	0.71		
	W4 + WO2	0.62	0.68	0.73	1.05	0.07	0.12
	W3 + WO3	0.58	0.45	0.84	0.96		
	W2 + WO4	0.53	0.48	0.67	0.83		
Ca	Pure stand	0.34	0.48	0.32	0.37		
	W4 + WO2	0.41	0.45	0.32	0.43	0.18	0.07
	W3 + WO3	0.32	0.47	0.36	0.37		
	W2 + WO4	0.36	0.44	0.25	0.44		
Mg	Pure stand	0.10	0.16	0.09	0.15		
	W4 + WO2	0.09	0.12	0.09	0.15	NS	NS
	W3 + WO3	0.08	0.13	0.09	0.15		
	W2 + WO4	0.09	0.14	0.09	0.15		

Table 3.40 Effects of plant ratio and P level on the nutrient concentrations (mMol/g shoot DW) in wheat (W) and barren brome (BB)

A. Effects of plant ratio
(Mean of P levels)

Nutrient	Species	Pure stand	W4+BB2	W3+BB3	W2+BB4	LSD(P 0.05)
P	W	0.24	0.23	0.23	0.23	NS
	BB	0.23	0.23	0.21	0.20	0.01
K	W	0.65	0.68	0.59	0.65	0.06
	BB	0.84	0.87	0.94	0.87	NS
Ca	W	0.33	0.37	0.39	0.36	NS
	BB	0.63	0.72	0.75	0.71	0.08
Mg	W	0.09	0.09	0.09	0.09	NS
	BB	0.12	0.13	0.14	0.14	0.02

B. Effects of P levels
(Mean of plant ratios)

Nutrient	Species	L1	L2	LSD ($P < 0.05$)
P	W	0.25	0.21	0.01
	BB	0.21	0.22	NS
K	W	0.52	0.76	0.04
	BB	0.64	1.12	0.07
Ca	W	0.37	0.35	NS
	BB	0.65	0.75	0.06
Mg	W	0.10	0.08	0.01
	BB	0.15	0.11	0.01

C. Effects of P levels x plant ratio

Nutrient	Species Frequency	L1		L2		LSD interaction ($P < 0.05$)	
		W	BB	W	BB	W	BB
P	Pure stand	0.25	0.21	0.23	0.24		
	W4 + BB2	0.25	0.21	0.21	0.24		
	W3 + BB3	0.25	0.22	0.21	0.20	NS	0.02
	W2 + BB4	0.26	0.22	0.20	0.19		
K	Pure stand	0.52	0.68	0.79	0.99		
	W4 + BB2	0.56	0.63	0.80	1.11		
	W3 + BB3	0.48	0.66	0.70	1.21	NS	0.14
	W2 + BB4	0.53	0.57	0.76	1.17		
Ca	Pure stand	0.34	0.61	0.32	0.64		
	W4 + BB2	0.34	0.65	0.39	0.78		
	W3 + BB3	0.42	0.68	0.36	0.83	NS	NS
	W2 + BB4	0.39	0.65	0.32	0.75		
Mg	Pure stand	0.10	0.13	0.09	0.10		
	W4 + BB2	0.09	0.14	0.08	0.11		
	W3 + BB3	0.10	0.17	0.08	0.12	NS	NS
	W2 + BB4	0.10	0.16	0.09	0.12		

Table 3.4i. Effects of planting frequency and P level on the nutrient concentration (mMol/g shoot DW) in wild (WO) and barren brome (BB)

A. Effects of plant ratio
(Mean of P levels)

Nutrient	Species	Pure stand	WO4+BB2	WO3+BB3	WO2+BB4	LSD(P 0.05)
P	WO	0.26	0.28	0.26	0.24	NS
	BB	0.23	0.29	0.23	0.21	0.02
K	WO	0.60	0.65	0.75	0.73	0.11
	BB	0.84	0.86	0.82	0.90	NS
Ca	WO	0.43	0.32	0.41	0.43	0.05
	BB	0.63	0.66	0.66	0.58	NS
Mg	WO	0.15	0.16	0.14	0.14	0.01
	BB	0.12	0.13	0.14	0.14	NS

B. Effects of P levels
(Mean of plant ratio)

Nutrient	Species	L1	L2	LSD (P 0.05)
P	WO	0.25	0.26	NS
	BB	0.23	0.24	NS
K	WO	0.49	0.88	0.08
	BB	0.62	1.09	0.08
Ca	WO	0.41	0.38	0.04
	BB	0.59	0.68	0.09
Mg	WO	0.14	0.15	0.01
	BB	0.14	0.12	0.02

C. Effects of plant ratio x P level

Nutrient	Species Frequency	L1		L2		LSD ($P < 0.05$, interactions)	
		WO	BB	WO	BB	WO	BB
P	Pure stand	0.26	0.21	0.26	0.24		
	WO4 + BB2	0.28	0.31	0.28	0.27	NS	0.03
	WO3 + BB3	0.25	0.20	0.28	0.26		
	WO2 + BB4	0.26	0.25	0.23	0.19		
K	Pure stand	0.47	0.68	0.73	0.99		
	WO4 + BB2	0.49	0.59	0.82	1.13		
	WO3 + BB3	0.54	0.60	0.97	1.19	0.16	NS
	WO2 + BB4	0.44	0.61	1.01	1.19		
Ca	Pure stand	0.48	0.61	0.37	0.64		
	WO4 + BB2	0.33	0.53	0.32	0.79		
	WO3 + BB3	0.44	0.61	0.37	0.70	0.07	NS
	WO2 + BB4	0.39	0.59	0.46	0.58		
Mg	Pure stand	0.15	0.13	0.15	0.10		
	WO4 + BB2	0.15	0.13	0.18	0.13		
	WO3 + BB3	0.14	0.16	0.14	0.13	0.02	NS
	WO2 + BB4	0.12	0.15	0.15	0.14		

Table 3.42. Effects of plant ratio and P level on the relative nutrient yields (RY) and relative yield totals (RYT) of wheat (W) and wild oat (WO) calculated for P contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYWO	RYT
L1	0.49	0.56	1.05
L2	0.45	0.47	0.92
LSD ($P < 0.05$)	NS	0.08	0.10

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYWO	RYT
W4 + WO2	0.56	0.29	0.85
W3 + WO3	0.44	0.53	0.97
W2 + WO4	0.39	0.73	0.12
LSD ($P < 0.05$)	0.08	0.10	0.12

C. Effects of P level x plant ratio

	L1			L2		
	RYW	RYWO	RYT	RYW	RYWO	RYT
W4 + WO2	0.55	0.29	0.84	0.57	0.28	0.85
W3 + WO3	0.48	0.57	1.05	0.40	0.49	0.89
W2 + WO4	0.40	0.83	1.23	0.38	0.64	1.02

LSD ($P < 0.05$, interaction)

RYW	NS
RYWO	NS
RYT	NS

and their products were close to unity, suggesting competitive interference between them.

(d) Nutrient concentrations in wheat and wild oat

The concentrations of P and Mg in both species and Ca in the weed were not affected by changes in their proportions. K concentration in both species, and Ca in the crop, however, differed significantly with plant ratio. The concentrations of these nutrients were higher in the weed in almost at all combinations (Table 3.39). Phosphorus level also significantly affected K and Ca concentrations in both species, P in wheat and Mg in wild oat. At both P levels, the concentrations of these elements were higher in the weed. The interaction between P levels and plant ratios also showed similar trends in both species.

(e) Relative yields (RYs) and relative yield totals (RYTs) for nutrient contents in wheat (W) and wild oat (WO)

The relative yields (RYs) for P content in wild oat (RYWO) and K content in wheat were significantly affected by levels of P. In both species relative yields were higher at higher P than lower. The level of phosphorus had no effect on the relative yields for Ca and Mg content in both species (Tables 3.42-3.45). RYTs differed between P levels only for P content. The results also showed that the relative yields for the nutrient contents of P, K, Ca and Mg in wheat and wild oat were affected by plant ratios. Both species showed higher relative yields when their numbers were higher than the competitor in the mixture. In such mixtures the relative yields of the weed were higher than those of the crop. When numbers of the two component species were equal, the RY of wild oat was greater than that of wheat for all four nutrients, indicating that it was more competitive than the crop. RYTs differed statistically between plant ratios, but only for P content (Tables 3.42-3.45). In most cases RYTs were close to unity (Figs. 3.1b, c, d and e) suggesting that the two species may be making the same demand on the environmental resources. In some situations RYTs were substantially greater than 1.0. This implies that the two species escape some measure of competition with each other which may take place when components are limited by different resources. Where the RYTs were <1.0, some mutual antagonism may be inferred.

Relative crowding coefficients (RCCs) of each species and their products were also close to 1.0. The RCC of wild oat towards the crop

Table 3.43 · Effects of plant ratio and P level on the relative nutrient yields (RY) and relative yield totals (RYT) of wheat (W) and wild oat (WO) calculated for K contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYWO	RYT
L1	0.56	0.58	1.14
L2	0.48	0.60	1.08
LSD ($P < 0.05$)	0.07	NS	NS

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYWO	RYT
W4 + WO2	0.67	0.45	1.12
W3 + WO3	0.52	0.60	1.12
W2 + WO4	0.37	0.73	1.10
LSD ($P < 0.05$)	0.09	0.12	NS

C. Effects of P level x plant ratio

	L1			L2		
	RYW	RYWO	RYT	RYW	RYWO	RYT
W4 + WO2	0.72	0.45	1.17	0.62	0.44	1.06
W3 + WO3	0.57	0.54	1.11	0.46	0.66	1.12
W2 + WO4	0.38	0.76	1.14	0.35	0.70	1.05

LSD ($P < 0.05$, interaction)

RYW	NS
RYWO	NS
RYT	NS

Table 3.44. Effects of plant ratio and P level on the relative nutrient yields (RY) and relative yield totals (RYT) of wheat (W) and wild oat (WO) calculated for Ca contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYWO	RYT
L1	0.53	0.50	1.03
L2	0.48	0.53	1.01
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYWO	RYT
W4 + WO2	0.66	0.32	0.98
W3 + WO3	0.50	0.53	1.03
W2 + WO4	0.36	0.71	1.07
LSD ($P < 0.05$)	0.12	0.09	NS

C. Effects of P level x plant ratio

	L1			L2		
	RYW	RYWO	RYT	RYW	RYWO	RYT
W4 + WO2	0.71	0.29	1.00	0.61	0.35	0.96
W3 + WO3	0.48	0.54	1.02	0.51	0.51	1.02
W2 + WO4	0.40	0.68	1.08	0.32	0.73	1.05

LSD ($P < 0.05$, interaction)

RYW	NS
RYWO	NS
RYT	NS

Table 3.45. Effects of plant ratio and P level on the relative nutrient yields(RY) and relative yield totals (RYT) of wheat (W) and wild oat (WO) calculated for Mg contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYWO	RYT
L1	0.42	0.47	0.89
L2	0.51	0.48	0.99
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYWO	RYT
W4 + WO2	0.57	0.30	0.87
W3 + WO3	0.44	0.49	0.93
W2 + WO4	0.38	0.64	1.02
LSD ($P < 0.05$)	0.12	0.10	NS

C. Effects of P levels x plant ratio

	L1			L2		
	RYW	RYWO	RYT	RYW	RYWO	RYT
W4 + WO2	0.52	0.27	0.79	0.62	0.32	0.94
W3 + WO3	0.41	0.47	0.88	0.47	0.51	0.98
W2 + WO4	0.33	0.69	1.02	0.43	0.60	1.03

LSD ($P < 0.05$, interaction)

RYW	NS
RYWO	NS
RYT	NS

was slightly higher for yields of dry matter, P and Mg contents at the higher P level and the crop was higher for K and Ca at that level. At low P, the weed showed higher values for P, K and Ca whilst those of the crop were higher for dry matter and Mg content.

2. Effects of planting frequency and P level on the competitive relationship between wheat and barren brome

(a) Dry matter yield

The dry matter yields (g/plant) of both species were significantly affected by the level of P applied (Table 3.46). The yields of these species were not different whether grown in pure stands or mixtures.

(b) Relative yields (RY) and relative yield totals (RYT)

The relative yields and their totals calculated for dry matter yields of the species were not affected by the level of P. The frequency of planting, significantly affected the relative yields of both species. Their RYTs did not vary with planting ratios, although they tended to increase with increase in the proportion of barren brome. In such mixtures the relative yield of wheat increased more than that of the weed, and contributed towards increase in RYT (Table 3.48, Fig. 3.2a).

(c) Nutrient concentration in wheat and barren brome in competition

P level significantly affected K and Mg concentrations of both species. P level did not affect P concentration in the weed and Ca concentration in the crop. The weed contained higher concentrations of K, Ca and Mg at both high and low levels of P (Table 3.40b). Planting proportion, however, did not change P, Ca and Mg concentrations in wheat, or those of K and Mg in the weed. The interactions of both factors affected the concentrations of P and K in the weed only. For any given element, the effects of P level, planting ratio and their interactions resulted in a slightly or significantly higher concentration in the weed for K, Ca and Mg (Table 40c) The Ca and Mg concentration of barren brome significantly increased in mixtures over pure stand, and that of K also increased slightly, while P decreased in mixtures. In wheat, the concentrations of these elements either slightly increased in competition with the weed or remained similar (Table 3.40a).

Table 3.46. Effects of plant ratio and P level on the mean dry matter yields of wheat (W) and barren brome (BB)

(Mean of 2 harvests)

A. Wheat yield (g/plant)

Plant ratio	P level L1	L2	Mean
W6 + BB0 (pure wheat)	1.17	0.78	0.98
W4 + BB2	1.18	0.78	0.99
W3 + BB3	1.24	0.88	1.06
W2 + BB4	1.19	1.02	1.10
Mean	1.20	0.87	

LSD ($P < 0.05$)

Plant ratio	NS
P level	0.11
Interaction	NS

B. Barren brome (g/plant)

Plant ratio	P level L1	L2	Mean
BB6 + W0 (pure b. brome)	0.95	0.56	0.75
BB4 + W2	0.89	0.59	0.74
BB3 + W3	0.95	0.47	0.71
BB2 + W4	0.83	0.59	0.71
Mean	0.90	0.55	

LSD ($P < 0.05$)

Plant ratio	NS
P level	0.08
Interaction	NS

Table 3.47. Effects of plant ratio and P level on the mean dry matter yield of wild oat (WO) and barren brome (BB)

(Mean of 2 harvests)

A. Wild oat yield (g/plant)

Plant ratio	P level L1	L2	Mean
SO6 + BB0 (pure wild oat)	1.35	0.92	1.14
SO4 + BB2	1.37	0.96	1.17
WO3 + BB3	1.53	0.94	1.24
WO2 + BB4	1.80	0.96	1.38
Mean	1.51	0.95	

LSD ($P < 0.05$)

Plant ratio	NS
P level	0.13
Interaction	NS

B. Barren brome yield (g/plant)

Plant ratio	P level L1	L2	Mean
BB6 + WO0 (pure b. brome)	0.95	0.56	0.75
BB4 + WO2	0.93	0.60	0.77
BB3 + WO3	0.88	0.50	0.69
BB2 + WO4	0.88	0.50	0.69
Mean	0.91	0.54	

LSD ($P < 0.05$)

Plant ratio	0.040
P level	0.29
Interaction	NS

Table 3.48 Effects of plant ratio and P level on mean relative (RY) and relative yield totals (RYT) of wheat (W) and barren brome (BB) calculated for shoot dry matter yields

A. Effects of P levels
(Mean of three plant ratio)

	RYW	RYBB	RYT
L1	0.51	0.47	0.98
L2	0.56	0.50	1.06
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Mean of two P levels)

	RYW	RYBB	RYT
W4 + BB2	0.67	0.32	0.99
W3 + BB3	0.55	0.46	1.01
W2 + BB4	0.39	0.68	1.07
LSD ($P < 0.05$)	0.10	0.09	NS

C. Effects of plant ratio x P level (interaction)

	L1			L2		
	RYW	RYBB	RYT	RYW	RYBB	RYT
W4 + BB2	0.67	0.29	0.96	0.67	0.36	1.03
W3 + BB3	0.53	0.50	1.03	0.56	0.42	0.98
W2 + BB4	0.34	0.62	0.96	0.43	0.71	1.14

LSD ($P < 0.05$)

RYW	NS
RYBB	NS
RYT	NS

Table 3.49. Effects of plant ratio and P level on mean relative yield (RY) and relative yield totals (RYT) for wild oat (WO) and barren brome (BB) calculated for shoot dry matter yield

A. Effects of P level
(Mean of three plant ratios)

	RYWO	RYBB	RYT
L1	0.56	0.47	1.03
L2	0.52	0.49	1.01
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Mean of two P levels)

	RYWO	RYBB	RYT
WO4 + BB2	0.68	0.30	0.98
WO3 + BB3	0.54	0.46	1.00
WO2 + BB4	0.39	0.69	1.08
LSD ($P < 0.05$)	0.08	0.04	0.09

C. Effects of plant ratio x P level

	L1			L2		
	RYWO	RYBB	RYT	RYWO	RYBB	RYT
WO4 + BB2	0.68	0.31	0.99	0.69	0.31	1.00
WO3 + BB3	0.57	0.46	1.03	0.51	0.46	0.97
WO2 + BB4	0.44	0.65	1.09	0.35	0.72	1.07

LSD interaction ($P < 0.05$)

RYWO	NS
RYBB	NS
RYT	NS

Table 3.50 Effects of plant ratio and P level on the relative nutrient yields (RY) and relative yield totals RYT) of wheat (W) and barren brome (BB) calculated for P contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYBB	RYT
L1	0.52	0.49	1.01
L2	0.50	0.42	0.92
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYBB	RYT
W4 + BB2	0.63	0.33	0.96
W3 + BB3	0.54	0.43	0.97
W2 + BB4	0.37	0.61	0.98
LSD ($P < 0.05$)	0.06	0.09	NS

C. Effects of plant ratio x P level

	L1			L2		
	RYW	RYBB	RYT	RYW	RYBB	RYT
W4 + BB2	0.66	0.29	0.95	0.60	0.37	0.97
W3 + BB3	0.57	0.52	1.09	0.52	0.34	0.86
W2 + BB4	0.34	0.65	0.99	0.39	0.56	0.95

LSD ($P < 0.05$, interaction)

RYW	NS
RYBB	0.13
RYT	NS

Table 3.51 Effects of plant ratio and P level on the relative nutrient yields (RY) and relative yield totals (RYT) of wheat (W) and barren brome (BB) calculated for K contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYBB	RYT
L1	0.54	0.43	0.97
L2	0.53	0.58	1.11
LSD ($P < 0.05$)	NS	0.09	0.13

B. Effects of plant ratio
(Means of 2 P levels)

	RYW	RYBB	RYT
W4 + BB2	0.70	0.33	1.03
W3 + BB3	0.52	0.50	1.02
W2 + BB4	0.38	0.68	1.06
LSD ($P < 0.05$)	0.08	0.11	NS

C. Effects of plant ratio x P level

	L1			L2		
	RYW	RYBB	RYT	RYW	RYBB	RYT
W4 + BB2	0.72	0.26	0.98	0.68	0.40	1.08
W3 + BB3	0.54	0.49	1.03	0.50	0.51	1.01
W2 + BB4	0.35	0.53	0.88	0.42	0.84	1.26

LSD ($P < 0.05$, interaction)

RYW	NS
RYBB	0.16
RYT	NS

Table 3.52 Effects of plant ratio and P level on the relative nutrient yields (RY) and relative nutrient yield totals (RYT) of wheat (W) and barren brome (BB) calculated for Ca contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYBB	RYT
L1	0.60	0.51	1.11
L2	0.62	0.61	1.23
LSD ($P < 0.05$)	NS	0.09	NS

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYBB	RYT
W4 + BB2	0.74	0.37	1.11
W3 + BB3	0.68	0.55	1.23
W2 + BB4	0.41	0.75	1.16
LSD ($P < 0.05$)	0.09	0.11	NS

C. Effects of plant ratio x P level

	L1			L2		
	RYW	RYBB	RYT	RYW	RYBB	RYT
W4 + BB2	0.67	0.31	0.98	0.81	0.44	1.25
W3 + BB3	0.74	0.55	1.29	0.62	0.56	1.18
W2 + BB4	0.39	0.67	1.06	0.44	0.83	1.27

LSD ($P < 0.05$, interaction)

RYW	0.13
RYBB	NS
RYT	NS

Table 3.53 Effects of plant ratio and P level on relative nutrient yields (RY) and relative yield totals (RYT) of wheat (W) and barren brome (BB) calculated for Mg contents

A. Effects of P level
(Means of three plant ratios)

	RYW	RYBB	RYT
L1	0.50	0.56	1.06
L2	0.51	0.57	1.08
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Means of two P levels)

	RYW	RYBB	RYT
W4 + BB2	0.61	0.34	0.95
W3 + BB3	0.53	0.57	1.10
W2 + BB4	0.39	0.78	1.17
LSD ($P < 0.05$)	0.07	0.13	NS

C. Effects of P levels x plant ratio

	L1			L2		
	RYW	RYBB	RYT	RYW	RYBB	RYT
W4 + BB2	0.61	0.32	0.93	0.61	0.36	0.97
W3 + BB3	0.56	0.63	1.19	0.50	0.51	1.01
W2 + BB4	0.35	0.73	1.08	0.42	0.83	1.25

LSD ($P < 0.05$, interaction)

RYW	NS
RYBB	NS
RYT	NS

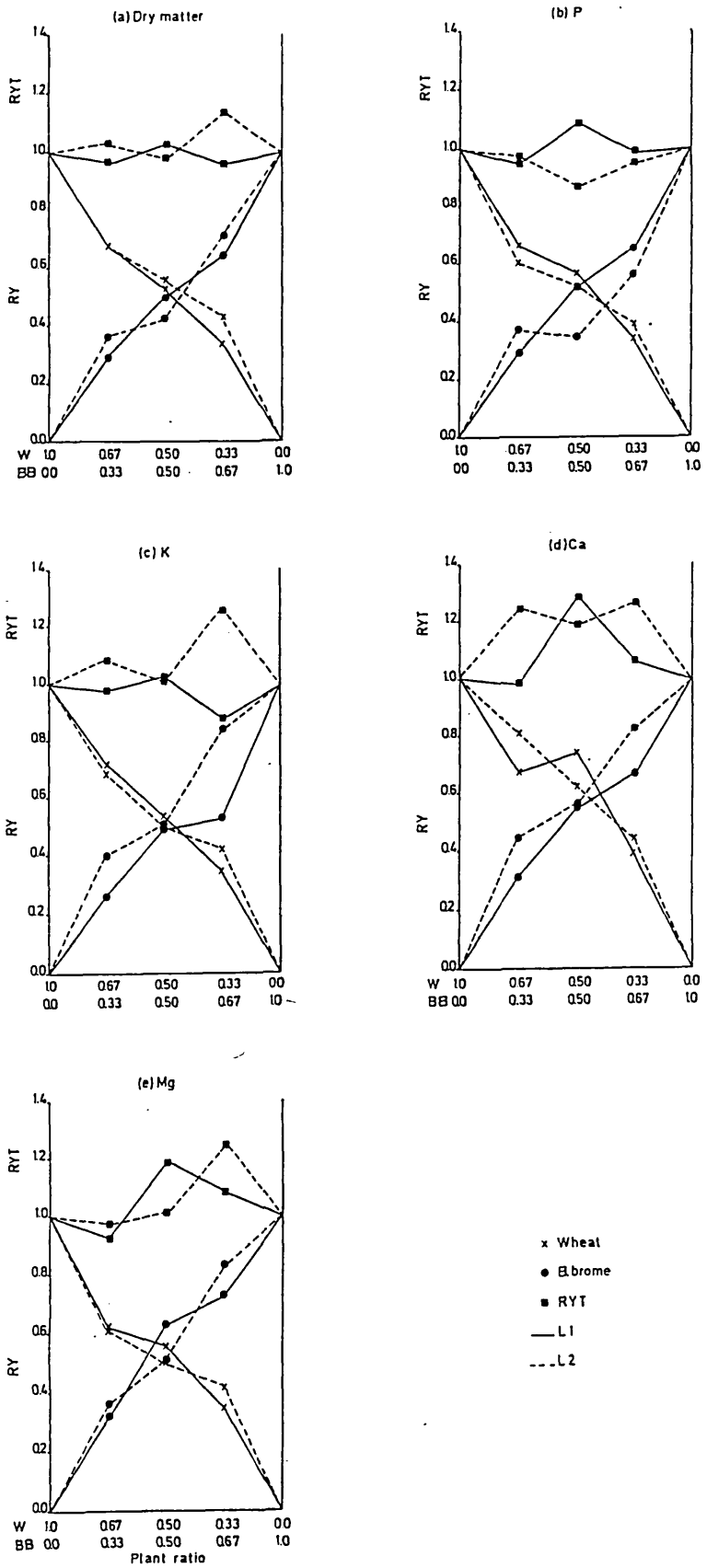


Figure 3.2 (a–e) Replacement series diagrams for wheat (W) and barren brome (BB) in response to levels of phosphorus

(d) Relative yields (RYs), relative yield totals (RYTs) and relative crowding coefficients (RCCs) for nutrient concentrations of wheat (W) and barren brome (BB)

The relative yields of wheat or barren brome for P and Mg contents did not differ significantly between the two P levels. The relative yields of wheat for K and Ca were not affected by levels of P, whilst that of barren brome was (Tables 3.50-3.53). RYTs did not differ between P levels except for K contents. RYTs for P contents were 1.0 at the lower P and for all species combinations. RYs of wheat and barren brome increased when their ratios were higher in the mixtures; where ratios were similar the RYs of the crop were greater than this weed, indicating its greater competitiveness. The interactions between plant ratio and P levels were significant in barren brome for the contents of P and K, whilst that of the crop was different for Ca only. RYTs varied with plant ratios and P levels (Tables 3.50-3.53; Figs 3.2b, c, d, and e). In general RYTs for Ca and Mg were greater than 1.0 for the main effects and their interactions.

Relative crowding coefficients were higher for the nutrients in wheat except for Mg and K contents at high and low levels of P respectively. The products of RCCs were either equal to 1.0 or slightly higher and may thus indicate both competitive and non-competitive interference. RCC for yields of dry matter in barren brome were $\geq$ 1.0 at both P levels whilst that of the crop was significantly higher and may also show greater competitive ability than the weed (Table 3.58b).

3. Effects of plant ratio and P level on the competitive relationships between wild oat (WO) and barren brome (BB)

(a) Dry matter yield (g/plant)

The dry matter yield accumulated by both weed species increased significantly at higher phosphorus. Planting proportion significantly affected the yield of barren brome, but not of wild oat. The pure stand yield in barren brome was higher than that in mixture with wild oat, except at the 50% combination, while that of the latter was lower in pure stand than in mixtures (Table 3.47a and b). Since wild oat was a larger plant than barren brome the possibility that some competition for light may have affected the outcome of competition cannot be totally excluded.

Table 3.54 Effects of plant ratio and P level on the relative nutrient yields (RY) and relative yield totals (RYT) of wild oat (WO) and barren brome (BB) calculated for P contents

A. Effects of P level
(Means of three plant ratios)

	RYWO	RYBB	RYT
L1	0.52	0.52	1.04
L2	0.53	0.48	1.01
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Means of two P levels)

	RYWO	RYBB	RYT
WO4 + BB2	0.74	0.41	1.15
WO3 + BB3	0.56	0.46	1.00
WO2 + BB4	0.38	0.64	1.02
LSD ($P < 0.05$)	0.10	0.08	0.12

C. Effects of P level x plant ratio

	L1			L2		
	RYWO	RYBB	RYT	RYWO	RYBB	RYT
WO4 + BB2	0.74	0.45	1.19	0.73	0.36	1.09
WO3 + BB3	0.57	0.43	1.00	0.55	0.48	1.03
WO2 + BB4	0.44	0.68	1.12	0.31	0.59	0.90

LSD ($P < 0.05$, interaction)

RYWO	NS
RYBB	NS
RYT	NS

Table 3.55 Effects of plant ratio and P level on the relative nutrient yields (RY) and relative nutrient yield totals (RYT) of wild oat (WO) and barren brome (BB) calculated for K contents

A. Effects of P level
(Means of three plant ratio)

	RYWO	RYBB	RYT
L1	0.61	0.42	1.03
L2	0.64	0.57	1.21
LSD ($P < 0.05$)	NS	0.06	0.11

B. Effects of plant ratio
(Means of two P levels)

	RYWO	RYBB	RYT
WO4 + BB2	0.77	0.31	1.08
WO3 + BB3	0.66	0.45	1.11
WO2 + BB4	0.45	0.73	1.18
LSD ($P < 0.05$)	0.10	0.07	NS

C. Effects of P level x plant ratio

	L1			L2		
	RYWO	RYBB	RYT	RYWO	RYBB	RYT
WO4 + BB2	0.77	0.27	1.04	0.77	0.36	1.13
WO3 + BB3	0.66	0.41	1.07	0.67	0.49	1.16
WO2 + BB4	0.41	0.58	0.99	0.49	0.87	1.36

LSD ($P < 0.05$, interaction)

RYWO	NS
RYBB	0.10
RYT	NS

Table 3.56 Effects of plant ratio and P level on the relative nutrient yield (RY) and relative yield totals (RYT) of wild oat (WO) and barren brome (BB) calculated for Ca content

A. Effects of P levels
(Means of three P levels)

	RYWO	RYBB	RYT
L1	0.44	0.45	0.89
L2	0.51	0.51	1.02
LSD ($P < 0.05$)	NS	0.06	0.12

B. Effects of plant ratio
(Means of two P levels)

	RYWO	RYBB	RYT
WO4 + BB2	0.53	0.33	0.86
WO3 + BB3	0.51	0.48	0.98
WO2 + BB4	0.40	0.63	1.03
LSD ($P < 0.05$)	0.11	0.07	0.14

C. Effects of plant ratio x P level

	L1			L2		
	RYWO	RYBB	RYT	RYWO	RYBB	RYT
WO4 + BB2	0.47	0.27	0.74	0.59	0.39	0.98
WO3 + BB3	0.52	0.47	0.99	0.51	0.49	1.00
WO2 + BB4	0.36	0.62	0.98	0.44	0.65	1.09

LSD ($P < 0.05$, interaction)

RYWO	NS
RYBB	NS
RYT	NS

Table 3.57 Effects of plant ratio and P level on the relative yields (RY) and relative yield totals (RYT) of wild oat (WO) and barren brome (BB) claculated for Mg contents

A. Effects of P level
(Means of three plant ratios)

	RYWO	RYBB	RYT
L1	0.51	0.53	1.04
L2	0.56	0.67	1.23
LSD ($P < 0.05$)	NS	0.07	0.14

B. Effects of plant ratio
(Means of two plant ratios)

	RYWO	RYBB	RYT
WO4 + BB2	0.75	0.35	1.10
WO3 + BB3	0.50	0.58	1.08
WO2 + BB4	0.36	0.87	1.25
LSD ($P < 0.05$)	0.08	0.09	NS

C. Effects of plant ratio x P levels

	L1			L2		
	RYWO	RYBB	RYT	RYWO	RYBB	RYT
WO4 + BB2	0.67	0.31	0.98	0.83	0.39	1.22
WO3 + BB3	0.52	0.56	1.08	0.49	0.60	1.09
WO2 + BB4	0.35	0.72	1.07	0.36	1.01	1.37

LSD ($P < 0.05$, interaction)

RYWO	NS
RYBB	0.12
RYT	NS

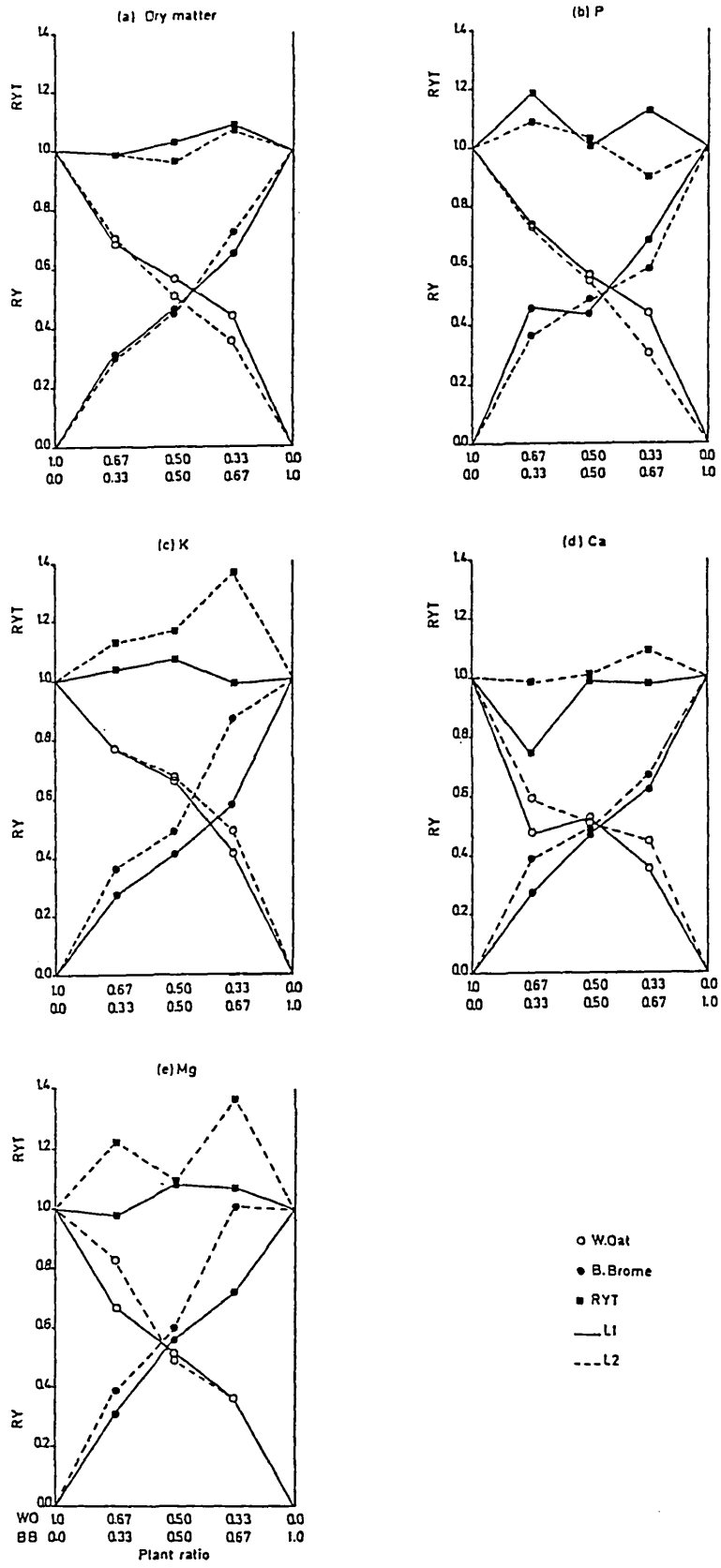


Figure 3.3 (a–e) Replacement series diagrams for wild oat (WO) and barren brome (BB) in response to levels of phosphorus

(b) Relative yields (RYs) and relative yield totals (RYTs)

The RYs and RYTs of these species were affected by plant ratios and phosphorus, but the interaction had no significant effect on either variate (Table 3.49, Fig. 3.3a). The RY of wild oat at the two levels of P and similar frequencies of planting was always higher for wild oat.

(c) Relative crowding coefficient (RCC) for dry matter yields of wild oat and barren brome

The mean RCC of wild oat with respect to barren brome at the two levels of P was greater than the converse (Table 3.58c). This supports the observation made for their relative yields.

(d) Nutrient concentrations

The planting frequencies affected K, Ca and Mg concentrations in wild oat only. Phosphorus concentration in barren brome was also affected by the planting frequency and its interaction with P levels. Interactions were significant in wild oat for K, Ca and mg (Tables 3.45a, b and c). Barren brome showed higher concentrations of K and Ca, whilst wild oat had slightly higher P and Mg concentrations. The pure stand K, Ca and Mg concentrations in barren brome were similar to those in mixtures, except for P in WO4 + BB2 where it was lower. In wild oat, P concentration was similar for all combinations and K concentration was lower in pure stands than in mixture with barren brome. Ca and Mg concentrations were either similar or higher in pure stands than in the mixtures with barren brome. The level of P affected concentrations of all nutrients except P in both weeds. At both levels K and Ca concentrations were higher in barren brome and wild oat had slightly higher concentrations for P and Mg. Interactions were similar for both species.

(e) Relative yields (RYs) and relative yield totals (RYTs) for nutrient contents in wild oat (WO) and barren brome (BB)

P level significantly affected relative yields of barren brome for the contents of K, Ca and Mg, whilst the RYs of wild oat for the contents of these elements and for P was not affected. The RY of barren brome for P was also not affected by P. The RYTs for the different nutrients also differed between P levels except for P content. RYs for both species and their totals differed between mixtures for all the elements. Exceptions

Table 3.58 (a) Effects of plant ratio and P level on the relative crowding coefficients (RCCs) of wheat (KWWO) and wild oat (KWOW) for yields of dry matter and some mineral nutrient contents (all figures per plant)

	P level					
	L1			L2		
	KWWO	KWOW	KWWO x KWOW	KWWO	KWOW	KWWO x KWOW
DM yield	0.97	1.06	1.03	1.14	0.95	1.08
P	0.92	1.09	1.00	0.98	1.05	1.03
K	1.11	1.09	1.21	0.79	1.31	1.03
Ca	1.11	0.91	1.01	0.95	1.06	1.00
Mg	0.94	1.07	1.01	1.15	0.88	1.02

Table 3.58 (b) Effects of plant ratio and P level on the relative crowding coefficients (RCCs) of wheat (KWBB) and barren brome (KBBW) calculated for yields of dry matter and some mineral nutrient contents (all figures per plant)

	P level					
	L1			L2		
	KWBB	KBBW	KWBB x KBBW	KWBB	KBBW	KWBB x KBBW
DM yield	1.13	0.92	1.04	1.17	0.89	1.04
P	1.06	0.94	1.00	1.24	0.86	1.08
K	1.22	0.83	1.00	1.24	0.87	1.08
Ca	1.20	0.83	1.00	1.07	0.94	1.01
Mg	0.87	1.18	1.03	1.05	0.97	1.02

Table 3.58 (c) Effects of plant ratio and P level on the relative crowding coefficients (RCCs) of wild oat (KWOBB) and barren brome (KBBWO) calculated for yields of dry matter and some mineral nutrient contents (all figures per plant)

	P level					
	L1			L2		
	KWOBB	KBBW0	KWOBBxKBBWO	KWOBB	KBBWO	KWOBBxKBBWO
DM yield	1.23	0.83	1.02	1.02	1.01	1.03
P	1.16	0.91	1.05	1.22	0.83	1.01
K	1.48	0.67	0.99	1.17	0.86	1.01
Ca	1.19	0.85	1.01	1.04	1.01	1.05
Mg	1.01	1.00	1.01	0.92	1.12	1.03

were RYTs for K and Mg (Tables 3.54-3.57). Interactions were not significant for the relative yields and their totals for the different elements except for RYs of barren brome for K and Mg. The results also indicate that the RYs of both weeds were higher when members of each in the component mixtures are greater than the other. The RY of wild oat in the 50:50 mixtures (i.e. WO3 + BB3) were always higher for wild oat except for Mg, where the RY of barren brome was greater (Fig. 3.3b, c, d, and e). The relative crowding coefficient of wild oat with respect to barren brome also showed greater values for the former for dry matter yields, P, K and Ca (Table 3.58c). The RCC of barren brome was greater than wild oat only for Mg. Thus evidence from RYs and RCCs suggested that wild oat is a stronger competitor than barren brome. Although barren brome showed higher concentrations for these elements in these experiments and elsewhere in response experiments (Section I), it was not superior in competition to either species, partly due to its small size.

7.5.2. Discussion

The competitive relationships of the three species in replacement/substitutive experiments were assessed in a number of ways. The ability of an individual species to accumulate dry matter (g/plant) in competition was assessed by analysis of variance carried out on the data for each species separately. The nutrient concentrations (mMols/g DW) were similarly analysed. In order to assess whether a species had made gains/losses in competition as a result of treatment effects in these type of experiment, relative yield (RY) of a species with respect to its yield in pure form was calculated. Relative yield totals (RYT) for any two competing species were also calculated. These were also subjected to analysis of variance and further presented in Replacement Diagrams, which are representations of the relative yields and the relative yield/totals of two competing species. Because graphical presentation of yield data allows the identification of the stronger competitor and the extent of niche overlap between species, replacement series experiments have proved useful and have been used widely to investigate competition for specific nutrients (Hall, 1974a, b). De Wit (1960) first introduced replacement series experimental models and according to him values of RYT = 1.0 imply that the two species are making demands on the same limiting resources of the environment. Values

of RYT 1.0 suggest that the species made different demands on resources, avoid competition with each other or are showing some form of 'symbiotic' relationship. Valaues of RYT of 1.0 imply mutual antagonism. In the present study, RYT of wheat in association with wild oat or barren brome, or wild oat with barren brome was very close to unity. This occurs when an increase in RY of one component in a mixture is exactly matched by the decrease in RY of the other component. When this occurs, the two species in a mixture are said by de Wit (1960) to be 'crowding for the same space' (or competing for the same resources) and are 'mutually exclusive'. Competition for the same resources could be for light above ground (i.e. shoot competition) and/or for nutrients and water below ground (i.e. root competition).

The competitive ability of the species was also assessed by another mathematical index - 'the relative crowding coefficient, K', first introduced by de Wit (1960), and used by many others e.g. Bakhuis and Kleter (1965) and Hall (1974a, b). The values of relative crowding coefficients (RCC) for each species and their products are used to describe the occurrence and extent of interference between a plant, or plant species and its neighbours. De Wit (1960) states that when the two species compete for the same space (competitive interference) the products of their relative crowding coefficients for yield should equal 1, and the two space are mutually exclusive. If the product is 1.0, although they may still be competing for the same resource or resources, they are also competing for different space i.e. non-competitive interference is perhaps taking place in addition to competitive interference. Relative crowding coefficient has been used to identify the limiting factor governing the growth of two species in association. In the present study, the RCCs were calculated for nutrient contents of the species, as well as for dry matter, and this data have been compared. The relative crowding coefficients for the various plant nutrients and dry matter data in these studies showed a wide range of values (Tables 3.58a and 3.63a, b and c).

Replacement series experiments have been widely used by a number of investigators in the study of competitive relationships of different species for various plant nutrients (Bhaskar and Vyas, 1988; Johnson, 1987; Hall, 1974a, b; Newman and Andrews, 1973; Tarawali, 1983; Wellbank, 1963). The earlier investigations of de Wit (1960, 1961) and de Wit and Van den Burgh (1965) involved the use of replacement series to study

'competition for space' - a composite of all growth resources and the interactions between them. This does not attempt to identify any particular growth limiting factor in the association of species. Hall (1974a) extended the concept to the identification of individual factors affecting competition. By expressing results in terms of total K uptake he examined the effects of K on the growth in monoculture and mixtures of the tropical species, Setaria anceps cv. Nandi and Desmodium intortum cv. Greenleaf. He was able to show the importance of the element in suppressing the growth of the legume by the tropical grass. Similarly he (Hall, 1974b) also studied the role of N in the relationships between another grass, Chloris gayana (Rhodes grass), and a legume, Stylosanthes humilis (Townsville stylo). In this association he was able to demonstrate the existence of competitive and non-competitive interference using the concepts of relative crowding coefficients (RCC) for dry matter yield and N concentrations in the two species.

In the present experiments RCCs for the competing species were calculated for their dry matter yields, P, K, Ca and Mg nutrient yields according to the formula given by de Wit (1960), and Harper (1977). Results of analyses on the mean relative crowding coefficients for yields of dry matter and some mineral nutrients also varied with the different elements, P levels and plant ratios. In general RCCs suggested competitive and/or non-competitive interference between species compared for the yields of dry matter and nutrient contents. Values of RYs and RCCs also suggested that wheat and wild oat may be competitively similar, and that both may be superior to barren brome.

In many studies using replacement technique results especially for such derived variates as RYs, and RYTs and aggressivity are interpreted without statistical analysis e.g. Bhaskar and Vyas (1988). In the present studies some of the results are discussed with this approach as a background but statistical analyses were also carried out where possible. This explains some cases where trends in the results are discussed even though statistical significance was not achieved. The lack of rigour noted above has also been criticised by Wilson (1988).

1. Competitive inter-relationships between wheat and wild oat

When wheat and wild oat were combined in replacement series, the ratio of planting had no significant effect on the weed species. The yield of the crop, however, was significantly different when two plants

of this species were grown with four of the weed. The pure stand yields of the weed and of the crop were similar to their yields in mixtures except that in wheat the per plant monoculture was lower than when four wild oat plants were combined with the crop. The yield of both species was significantly reduced by low available phosphorus suggesting that the nutrient was important in limiting their growth. In general individual weed plants were heavier than those of the crop and some element of competition for light may have been involved.

The RYTs varied with planting ratios and when four wheat and two plants of the weed were associated, the RYT value was significantly lower than the rest and was also lower than 1.0. This may have been due partially to competition for light or some other factor, since P level had no effect on the RYs or RYTs. The lower relative crowding coefficient (RCC) of the crop than the weed at higher P may also suggest that, under such circumstances, the latter had grown large enough to interfere with the light supply of the former. At lower P, however, the supply of this element would have been more important. Here, the RCC for the crop was larger than for the weed and it may thus be said that the former is more competitive than the latter. In general, the product of RCCs of both species for dry matter yield were slightly greater than 1.0, suggesting that P may not have been important in limiting growth and that its effect could have been confounded with that of light interception. Values for the relative crowding coefficients of wild oat with respect to crop indicate higher ability of the weed to accumulate P at both high and low external levels. The products of their relative crowding coefficients also imply competitive interference at higher P and non-competitive and/or competitive interference between them at the deficient phosphorus level. According to de Wit's terminology the species were mutually exclusive and thus compete more fully at higher P than at lower. In pot culture, as in the present experiment, it could be assumed that P at the higher level is potentially available for both species, but the size and the efficiency of their roots may have resulted in intense competition for the element, both intra- and interspecifically. Although the weed was unresponsive to levels of P (Section I), the size of its root system was usually larger than that of the crop and contained higher or similar quantities of P, K, Ca and Mg. In competition as in these experiments the weed had higher concentrations of these nutrients (Tables 3.43a, b and c). In the pure stand its K concentration was significantly

reduced while P remained similar to the mixture concentrations. The concentrations of Ca and Mg of the weed also remain unaffected in mixture, suggesting intra- and interspecific competition of similar magnitude or no competition at all both in pure and mixed stands for these nutrients. Higher level of intraspecific competition may be shown by plants which show high competitive ability in interspecific situations. The concentration of K and to some extent P in the weed increased in mixture than in monoculture. Instances of higher levels of intraspecific competition which lead to greater competitive ability are common in literature. For example, Jolliffe et al. (1984) reported that barnyard grass (Echinochloa crusgalli L. Beauv.) showed a greater amount of intraspecific competition also was more efficient in depressing yields of green foxtail (Setaria viridis L. Beauv.) and other species studied in mixtures. They also found that in most mixtures, the relative monoculture effect was greater than the relative mixture effect. Other studies (e.g. Haizel and Harper, 1973; Thomas and Allison, 1975) have shown that species often respond more strongly to increasisng densities of their own rather than other species. Tarawali (1983) also found that the yield of blackgrass was greater in competition with wheat than with equal densities of itself. Contrary to the findings of Tarawali, Johnson (1987) reported that the crop accumulated more dry matter yield in mixture with blackgrass than in pure stand. The results of the present experiments are in line with those of Johnson, in that at least dry matter yield of wheat increased in mixture with four plants of wild oat over than in monoculture, whilst that of wild oat was unaffected. Nutrient concentrations of the crop in pure stand remain similar to mixtures for P, Ca and Mg, although its concentration for Ca at the combination where two wheat and four wild oat plants compete was lower than at four wheat and two wild oat plants. The K concentration of the crop was also lower in the mixture where the number of wild oat plants exceeded wheat. This suggests that higher densities of the weed may only reduce uptake of the two elements in the crop, whilst higher density of the crop itself can reduce its P and Mg concentrations by a similar magnitude to competition from wild oat plants.

In general relative yields and relative yield totals for nutrient contents were not significantly affected by P levels. However, the P effect was significant for the relative yields and relative yield totals for P content and RY for K. In both species the relative yields and

their totals were higher at the higher level of P, indicating that growth was impeded by limiting P in the medium. The results also clearly show that relative yields for nutrient contents of P, K, Ca and Mg in wheat and wild oat were affected by plant ratios. Both species showed higher RYs when numbers of one component were lower than the other in the mixture. In such mixtures and those where the number of wheat plants were similar to wild oat, the RYs of the weed were greater than the crop. This suggests that wild oat has absorbed and utilized more of the nutrients potentially available for both species in the pot. The ability of the weed efficiently to absorb and utilize these elements has also been seen earlier in Section I. The P RYTs of the two species varied significantly with P levels and plant ratios and slightly with their interactions. In most cases they were close to unity (Figs. 3.1b, c, d and e). this suggests the two species may be making the same demand on the environmental resources available to them. RYTs for P contents at the deficient level of P and Mg at both levels were substantially lower than 1.0 in mixtures where four and two, and three and three plants of wheat and wild oat were grown. In such situations mutual antagonism between the species (for example as a result of the release of phytotoxins by either species) may be inferred. RYTs 1.0 may also be the result of very intense species competition, both intra- and interspecific, leading to seriously reduced growth of either and/or both species, including the death of plants or parts of plants. It is clear that the two species competed intensively for the deficient level of P in these experiments and since the RYTs were 1.0, at plant ratios where the number of wheat plants were greater than or similar to those of wild oat, intraspecific competition amongst wheat plants could have been strong enough to reduce the RYs of both species. The lack of response of the weed to low level of P in competition with the crop is in agreement with the earlier observation for the response of the species in water culture experiments. The obvious practical implication is that in soils where the fertility status is low the yield of wheat would be reduced due to intraspecific competition and to competition with the weed for P as well as other soil nutrients and light. The effect of light could be significant as a result of the ability of the weed to grow larger than the crop in P-limiting conditions though this matter was not investigated here. The RY of wild oat, being much higher at the higher P level (20.5 mM P) also shows the ability of the weed to absorb and utilize P when it is available at adequate concentrations for both species. This

also implies that the fertilization of a wheat field infested by wild oat may also benefit the weed, especially when the density of the crop in relation to wild oat is not large enough to depress the weed.

The RYTs for wheat and wild oat for K contents were greater than 1.0 for P levels, plant ratios and their interactions and may imply non-competitive interference between the two species for the element. The contribution of wild oat to the RYT, was, however, greater than the crop at all combinations indicating efficiency of the weed in taking up and utilizing K.

The occurrence of non-competitive interference between wheat and Chenopodium album for K was also demonstrated by Bhaskar and Vyas (1988) using the concept of relative crowding coefficient based on potassium yields per plant. They reported RCCs greater than 1.0, indicating that there was some non-competitive interference for K between the two species. The higher values of RYs and RCCs of wild oat at low available P with respect to wheat in mixtures may thus indicate its non-competitive ability in restricting the uptake of the nutrient by the crop. On the other hand, similarities in their respective RYs and RCCs at some combination imply similar magnitude of competitive abilities.

RCCs of the two species also differed. At higher P the RCC of the crop for Ca was higher than the weed and the reverse was true at low P. The RCC of the crop towards the weed for Mg contents was lower at higher P and higher at lower availability. The opposite happened with the weed at the two P levels. The products of RCC were very close to one for both Ca and Mg contents of the species suggesting competitive interference, non-competitive interference or both between wheat and wild oat. At the higher P level the growth of the crop was reduced due to competition effects of the weed. The weed, however, did not reduce the Ca contents of the crop, although the weed grew larger than the latter. At low P, however, Ca content of the crop was more affected than its growth. The competitive effects of the weed on the crop with respective to Mg resulted in lower RCC values for crop than the weed and thus similarly affected dry matter yields of the crop and its P and Mg contents at the higher P level. At the lower level the crop was more competitive than the weed and this effect was reflected in RCC values for dry matter and Mg, which were greater than those for the weed.

2. Competitive inter-relationships between wheat and barren brome

The responses of both species to P level were similar. Dry matter accumulation (g/plant) was significantly higher at the higher P. Their mean yields in pure and mixed stands, however, were not significantly different. The yield of the crop slightly increased with increase in the number of associated barren brome plants over its monoculture yield or that when four wheat and two barren brome plants were combined. The reverse happened with the weed, indicating that it is less competitive than the crop. Increases in the sizes of individual wheat plants with increases in the proportions of the weed clearly suggest that intraspecific competition among wheat plants was greater than interspecific competition with the weed. This is contrary to the findings of intercompetitive relationships between wheat and wild oat, where individual plants of the latter appeared to have benefited from the association with the crop in terms of increased dry matter accumulation. The results reported here for wheat and barren brome for the yields of dry matter are similar to those found for wheat and blackgrass in competition (Johnson, 1987). He reported that the mean shoot dry matter weight of wheat increased in competition, whilst that of blackgrass decreased, and concluded that the crop was the more aggressive species, the weed being subordinate. Contrary to the results of the present experiments, Tarawali (1983), however, found that individual A. myosuroides plants became bigger with increasisng proportions of wheat while those of the crop became smaller with increasisng A. myosuroides plants. A number of investigators have shown that individual plants of the aggressor species became bigger with increasing proportions of the weaker competitors, e.g. Hall, 1974a and 1974b; Tarawali, 1983; Johnson, 1987.

The observed trends for the shoot dry matter yields of wheat and barren brome were also clearly shown in their relative yields. Mean RYs for the crop were higher in all combinations and both P levels, implying that the crop is more competitive than the weed. In general the RYT of the two species approximated to a straight line (Fig. 3.2a) suggesting they were mutually exclusive and were thus competing for the same resources. Differences in the relative competitive power of the two species were also clearly shown by differences in the mean relative crowding coefficients calculated for shoot dry matter. Wheat again had higher values in all combinations and both P levels. The products of the

RCC of the two species at both P levels were similar and were slightly higher than 1.0, indicating that both competitive and non-competitive effects may well have been operating.

It should be noted that in such experiments both nutrient and light effects may be involved. This matter is considered further in Section 4.

The trends in the competitive relationships of wheat and barren brome with respect to dry matter accumulation differed for their nutrient concentrations. The weed contained higher concentrations of K, Ca and Mg at all combinations and both P levels. Except for P, the concentrations of the weed for K, Ca and Mg increased in competition with the crop while that of the latter did not differ significantly from the pure stand, the only exception being K which was higher, lower or similar depending on the ratio of plants between these species. This suggests that the weed is more competitive for growth resources in the soil while the ability of the crop to compete for aerial resources is greater. The higher competitive ability of the weed for below ground resources also supports the observation in responses and in competition in additive experiments that the weed contained higher concentrations of P, Ca and Mg. The highest concentrations in the weed (except for Mg) occurred at the deficient level of P. The concentrations of all nutrients except K were higher at the higher P level. The reduction in the concentration of these elements at higher P in the weed may be due partly to tissue dilution effect resulting from more rapid growth and dry matter accumulation which occur at such levels. Similar observations were also made by Johnson (1987) who reported higher concentrations of N, P, K, Ca and Mg in blackgrass in competition with wheat at the lowest P level tested. This obviously suggests that in soils where a specific element like P may be limiting, the efficiency of the weed in taking up other elements may be greater than the crop. The practical implication is that the competition between these two species for below ground resources may lead to the benefit of the weed as well as to the detriment of the crop.

The trends found for the nutrient concentrations differed from their relative yield calculated for their nutrient yields. The replacement diagrams for nutrients contents (Fig. 3.2b, c, d and e and Tables 3.50-53) showed that crop is more competitive than the weed for P, K and Ca and the latter for Mg. Since the calculation of nutrient content yields take into consideration the dry matter yield of the component species,

those of the crop would be expected to be greater than the weed which usually grows less than the crop. The fact that the crop appeared to have higher relative yields than the weed for P, K and Ca suggests that it was tending to dominate in competition for these elements between the two species. The same may be true for the weed in the case of Mg, for which it showed higher RY. The lower relative yield of the weed in the mixtures tended to be compensated for by a corresponding increase in the relative yield of the crop for P, K and Ca. The same was also true for RYs of both species for Mg. The relative yield totals of these species were in general slightly 1.0 for the nutrients K, Ca and Mg and may again indicate that either the gain by one species exceeds the loss by the other or both species are benefiting from the relationship. In this case the former explanation appears to hold. The RYT for P contents of these species at the higher P approximated to unity while at the lower level these were much less than 1.0, implying competitive interference and the possibility of mutual inhibition between them respectively. In general P level in the pot did not affect the relative nutrient yield totals of these species significantly, except for K, which showed higher RYT at the lower P. P level also significantly affected the RY of the weed for K and Ca contents, whilst that of the crop remained similar for the four elements.

Fleming et al. (1988) studied competitive relationships among winter wheat (Triticum aestivum), jointed goatgrass (Aegilops cylindrica) and downy brome (Bromus tectorum) under growth chamber conditions of ample fertility and soil moisture and day/night temperatures of 18/10°C. They reported similar relative yield totals for the three species, indicating that they competed for the same resources. Both winter wheat and jointed goatgrass grew more rapidly and had higher relative crowding coefficients than downy brome, which indicated a hierarchy of relative competitiveness of winter wheat jointed grass goatgrass downy brome. In the present experiments also, the relative crowding coefficients of wheat for yields of dry matter is higher than that of barren brome at both levels of phosphorus. The products of their RCCs were slightly greater than one, implying that competitive effects in addition to non-competitive interference may have operated. The crop also showed higher values of RCCs for the nutrient elements P, K and Ca at higher P level, whilst the weed had a greater coefficient for Mg at that level. At the lower P, the weed had higher RCCs for K and the crop for the other three nutrients.

The product of RCCs varied between P levels and nutrients. At the higher P level, these were either equal to 1.0 (P and Ca) or slightly higher than 1.0 (K and Mg). At the lower P level the RCC product for K was approximately equal to 1.0. For the other elements they were slightly higher than 1.0 which suggests non-competitive interference in addition to competitive interference. The higher RYs and RCC of the crop for yields of dry matter and P, M and Ca indicates this species dominating in competition. The same may also be true for the weed which showed greater val ues of RY and RCC for the contents of Mg in competition. In the study of Johnson mentioned above, the RY of blackgrass for Mg was higher than for wheat and hence the weed was the aggressor in competition for this element. Barren brome in the present experiments also showed higher concentrations of K, Ca and Mg in competition, but owing to the fact that the weed had a lower dry matter yields than the crop, its RYs and RCCs were usually lower than the crop. Considering tissue concentrations of the two species, the weed is more efficient in absorbing and translocating these nutrients than the crop and is thus an accumulator. The ability to accumulate K, Ca and Mg by barren brome may be attributed to its finer root system or to its root physiological characteristics. A number of investigators have studied the importance of the root system in competition e.g. Martin and Field (1987 and 1988) investigated competitive relationships between wheat and wild oat. They reported greater competitive ability in the weed and this was attributed to greater root competition than shoot competition. Similarly Baan-Hofman and Ennik (1982) attributed the greater competitive ability of ryegrass (Lolium. perenne) in competition with couch grass (Elytrigia. repens (L.) Desv.) to the greater root mass of the former. The effects of root and shoot competition is considered further in Section 4.

3. Competitive inter-relationships between wild oat and barren brome (weeds)

The greater amount of dry matter accumulated in wild oat, its high relative yields and relative crowding coefficients (Tables 3.47a, b and c; 3.13; 3.23; Fig. 3.3a) suggest that this weed is a stronger competitor than barren brome. The level of P had no effect on the competitive ability of either species. This is shown by the non-significant difference in their RYs. The frequency of planting, however, had significant effect on both RYs and RCCs of barren brome which were lower

in this weed than in wild oat. RYTs were not affected by P level and interactions. The products of RCCs for the yield of dry matter were similar at the two P levels and did not deviate significantly from unity, implying that both species compete for aerial resources and they are mutually exclusive. According to de Wit and Van den Bergh (1965), the outcome of their competitive relationship is that wild oat is the aggressor and barren brome the subordinate species.

The concentration of some nutrients in both weeds were affected by P level, planting frequency and their interactions. In barren brome K and Ca concentrations were significantly higher whilst in wild oat, P and Mg appeared to be slightly higher. In pure stands the concentrations of K, Ca and Mg in wild oat were significantly different from those in mixtures. Concentrations did not change in barren brome except for P which was similar at the density where three plants of each species were grown, lower at WO4 + BB2 and higher at the combination WO2 + BB4.

Although monoculture nutrient concentrations in barren brome were similar to their concentrations in mixtures, RYs based on nutrient yields did not show a more efficient competitive ability of this weed than the other. For example, although barren brome contained higher K than wild oat, its RY for the element was smaller than that of the latter at all three combinations. Thus it may be assumed that wild oat is a stronger competitor for K than barren brome. The fact that RYTs 1.0 suggests that non-competitive interference may have occurred between these weeds. Relative crowding coefficients and their products calculated for the two weeds for K yield, however, showed that competition took place for the element at the lower level and the competitive power of wild oat was greater than that of barren brome. Relative crowding coefficients and their products also showed that competition for P occurred at the lower P and wild oat was more competitive than barren brome. The greater competitive power in wild oat for these elements in general may be attributed to its prolific development of crown roots resulting in the absorption of a major share of the nutrients. This may have led to better growth of tops and hence better light capture, producing more assimilates which may, of course, reinforce the greater development of roots. The opposite sequence of events may well have occurred in barren brome leading to its suppression by wild oat.

The relative yields for Ca in the two species suggest that both

appeared to have a similar share of the element, at both P levels, although barren brome had a slightly higher Ca concentration. Competition between the two species may have taken place in some mixtures where the values for RYTs approximated to 1.0 (Table 3.13c; Fig. 3.3d). The relative crowding coefficient for Ca for wild oat was, however, greater than that of barren brome at both P levels suggesting that the former species may have competed more strongly for the element. The products of RCC were higher than 1.0, and may thus suggest that some non-competitive interference for the element may be involved.

Although higher concentrations of Mg were found in wild oat than in barren brome both in pure stands and in mixtures, RYs were higher for barren brome, whose Mg concentration increased in competition over those in monoculture. At low P values of relative crowding coefficients were higher for barren brome than wild oat, showing its ability to compete better for the element at that level. At the higher level these were similar. The products of RCC was equal to 1.0, at the higher P implying competitive interference. At the low P level RCC was slightly 1.0, and might suggest some competitive and non-competitive effects between the species.

It may be concluded that under low P soil conditions the species may have escaped some measure of competition with each other for this element. This may occur if the growth of the two species is separated in time or if the species differ in their demands for the element. Although barren brome contained higher concentrations for some of the nutrients e.g. for K and Ca than wild oat values for relative yields and relative crowding coefficients of the weeds calculated for their yields of dry matter and P, K and Ca suggest that wild oat is competitively superior to barren brome. Tissue nutrient concentrations of component species in competition clearly do not reflect the competitive ability of such species. The performance of paired species may be evaluated using other factors such as total nutrient contents, relative growth rates, relative yields, relative crowding coefficients and root morphological and physiological characteristics.

In the present experiments, although barren brome had higher tissue nutrient concentrations for the majority of the elements determined than either the crop or wild oat, all evidence for relative yields and relative crowding coefficients suggest that it is competitively inferior

to both species. The competitive relationship between wheat and wild oat clearly shows that concentrations of P, K, Ca and Mg, the relative yields and relative crowding coefficients for these nutrients and yields of dry matter are higher for the weed in general conferring its competitive dominance on the crop. Martin and Field (1988) also investigated competitive inter-relationships between wheat and wild oat and reported that when both species were sown at the same time, wild oat was the more competitive species due largely to its larger root system compared with wheat (Pavlychenko and Harrington, 1934; Pavlychenko, 1937) and especially to the prolific development of crown roots (Chancellor, 1976). The competitive superiority of wild oat over wheat has also been shown in the work of Hannah (1964), Chancellor and Peters (1974) and Martin and Field (1987).

Substitutive Experiments

7.5.3. Results

Experiment 3.5: Replacement series at different K levels

Welbank (1963) states that the competitive ability of a plant can be thought of as its ability to depress the growth of other plants. Thus the competitive relationship between any paired species in these experiments were determined based on the quantity of dry matter (g shoot/plant) produced. It is not possible to include root dry weights in the anal ysis because in mixed stands separation of the roots of the different species is not practicable. The data for the dry matter yields were analaysed for two harvests and showed similar trends. Thus the results of the first harvest only are presented and discussed.

1. Effects of K level and plant ratio on the competitive relationships between wheat (W) and wild oat (WO) at the first harvest

(a) Dry matter yield (g/plant)

The level of potassium applied had no effect on the shoot dry matter yield of the crop, whilst this was affected significantly by the ratio of plants. The monoculture yield of the crop was lower than when the ratio of the crop to the weed was 2:4 or 4:2 crop to weed mixtures; the yield

Table 3.59 (a) Effects of plant ratio and K level on the shoot dry matter yield (g/plant) of wheat (W) in competition with wild oat (WO) and barren brome (BB) at the first harvest

	K level							
	L1		L2		L3		Mean	
Plant ratio	WO	BB	WO	BB	WO	BB	WO	BB
Pure wheat(W)	0.77		0.78		0.71		0.75	
W4 + WO2	0.88		0.76		0.79		0.78	
W2 + WO4	1.10		0.93		0.95		0.99	
W4 + BB2		1.07		1.04		0.90		1.00
W2 + BB4		1.26		1.26		1.43		1.31
Mean	0.89	1.03	0.82	1.02	0.81	1.01		

LSD ($P < 0.05$)

	WO	BB
K levels	NS	NS
Plant ratio	0.07	0.10
Interaction	NS	NS

Table 3.59 (b) Effects of plant ratio and K level on the shoot dry matter yield (g/plant) of wild oat (WO) in competition with wheat (W) and barren brome at the first harvest

	K level							
	L1		L2		L3		Mean	
Plant ratio	W	BB	W	BB	W	BB	W	BB
Pure wild oat	1.13		1.15		1.13		1.14	
WO4 + W2	0.99.		1.04		1.08		1.04	
WO2 + W4	1.13.		1.20		1.03		1.12	
WO4 + BB2		1.40		1.54		1.47		1.47
WO2 + BB4		1.69		1.58		1.95		1.74
Mean	1.08	1.41	1.13	1.42	1.08	1.52		

LSD ($P < 0.05$)

	W	BB
K levels	NS	NS
Plant ratio	NS	0.17
Interaction	NS	NS

Table 3.59 (c) Effects of plant ratio and K level on the shoot dry matter yield (g/plant) of barren brome (BB) in competition with wheat (W) and wild oat (WO) at the first harvest

	K level							
	L1		L2		L3		Mean	
Plant ratio	W	WO	W	WO	W	WO	W	WOW
Pure b. borme	0.68		0.66		0.66		0.67	
BB4 + W2	0.39		0.44		0.44		0.42	
BB2 + W4	0.14.		0.20		0.13		0.15	
BB4 + WO2	0.44		0.53		0.47		0.48	
BB2 + WO4	0.44		0.38		0.37		0.40	
Mean	0.40	0.52	0.43	0.52	0.41	0.50		

	LSD ($P < 0.05$)	
	W	WO
K levels	NS	NS
Plant ratio	0.04	0.05
Interaction	NS	NS

Table 3.60 Effects of plant ratio and K level on the mean relative yield (RY) and relative yield totals (RYT) of wheat (W) and wild oat (WO) calculated for dry matter yield of shoots at the first harvest

A. Effects of K level
(Mean of two planting frequencies)

	RYW	RYWO	RYT
L1	0.58	0.46	1.04
L2	0.52	0.48	1.00
L3	0.59	0.47	1.07
LSD (5%)	NS	NS	NS

B. Effects of planting frequency
(Means of three potassium levels)

	RYW	RYWO	RYT
W4 + WO2	0.69	0.33	1.02
W2 + WO4	0.44	0.61	1.05
LSD (P 0.05)	0.06	0.06	NS

C. Effects of plant ratio x K level

	L1			L2			L3		
	RYW	RYWO	RYT	RYW	RYWO	RYT	RYW	RYWO	RYT
W4 + WO2	0.69	0.33	1.02	0.65	0.35	1.00	0.74	0.31	1.05
W2 + WO4	0.48	0.59	1.07	0.40	0.60	1.00	0.45	0.63	1.08

LSD ($P < 0.05$)

RYW	NS
RYWO	NS
RYT	NS

of the crop was not different from its yield in monoculture (Table 3.59a). The yield of the weed was affected by neither factor.

(b) Relative yield and relative yield totals

RYs of both species and their RYTs were unaffected by K level. RY values were greater for the crop at all three levels of K. The RYTs were much greater than 1.0, suggesting both competitive and non-competitive interference.

The ratio of planting significantly affected RYs of both species and this effect was also greater for the crop. RYTs were not affected by plant ratio and were greater than 1.0 (Table 3.60). The interactions were not significant for RYs or RYTs (Fig. 3.4a).

(c) Relative crowding coefficient of wheat (KWWO) and wild oat (KWOW)

RCC values were higher for the crop than the weed at both planting ratios and K levels. The product of RCCs was greater than 1.0, except for the combination 2:4 wheat to wild oat, where it was equal to one. These values suggest that both competitive and non-competitive interference was taking place between wheat and wild oat plants.

2. Effects of K level and plant ratio on the competitive relationship between wheat (W) and barren brome (BB) at the first harvest

(a) Dry matter yield (g/plant)

The mean dry matter yield of wheat increased with increase in the number of barren brome plants so that its yield in monoculture was significantly lower than in the mixtures (Table 3.59a). The reverse happened with barren brome (Table 3.59c).

(b) Relative yields and relative yield totals (RYTs)

K level affected the relative yield of barren brome only, while the ratio of planting affected the relative yields of both species and their relative yield totals (Table 3.61). The interactions were significant for RYTs .

(c) Relative crowding coefficients of wheat (KWBB) and barren brome (KBBW)

The RCC of the crop with respect to the weed was very much greater at all K levels and both combinations (Table 3.63b). The product of the

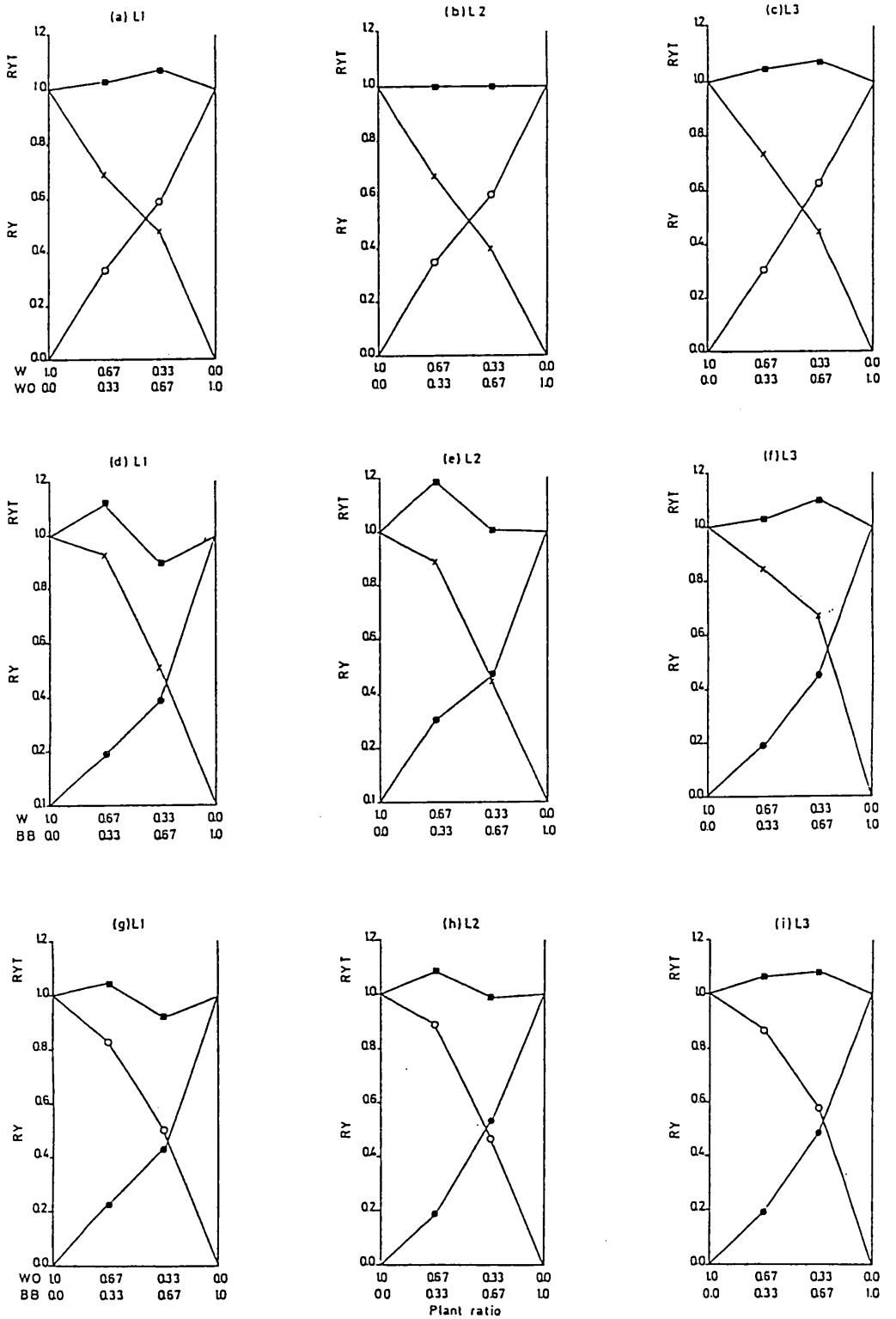


Figure 3.4 (a–i) Replacement series diagrams for wheat (W) and wild oat (WO), wheat (W) and barren brome (BB) and wild oat (WO) and barren brome in response to levels of K

Table 3.61 Effects of plant ratio and K level on the mean relative yields (RY) and relative yield totals (RYT) of wheat (RYW) and barren brome (RYBB) at the first harvest

A. Effects of K level
(Mean of two planting ratios)

	RYW	RYBB	RYT
L1	0.72	0.29	1.01
L2	0.71	0.38	1.09
L3	0.74	0.32	1.06
LSD ($P < 0.05$)	NS	0.05	NS

B. Effects of planting ratio
(Mean of three K levels)

	RYW	RYBB	RYT
W4 + BB2	0.89	0.23	1.12
W2 + BB4	0.56	0.44	1.00
LSD ($P < 0.05$)	0.09	0.04	0.08

C. Effects of plant ratio x K level

	L1			L2			L3		
	RYW	RYBB	RYT	RYW	RYBB	RYT	RYW	RYBB	RYT
W4 + BB2	0.93	0.19	1.12	0.89	0.30	1.19	0.84	0.19	1.03
W2 + BB4	0.51	0.39	0.90	0.54	0.47	1.01	0.65	0.45	1.10

LSD ($P < 0.05$)

RYW	NS
RYBB	NS
RYT	0.14

Table 3.62 Effects of plant ratio and K level on the mean relative yields and relative yield totals (RYTs) of wild oat (RYWO) and barren brome (RYBB) at the first harvest

A. Effects of K level
(Mean of two planting frequencies)

	RYWO	RYBB	RYT
L1	0.66	0.32	0.98
L2	0.68	0.36	1.04
L3	0.72	0.33	1.05
LSD ($P < 0.05$)	NS	NS	NS

B. Effects of plant ratio
(Mean of three K levels)

	RYWO	RYBB	RYT
WO4 + BB2	0.86	0.20	1.06
WO2 + BB4	0.51	0.48	0.99
LSD (5%)	0.07	0.04	NS

C. Effects of plant ratio x K level

	L1			L2			L3		
	RYWO	RYBB	RYT	RYWO	RYBB	RYT	RYWO	RYBB	RYT
WO4 + BB2	0.83	0.22	1.05	0.89	0.19	1.08	0.87	0.19	1.06
WO2 + BB4	0.50	0.43	0.93	0.46	0.53	0.99	0.58	0.48	1.06

LSD ($P < 0.05$)

RYWO	NS
RYBB	0.06
RYT	NS

Table 3.63 (a) Effects of plant ratio and K level on the relative crowding coefficients of wheat (KWWO) and wild oat (KWOW) calculated for shoot dry matter yield at the first harvest

	Relative crowding coefficient (RCC)								
	L1			L2			L3		
	KWWO	KWOW	KWWOxKWOW	KWWO	KWOW	KWWOxKWOW	KWWO	KWOW	KWWOxKWOW
W4+WO2	1.05	1.01	1.06	1.00	1.12	1.12	1.32	0.84	1.11
W2+WO4	1.62	0.62	1.00	1.37	0.78	1.07	1.51	0.81	1.22

Table 3.63 (b) Effects of plant ratio and K level on the RCC of wheat (KWBB) and barren brome (KBBW) calculated for shoot dry matter yield at the first harvest

	L1			L2			L3		
	KWBB	KBBW	KWBBxKBBW	KWBB	KBBW	KWBBxKBBW	KWBB	KBBW	KWBBxKBBW
W4+BB2	7.35	0.15	1.10	3.56	0.23	0.82	6.70	0.15	1.01
W2+BB4	2.96	0.36	1.07	2.44	0.43	1.05	.306	0.34	1.04

Table 3.63 (c) Effects of plant ratio and K level on the RCC crowding coefficients of wild oat (KWOBB) and barren brome (KBBWO) calculated for shoot dry matter yield at the first harvest

	L1			L2			L3		
	KWOBB	KBBWO	KWOBBxKBBWO	KWOBB	KBBWO	KWOBBxKBBWO	KWOBB	KBBWO	KWOBBxKBBWO
WO4+BB2	1.89	0.59	1.12	2.43	0.42	1.02	2.49	0.45	1.12
WO2+BB4	2.37	0.48	1.14	1.88	0.67	1.26	2.44	0.42	1.02

RCCs was higher than 1.0, except at L2, at 4:2 wheat to barren brome. This may indicate that the intensity of competition at higher populations of the crop reduced the competitive power of the weed.

3. Effects of K level and plant ratio on the competitive relationships between wild oat (WO) and barren brome at the first harvest

Dry matter yield

The mean dry matter yield of wild oat (WO) in mixture with barren brome was greater than in monoculture whilst that of barren brome decreased significantly (Table 3.59b and c). The level of K had no effect on either species.

Relative yields and relative yield totals

The RYs of wild oat were also clearly greater than those of barren brome. Potassium level had no effect on the RYs and the RYTs of either species. The ratio of planting affected their respective relative yields, but not their totals. The interaction was significant for the RY of barren brome only (Table 3.62).

Relative crowding coefficients of wild oat (KWOBB) and barren brome (KBBWO)

Values of RCCs were also greater for wild oa at all K levels and in both species mixtures (Table 3.63c). The products of RCC of the species were also greater than 1.0, implying both competitive and non-competitive inter-relationship between the species.

7.5.4. Discussion

1. Competitive inter-relationships between wheat and wild oat

The greater intensity of intraspecific competition in wheat than interspecific competition with wild oat, was clearly shown by its lower dry matter yield in the pure stand and significantly higher yield when the weed predominated. The yield of the weed did not differ between pure stands and mixtures. Values for relative yields and relative crowding coefficients were also higher for the crop. Relative yield totals and relative crowding coefficients were greater than 1.0, situations which may indicate that the two species make different demands on resources or

avoid competition with each other. Although the resu. lts indicate a greater gain in dry matter yield of the crop than the weed, the growth of the latter was not reduced by the presence and growth of former. An important observation is that the level of K did not have any influence on the competitive relationship between the two species, at least on dry matter yield. The higher yield of the crop in mixed stands than in monoculture could thus not be attributed to its efficiency in taking up limiting K. In the study of the responses of the species to K in water culture, the crop had shown higher efficiencies of uptake and utilization than the weed. The greater relative yield values for the dry matter yield of the crop at all K levels and both combinations may be due partly to non-competitive and competitive interference for some other growth factors. Although the per plant yield of the weed in pure stands was greater than for the crop, it is worth noting that the species yielding most in pure stand need not be more competitive in mixtures.

The use of de Wit's (1960) replacement series method to measure the magnitude of effects of one species on the other may also be used to study the competitive relationships among the three species in relation to K supply. Hall (1974b) used the yields of K in such experiments to study the influence of K on the growth of Setaria anceps cv. Nandi and Desmodium intortum cv. Green Leaf and showed that at low levels of K, S. anceps severely restricted the growth of the legume Desmodium by competing for K, and this was reflected by high RY values for the grass. A number of other investigators have used the RYs to study competitive relationships among and between species e.g. Ivens and Mlowe (1980); Berendse (1982); Martin and Field (1987, 1988); Bhaskar and Vyas (1988). In this laboratory, Tarawali (1983) investigated the competitive relationships between winter wheat and blackgrass. His approach involved the direct foliar feeding of the crop but not the weed with K as a means of overcoming below ground competition and to see the effects of such a method on the RY and RYTs of the weed and the crop. He found that A. myosuroides had a higher RY than wheat and the RYT of plants in which the crop was not fed with K approximated to a straight line. He implied that the two species were mutually exclusive and were competing for the element. Foliar feeding the crop with K increased the RY of the crop significantly in monoculture and the RYT of the mixture slightly and the author suggested that this may have decreased both intraspecific competition among wheat plants and interspecific interaction between the

weed and the crop. In the study of Hall (1974b) he was able to show that the competitive effects between Setaria and Desmodium can be removed by adding K to the system and this was reflected in higher RYTs and RCCs. Also in this laboratory, Johnson (1987) investigated the competitive abilities of wheat and blackgrass in relation to P and N using de Wit's replacement series technique. He found wheat more aggressive than blackgrass and that its competitive ability increased with higher levels of phosphorus, whilst that of the weed remained unaffected. His chemical analysis of plants showed that blackgrass was more efficient in absorbing N, P, K, Ca and Mg than wheat at low N and P. He concluded that competition for P and especially N were more important than for any other elements.

The resu lts indicate that K level has no significant effect on the DM yield of the crop or either weed. This is very difficult to explain but stresses the need for further detailed studies on the role of this nutrient and others in competition. In the study of Tarawali referred to earlier, a lack of significant response to K in wheat plants growing in association with the weed was reported. He concluded that it was possible that below ground competition for some other factor may be more important in the relationship between the two species than this mineral element.

Individual plants of the crop became bigger with increasing proportions of wild oat in the mixtures, while that of the weed remained similar to its yield in pure stand, indicating the effect of the crop on the weed was stronger than the weed on the crop. Wheat plants were also heavier in association with barren brome while plants of this weed became smaller with increasing numbers of plants of the crop. This also shows that the effects of intraspecific competition in wheat was greater than competition with either weed. Intra- and interspecific competition in wild oat is similar while in barren brome these were different, competition with the crop resulting in more reduced yield than in competition with itself. Hence in competition with either weed the crop tended to dominate, depressing their yields although the reduction in the yield of wild oat was not significant.

2. Competitive inter-relationships between wheat and barren brome

The results for dry matter yield of the crop showed that individual

wheat plants became heavier with increase in the population of the weed. The reverse was true for the weed. This clearly implies that intraspecific competition in the crop is stronger and thus it benefits from association with the weed, while the latter suffers from such an association. The relative yields of the species also clearly showed this relationship. The higher RY of the crop at all K levels and in both mixture populations imply that it tended to dominate the weed in competition. The relative crowding coefficient also showed values for the crop which were several times higher than that of the weed, indicating that it is the dominating species in competition. The competitive effect of wheat appeared to increase with the level of K used i.e. at the higher level (L1) of the nutrient, the value of RCC was higher than at L2 or L3. This shows that the growth of the crop may be enhanced at higher levels of the nutrient, which also led to greater acquisition of other resources. The common assumption that adding environmental resources reduces competitive effects may not be always true (Snaydon, 1982). It has often been suggested (e.g. Welbank, 1962) that if two species compete for a given resource addition of that resource will reduce its deficiency and so reduce the intensity of competition. Wilson (1988) found little evidence to support this. He often found 'competitive imbalance' greater at higher resource levels. The competitive balance index (Cb) used by Wilson is defined as the log of de Wit and Goudriaan's (1974) 'Relative Crowding Coefficient'. The antilog of Cb is the same as the 'Competitive Ratio' of Willey and Rao (1980).

Relative yield totals for K levels and plant ratio and their interactions were greater than unity except for interaction at L1, suggesting that the components used at least partially different resources and thus escaped some measure of competition. The values for the products of RCCs of the species were slightly greater than 1.0, and thus conclusions similar to their RYTs may be drawn.

3. Competitive relationships between wild oat (WO) and barren brome (BB), with some discussion of wheat

In the presence of barren brome, the shoot dry matter yield (g/plant) of the second weed significantly increased over its monoculture yield. The increase in wild oat in association with barren brome

resulted in significant yield reduction in the latter. This result is similar to the relationship found between wheat and barren brome. This indicates that the competitive ability of barren brome is lower than either of the other species. Similar relationships were also established between and among these species in replacement series at different levels of phosphorus (see Experiment 4). If the competitive ability of these species is to be determined by the amount of dry matter accumulation, the order of competitive ability would be wheat followed by wild oat followed by barren brome. In the competitive relationships between wheat and wild oat, the yield of the latter was unaffected by increase in the population of the former. Nevertheless, the dry matter yield of the crop was increased. Such relationships may or may not indicate competitive interference between the two species. Hill and Shimamoto (1973) have described the situation where the yield per plant in mixture is similar to that in monoculture as being one in which there is 'no competition'.

Relative yields and relative crowding coefficients were higher for wild oat than for barren brome at all K levels and plant ratios, indicating dominance of the former species. RYTs and the products of RCCs of the species yielded values approximating to or greater than 1.0, suggesting competitive or both competitive and non-competitive interference. If crowding coefficients are interpreted as a measure of the intensity of competition (Hall, 1974a), competition between the weeds would appear not to have been intense; because the products for their RCCs were 1.0. This may also be true for competitive relationships between wheat and barren brome and wheat and wild oat. In the competition between the crop and wild oat, respective RCCs tended to be similar, suggesting similar competitive abilities. When four wild oat and two wheat plants competed the product of RCCs was approximately 1.0, at the highest level of potassium. At that combination the RCC of the weed with respect to the crop showed values lower than 1.0 at all K levels. This indicates that competition between the two may have been intense. The considerable similarities of the two species in their growth habits may explain the fact that competition was more intense than between wheat and barren brome. It is likely that wheat and wild oat may be confined to the same ecological niche at least at some stages of growth.

More intensive research both under field and glasshouse conditions in these areas could be rewarding. Investigations into the relationships

between competing species should preferably include chemical analysis in order to be able to identify the objects of competition. Unfortunately such analyses were not done in the present experiments and the relative importance of the nutrient elements could not be established. The importance of light in the competition between wheat and brome and wild oat and brome could also have been significant, because the observed large differences in their RCCs for yields of dry matter and the differences in the overall sizes of the plants.

7.6. Conclusions

In general differences in dry matter accumulation of the three species in responses to density and P levels were noted. At the lower P level intense intraspecific competition resulted in similarities in dry matter accumulation per pot at higher and lower densities of all species (Tables 3.1, 3.2, 3.5 and 3.6). This was especially true for wheat and barren brome. Wild oat tended to be less sensitive to intraspecific competition particularly at early stages of growth. The higher values for regression coefficients and for the ratio of regression coefficient to the intercept suggested greater intraspecific competition in barren brome than the other species. Higher values for regression coefficients were also shown at low P than at high P, also indicating greater intraspecific competition at low P. Thus there is a greater dry matter reduction for each single plant added to the population at the low than at high P. The greater intraspecific competition in barren brome could be attributed to greater root competition of the weed due to its different root morphology. In earlier experiments (Section I), this weed tended to show higher requirements for P and the reduction in dry matter than either species could be expected.

When the crop (indicator) was surrounded by increasing numbers of either weed (competitors) dry matter yield, tiller number/plant and tissue nutrient concentrations of the crop was affected differently by the two weeds (Tables 3.9-3.14, and 3.16-3.26). In general orthogonal contrasts often showed similar effects of the weeds and increase in their densities reduced the measured variates linearly. An exception was the non-significant effect of either weed on the K uptake of the crop. This suggested a higher competitive ability of the crop than the weeds for K,

or that this element may not have been an important factor in competition.

Another significant point emerging from these experiments was that barren brome again showed higher concentrations of P, K, Ca and Mg than the crop and this was accompanied by correspondingly lower values for the crop. The weeds also differed in their overall effects on Mg uptake of the crop. Increasing barren brome density significantly reduced the element taken up by the crop. The smaller effect of wild oat may be associated with its lower sensitivity to variations in Mg in water culture (Section I).

Repetition of the experiment in a natural soil deficient in P showed trends similar to observations made in the experiment just described (Tables 3.27-3.35). Higher nutrient concentrations in the weeds, especially barren brome at lower P level again suggest the ability of the weed efficiently to take up the other elements. The implications of such findings have been discussed. Higher rates of uptake per unit root fresh weight and greater rates of depletion of the solution by the crop than the weeds as shown by the experiments in Section II, may also account for the insensitivity of the crop in increases in the density of the weeds shown here.

Further investigations on the competitive ability of the crop with varying levels of K in replacement series experiments also showed that crop yields were reduced by competition. Dry matter yield, relative yields and relative crowding coefficients were higher for the crop (Tables 3.59a-c and Figure 3.4d-i) confirming its superior ability to compete for K. K level did not significantly affect the yield of either weed species. This was very difficult to explain especially when RYTs and the products of RCCs did not usually deviate from unity significantly, suggesting that there was competitive interference between the crop and the weeds for K. Further examination on the role of this element in comparison with other major elements could be rewarding.

Replacement series experiments were also carried out at two P levels. Differences in competitive abilities between the species were clear. Dry matter accumulation in the crop again increased with increasing density of the weeds, especially barren brome. The trends in dry matter increase in the crop was also clearly shown in relative yields and relative crowding coefficients (Tables 3.48 and 3.61, Tables 3.58a

and b). RYs usually followed plant ratios of the component species i.e. the species with the higher proportion in the mixture had a higher RY value, but at equal proportions the order of competitive abilities of the species may be summarised as wild oat > wheat > barren brome. In general, the outcome of competition for the various nutrients as demonstrated by RYs and RCCs for total nutrient yields followed the competitive order for dry matter accumulation. It is noteworthy that although barren brome showed higher nutrient concentrations for all elements, except K, perhaps as the result of its root characteristics, it was the weakest competitor in competition. Under P and K limiting conditions, therefore, wild oat and wheat respectively became the aggressor species and barren brome clearly the subordinate, both in additive and replacement series experiments.

SECTION IV

SECTION IV

Some studies relating to the root systems of *Avena fatua*, *Bromus sterilis* and wheat

8.1. ABSTRACT

Separation of the effects of roots and shoots generally showed that competition for underground resources (nutrients) tended to be more important than those for above ground (mainly light). Dry matter and nutrient yields and values for relative yields and aggressivity indicated the order of competitiveness to be WO > W > BB.

Studies on the effects of root restriction showed that wild oat was generally tolerant to such treatment, whilst barren brome was the species most affected. The addition of a higher level of P to smaller pot sizes appeared partially to reduce the effects of root restriction in all the three species.

Investigations on the distribution and penetration of roots of the three species indicated that although the roots of wheat and barren brome generally occupied similar layers of the soil profile, the latter was the species with the shallowest roots. Wild oat showed a greater ability to root at deeper layers of the soil profile than the other species.

These results are discussed in the light of the species' ability effectively to extract limiting resources of the soil and their ultimate inter-relationships in competition.

Section IV Some studies relating to the root systems of wheat, *Avena fatua* and *Bromus sterilis*

8.2 Introduction

(i) Separating the Effects of Shoot Competition and Root Competition

Plant species compete for both aerial resources (mainly light) and soil resources (various mineral nutrients and water), and it is likely that competition normally occurs for several of these resources simultaneously (Donald, 1963). A technique for separating the effects of competition for aerial resources (i.e. shoot competition) from the effects of competition for soil resources (i.e. root competition) was devised by Donald (1958) for use in pot experiments. Using dividers to separate the shoot and root systems independently, he examined the effects of shoot and root competitions on the interaction between *Lolium perenne* and *Phalaris tuberosa*. Following the lead of Donald, various workers have also attempted to disentangle the effects of competition for light and nutrients and thereby studied the nature of competition between crops and weeds and between other species and pasture plants (e.g. Eagle, 1972; Remison and Snaydon, 1980; Scott and Lowther, 1980; Martin and Snaydon, 1982; Cook and Ratcliffe, 1984; Martin and Field, 1984; McGraw, 1985; Snaydon and Howe, 1986). In modifying Donald's technique various experimenters used containers of different sizes (e.g. Snaydon, 1979; Remison and Snaydon, 1980;, Martin and Snaydon, 1982; Martin and Field, 1984). The method was also extended to the separation of shoot and root effects in field experiments (e.g. Cook and Ratcliffe, 1984). Snaydon (1979) used the complementary techniques of Donald (1958) and de Wit (1960). By unifying the two methods he was able to separate shoot competition and root competition and define the nature of root and shoot interactions whilst it was possible to manipulate mineral nutrient supply (Donald, 1958; Hall, 1974a, b), soil water, light and use to obtain further information by plant chemical analysis (Snaydon, 1971; Hall, 1974a, b). More recently Johnson, 1987) adopted the complementary technique developed by Snaydon. He was able to vary the relative density of the interacting species and level of P nutrition to study root competition as well as full competition.

Most of the evidence from these studies indicated that the effects of root competition were greater than those of shoot competition, at least during the early growth period of plants. Hence, the greater

competitive ability of species in competition was reported to be due almost entirely to the greater competitive ability of the roots (Baan-Hoffman and Ennik, 1982; Martin and Snaydon, 1982; Cook and Ratcliffe, 1984). Donald (1958) pointed out that shoot competition would probably influence the size of the root system and the ability of the root to extract nutrients and that this might account for the apparent effect of the shoot competition upon chemical composition. Although the mechanisms of root competition are not clearly understood, Eagles (1972) suggested that the possible explanation for the major role of root competition may be because competition in the soil environment begins at a much earlier stage than competition for light. Hence, any difference between competing species in the efficiency of uptake and utilization can ultimately lead to the reduced growth of the shoots and the shading of one of the component species. It may be thought, therefore, that the relative effects of roots or shoots separately is less than the compounded effects of both under full competition conditions.

The performance of species in the various treatments, (i.e. shoot competition, root competition and full competition) was determined by calculating the relative yields and RYT (de Wit and van den Burgh, 1965). They concluded that when RYTs exceed 1.0, the species partially utilise different environmental resources. Martin and Snaydon (1982) found different RYT values for the different treatments studied with barley and field beans. They found RYT 1 and some values were twice as large when roots of barley and beans were inter-mixed though when the shoots were intermingled RYTs did not exceed 1.0 and hence concluded that the species apparently competed fully for light and that the roots appeared to exploit different resosurces below ground. It was explained that the beans fixed N symbiotically and left more soil N to be utilised by the barley. The aggressivity (competitive ability) of the species were also calculated with respect to the different treatments and interpreted according to McGilchrist and Trenbath (1971). For example Martin and Snaydon (1982) found similar aggressivity (A=0) when the shoots of beans and barley interacted, but barley was more competitive (A 0) than beans when the root systems interacted. Remison and Snaydon (1980) also reported that the aggressivity of Holcus lanatus relative to Dactylis glomerata was greatest under conditions of root competition and least under conditions of shoot competition.

(ii) Effects of root restriction on the growth and nutrient uptake of wheat, *A. fatua* and *B. sterilis*

The absorption of water and soil mineral nutrients is the most obvious function of the plant root system. The study of the rooting habits and activities of these organs is essential in order to understand the performance of species in competitive environments. Pavlychenko (1937) stated that the root is the first part to be affected by environmental changes and that the successful establishment of a plant depends largely on the adaptability of the root system. Thus knowledge of the depth, pattern and extent of root systems is important in determining the competitive abilities of weeds. Knowledge of the existence of wide variations among crop plants in their rooting densities, both vertically and horizontally, may lead to the most effective placement of fertilizers. Furthermore, such studies of species may help explain why stable equilibria may exist in homogeneous environments (Harper and MacNaughton, 1962).

Several workers have studied the root systems of various plant species and reported differences between species and among varieties for root characteristics such as branching, distribution patterns, surface area, dry weight, length, volume and even hair density (e.g. Pavlychenko and Harrington, 1934; Lyness, 1936; Pavlychenko, 1937, Ellern *et al.*, 1970; Gerloff, 1977; Shenk and Barber, 1980; Tarawali, 1983; Qasem, 1987). It has been widely assumed for many years that the amount of root on a plant will influence its ability to take up nutrients, and evidence of the importance of roots in competition may be found from the description of root system distributions, or in some cases from soil moisture or nutrient utilization patterns. Methods such as the placement of radioactive materials in the soil or their injection into stems and the following of their distribution in the root system have been used (e.g. Boggie and Knight, 1960; Racz *et al.*, 1964; Goodman and Collison, 1982; Tarawali, 1983). Earlier methods involved tedious excavation of root profiles (e.g. Bohm, 1979). The use of isotopes in root ecological investigations has declined in recent years, because working with these substances has been more successful in the studies of problems relating to root physiology than with root ecology (Bohm, 1979).

The extensive intermingling of the root systems of different species was demonstrated by Clements *et al.* (1929). They stated that species

with a large, deep and active root system have a greater ability to absorb water in large quantities from deep layers of the soil, thus affecting the growth of neighbouring plants. The fact that root morphological characteristics, particularly rooting density, have a greater influence on the uptake rates of soil moisture and nutrients than their physiological absorption capacities has been emphasised by Caldwell and Richards (1986) and Clarkson (1985). There is sosme circumstantial evidence that greater rooting density is an advantage in competition, because species which produce massive root systems are more effective in depleting soil resources. For example, Baan Hoffman and Ennik (1980, 1982) and Ennik and Baan Hoffman (1983) studied the variation in the root mass production of ryegrass lines and their competitive abilities with respect to couchgrass (Elymus repens). They found that ryegrass lines differed consistently in shoot/root ratios and the most competitive types produced more root mass and smaller shoot/root ratios. They concluded that the greater competitive ability of some lines could be attributed to their greater root mass which may have been effective in depleting soil resources, at least in localized zones, or they may have occup+ed more of the soil volume to the partial exclusion of the competitor's root system. Rhodes (1968) also studied the competitive relationships between ryegrass and the poor competitor, tall Fescue (Festuca arundinacea Schreber) and cocksfoot (Dactlylis glomerata L.) under nutrient deficient conditions. He found that ryegrass had a greater lateral spread of roots and longer roots and concluded that this was associated with its more aggressive habit.

An important characteristic of the root system of some plant species is the ability to change growth patterns and relocate zones of nutrient absorption (Goodman and Collison, 1982). Using ^{32}P they were able to demonstrate that the major zones of P uptake by ryegrass were deeper in the presence of clover than when the grass was growing in monoculture. The proliferation of roots in fertile zones of the soil layer has also been shown in field experiments (Fitter and Bradshaw, 1974). Under controlled conditions, Hackett (1968) and Drew et al. (1978) also showed increase in root density to be very localized and laterals were produced where high levels of nutrients were supplied.

Hartman and Allard (1964) compared the competitive ability of two barley varieties and reported that the variety with the more extensive root system was a better competitor for limiting soil nutrients and

moisture. When these factors were in ample supply the variety with less roots was capable of accumulating more nutrients than that with more roots. Soil environmental conditions may affect the production of the root mass and its properties. Racz et al. (1964) showed that low moisture levels in the soil can stimulate roots to grow deeper and extract moisture from the subsoil level. It has also been shown that root production was affected by low nutrient conditions in the media. Under these circumstances longer and deeper roots were produced (Ennik and Hofman, 1983).

Nye and Tinker (1977) claimed that plants apportion more biomass to the root system under soil moisture and nutrient deficient conditions, enabling them to compete more effectively.

The soil surrounding individual roots may become depleted of nutrients, the rate of depletion depending on the mobility of the resource (Nye and Tinker, 1977). For an immobile nutrient such as phosphate a marked depletion immediately near an active root may be expected in the soil. However, unless roots overlap, competition among roots for such nutrients may not be intensive. On the other hand, if roots are restricted with respect to the volume of soil so that depletion zones overlap, competition for soil resource may be intense. Gerloff (1976) stated that if access to soil nutrients is a limiting factor, then morphological features of the root systems of plants will be critical for ion uptake. As species vary in their rooting habits, their ability to obtain immobile nutrients and hence their nutritional requirements may be expected to be different.

The density of roots of plants at various soil depths during growth and development has been investigated. It has been indicated that aggressive weed species tend to produce much-branched and dense roots in deeper than in shallower layers of soil. For example Ellern et al. (1970) compared the growth of the root systems of Avena fatua L. and Avena strigosa L. at different depths of soil. They found that A. fatua had a higher percentage of its roots at greater depth, whilst roots of A. strigosa were mostly found in the upper layer of the soil. The percentage contribution to the total root weight at the various depths of soil by each species was different, particularly during the early period of growth. Tarawali (1987) examined some features of the root systems of

wheat and A. myosuroides both in the field and glasshouse. He found a higher root volume and weight in A. myosuroides than in wheat and attributed the ability of the weed to take up nutrients to its root characteristics. Qasem (1987) also studied the distribution in the soil of the root systems of tomato, fat-hen (Chenopodium album L.) and groundsel (Senecio vulgaris L.) with time. He found that fat-hen and tomato had almost the same percentage of roots at a depth of 40-50 cm. Groundsel had a higher percentage of its roots in the top 20 cm and a very low density at depths below 30 cm. In all three species root density was highest in the first 10 cm of soil. He also noted that the distribution of roots varied with plant age. Similar studies were made on the root distribution of corn (Zea mays) and soybean roots by Barber (1974a). When corn plants were 30 days old, he found more than half of the roots in the top 15 cm of the soil, but this dropped to 30% at plant maturity. In the case of soybean he found 31% of the roots in the top 15 cm of the soil at 60 days and at 117 days this had increased to 59%. Johnson (1981) studied the distribution of the root system of reed canary grass (Phalaris canariensis) and found many of the roots in the 0.2 cm soil layer and that the amount decreased exponentially with depth. He reported root density in the 0-5 cm layer to be greater than 25 cm/cm^3, but only 2.5 cm/cm^3 between 15 and 35 cm.

Stevenson (1967) has shown that roots of a plant will compete with each other for water if their density is too high, i.e. if roots are restricted by soil volume. He found that the root and top growth of clover, wheat and sunflower plants consistently and quantitatively varied with soil volume. Baker and Woodruff (1962) also studied the effect of soil volume and P nutrition on the growth of corn (Zea mays). They concluded that for optimum plant growth in small containers a greater P concentration is required than in large ones. How the volume of soil available to roots influences yields, response to added nutrients and the uptake of nutrients of contrasting mobility was also demonstrated by Cornforth (1968). He showed that the extra fertilizer added can make up for the small volume of soil available to the roots. He found the response to P to be greater in large volumes, while that of N was greater in small volumes. Although he found uptake of N and P to increase with increase in soil volume, uptake per unit volume of soil decreased as the volume of soil incresed (i.e. presumably as the root density decreased). Mitscherlich (1949, cited by Cornforth, 1968) also reported that P uptake

by seedlings was not proportional to the amount of soil used, but more P was extracted per unit volume of soil from small than large volumes. Newman and Andrew (1973) found that K uptake per unit mass of root was lower in small volumes of soil.

The importance of roots relative to shoots in determining the competitive abilities of wheat, wild oats and barren brome is shown elsewhere in Section IV. The main objective of the series of experiments reported in this section was to reveal any differences in the root morphology of these species which may help to explain the observed differences in their abilities to compete and absorb nutrients. These experiments were also carried out in order to obtain specific information on:

(1) the development of the root system in relation to the growth of the shoot and whole plant.

(2) the root distribution, depth, density, i.e. root volume weight and length with time. Vengris et al. (1955) stated that estimates of the amount of root/unit volume of soil are required to study water and nutrient uptake of species.

(3) the effect of root restriction on plant growth and nutrient uptake.

(4) the effect of nutrient supply (P) in compensating for root restriction.

(5) the visual differences in the root morphological features of the species and

(6) to separate the effects of root competition, shoot competition and their interactions and to assess the relative importance of above (shoot) and below-ground (root) competition in determining the competitive abilities of these species in terms of dry matter yields, nutrient concentration and total uptake.

8.3 Materials and Methods (General)

The soil used in experiments 2 and 4 was collected from College experimental plots which had not been cropped in the previous year. The

soil was left on the floor of the glasshouse to dry under a hot air fan for a few days. Large lumps were crushed and the soil sieved through a 9.5 mm mesh sieve. Some samples were taken for analysis by ADAS and the result showed that the soil was rich in phosphorus (86 ppm or 2.77 mM), potassium (287 ppm or 7.36 mM), magnesium (104 ppm or 4.33 mM) and had a pH of 7.9. Calcium status of the soil was expressed in terms of lime requirement (tonne/ha) and liming was not necessary. The soil nitrogen status was not determined but plants were fed with solutions containing supplementary nitrogen at the level of the full strength Long Ashton nutrient recipe. In order to facilitate aeration and washing out of the root systems nine parts of soil were mixed with one of river sand. In experiments 2 and 3 different pot sizes were used but all were of similar shape. Details of the pots are given in Table 4.1. The ratio of weight of soil in a pot to that in the smallest pot (Table 4.1) was described as the soil weight ratio by Qasem (1987).

Table 4.1 Dimensions, surface area, soil weight, soil ratio and capacity of pots used in experiments 2 and 3

Pot size	Height (cm)	Top diameter (cm)	Bottom diameter (cm)	Surface area (cm2)	Soil wt (kg/pot)	Soil wt ratio	Capacity (cm3)
1	18.75	18.75	13.25	276.20	4.68	13.77	5178.75
2	15.00	15.00	10.75	176.77	2.21	6.50	2651.55
3	12.50	12.50	8.50	122.76	1.22	3.59	1534.46
4	8.75	8.75	5.25	60.15	0.34	1.00	526.32

The medium used in experiments 1 and 3 consisted of 70% medium grade peat, 20% grit and 10% river sand. In all the experiments, sterile brome was sown up to five days earlier than wild oat and wheat. The only exception is in experiment 4 section (b) where sterile brome and wild oat were sown directly into boxes on the same day. In experiments 2 and 4 roots were harvested and the different root parameters recorded. The total root length of the root systems of the three species was determined either by Comair Root Length Scanner, or by the root intercept method (Tennant, 1975). Before determining total root length using the scanner,

the root system was cut into lengths of approximately 20-30 millimeters. The volume of the root systems was obtained by a displacement method. The mean root radius (ro) was calculated from the formula $ro=(FW/L)^{\frac{1}{2}}$ (Fontes et al., 1986), where, FW was the root fresh weight (g) and L the total root length in cm. This formula assumes that the root system is a uniform cylinder with a constant diameter. The total surface area of the root system was calculated from the mean radius and the total root length using the formula $2roL$. In all experiments, for each harvest, shoot parameters such as the number of shoots and fresh and dry weights were recorded. Root fresh and dry weights were also taken for experiments 2 and 4 only. Analysis for shoot and root nutrient concentrations were carried out. The shoots and roots were dried in an oven at 70°C for up to three days and finely ground using a ball mill. Approximately 150-200 mg of the ground sample was weighed into vials and ashed in a furnace at 450-480°C. The ashed sample was dissolved in a few drops of concentrated hydrochloric acid and transferred to volumetric flasks and made up to the mark with deionized water. These solutions were used to determine phosphorus, potassium, calcium and magnesium as described in Section I.

Experiment 4.1: Separating the effects of root competition and shoot competition

Materials and Methods

Barren brome seeds were sown on 6/5/88 and those of wheat and wild oats on 9/5/88. The seedlings were raised in nutrient-free compost mixtures and transferred on 18/5/88 to 15 cm pots filled with the same mixture to a level 2.5 cm below the rim. The plants were grown in the glasshouse with maximum, minimum and mean air temperatures of 26.5, 16.5 and 21.5°C respectively. Irradiation was only from natural light.

A technique for separating competition into components relating to the roots and to the shoot was developed by Donald (1958) for use in pot experiments and the technique adopted here was basically similar in that separating panels were placed above and below the soil allowing plants to be grown under conditions of no competition, root competition only, shoot competition only, and both shoot and root competition. The technique used differed from that of Donald in that pure stands of each species at the same densities as in the mixtures were grown in separate pots.

The separation of the root system of the species was achieved by means of formica sheet held vertical by a window frame sealant. The aerial parts of the plants was also separated using the same material extended up to 30 cm (12 in) above the pot. A stick glued to the formica sheet and inserted in the soil mixture in the middle of the pot held the formica in position. To decrease shading the sheet dividing the aerial part was covered with reflective aluminium foil. By different arrangements of the partitions the following four modes of competition (treatments) were obtained.

(T1) Full competition: no divisions of the soil or the aerial environment so that the root and shoot systems of the plants intermingled.

(T2) Root competition: the root systems were allowed to intermingle but the shoots of adjacent plants were separated.

(T3) Shoot competition: the shoot systems were allowed to mix but the root systems of adjacent plants were separated.

(T4) The species were not mixed above or below the soil. Hence, there was no interspecific competition, but intraspecific competition can be assumed.

12 treatment and species combinations could be obtained. However, due to lack of space, only 10 combinations were investigated. The treatment and species combinations were as follows. The mixtures consisted of two plants of the competing species:

(T1) Full competition
(a) wheat and wild oat competing (w2+wo2)
(b) wheat and barren brome competing (w2+bb2)
(c) wild oat and barren brome competing (wo2+bb2)

(T2) Root competition
(d) wheat and wild oat competing (w2+wo2)
(e) wheat and barren brome competing (w2+bb2)

(T3) Shoot competition
(f) wheat and wild oat competing (w2+wo2)
(g) wheat and barren brome competing (w2+bb2)

(T4) No competition - pure stands (4 plants/pot)

(h) wheat alone (w4)

(i) wild oat alone (wo4)

(j) barren brome alone (bb4)

The pots were separated into three blocks with every treatment combination represented in all blocks and randomised within each block. The aerial partitions were orientated in a north-south direction to minimise any shading effects. The rectangular blocks themselves were orientated similarly. The plants were fed with the full concentration Long Ashton nutrient solution at 200 ml/pot/week. When the pot was divided into two equal parts (T3), then each partition received 100 ml/week. Three harvests were made at 28, 35, and 42 days after transplanting. The number of tillers/plant and shoot dry weights were recorded. The shoot dry matter yield for the second harvest was analysed for P, K, Ca and Mg tissue concentrations. The data were subjected to analysis of variance. The performance of the mixture in the various combinations was expressed as the relative yield total (RYT) (de Wit and van den Burgh, 1965). The competitive ability of the species was expressed as the aggressivity (McGilchrist and Trenbath, 1971).

Experiment 4.2: Responses of A. fatua, barren brome and wheat to root restriction

Seeds of the three species were germinated in soilless compost containing the usual nutrients and watered with tap water as required. When seedlings reached the transplanting stage, two seedlings were planted in each pot irrespective of pot size on 24/8/87. Nitrogen was used in the form of $NaNO_3$ and pots received 50 ml per pot per week. Distilled water only was used between nitrogen applications. The different pots were arranged in a randomized block design with four replicates. Three harvests were made at 39, 49 and 59 days after transplanting. During each harvest, the number of tillers and shoot fresh and dry weights were recorded. The root systems were harvested for the first and third harvest only. The soil particles were washed off the roots with tap water in a 5.00 mm mesh sieve and the roots rinsed with distilled water twice before length, volume and fresh and dry weights were recorded.

Experiment 4.3: Response of Avena fatua barren brome and wheat to root restriction and phosphorus level

Sterile brome seeds were sown on 29/1/88 and those of wheat and wild oat on 3/2/88. A nutrient free soilless compost mixture was used for germinating the seeds. When the seedlings reached the stage of transplanting two were transplanted per pot on 18/2/88. Three pot sizes (1, 2 x 3) only were used in this experiment. Two phosphorus levels prepared on the basis of the Long Ashton nutrient recipe were used:

(L1) 0.645 mM (20.5 ppm P) and

(L2) 0.0645 mM (2.0 ppm P)

Solutions were prepared containing these concentrations of phosphorus and the other required elements as in the Long Ashton recipe and were given to plants on a weekly basis at 100 ml per pot starting at the end of the second week after transplanting. The pots were watered with distilled water between nutrient application. Three harvests 4, 6 and 8 wegks were made after the first date of application of nutrients. At each harvest data were collected for tiller number, shoot fresh and dry weights and tissue nutrient concentrations.

Experiment 4.4 a and b : Root growth, development and depth distribution of species at different stages of growth

Experiment 4a was carried out in cylindrical polyvinyl chloride (PVC) tubes 50 cm long and 10 cm wide. These tubes had about 3928 cm^3 capacity and were filled with approximately 4.94 kg of soil. One seedling was transplanted into each tube on 18/11/87 and there were six tubes per species arranged in a completely randomized design. Because the natural light conditions were inadequate during the time the experiment was carried out, the plants were given up to ten hours of supplementary illumination period per day by 400 W mercury vapour lamps. The tubes received 200 ml of the full strength Long Ashton nutrient solution per week. Tap water was used for watering the plants and leachates collected on saucers returned to relevant tubes. Harvests were taken at 12 and 16 weeks after transplanting. The shoots were clipped off at soil level and the data for tiller number and shoot fresh weight recorded. The soil was soaked with plenty of tap water and left overnight before the roots were harvested. The tubes were then gently

tapped and the soil profile carefully dislodged without breaking. The column was separated at depths of 10, 20, 30, 40 and 50 cm from the surface and the roots harvested together with the adhering soil. The soil was washed off carefully with a hose in a 5.0 mm mesh sieve. The roots were then rinsed twice with distilled water and their fresh weights recorded after surface water was removed using a paper towel. The dry weight data for shoots and roots were taken after drying at 70°C for three days in an oven.

In experiment 4b, wild oat and sterile brome were sown on 27/1/88 directly into deep metal boxed (55x20x91.5 cm deep) with soilless compost containing all the required plant nutrients. There were two seedlings per box and these were grown for up to four months. No additional nutrients were given and the plants were watered with tap water. Because only two boxes were available at a time wheat was grown in these boxes during the period May to July 1988. Just before harvest the boxes were opened on one side and the exposed soil profile revealed and the distribution of the roots systems were photographed. The root system of each species was carefully washed free from the growth mixture and the root fresh weights measured. Estimates of the total root length were made by the line intercept method. The shoot and root dry weights were also recorded.

8.4. Results

Experiment 4.1 Separating the effects of shoot competition and root competition

(i) Effects of forms of competition on the relative performance of wheat and wild oat

Dry weight (g/plant)

The responses of the two species to forms of competition were similar, i.e. yields in pure stands were greater than in competition at all three harvests. The amount of dry matter produced by the species also differed at all harvests, but interactions were significantly different at the first two harvests only (Table 4.2). In wheat, dry matter accumulation appeared to be more reduced when the species compete for root resources, whilst in wild oat the effect appeared to be of similar magnitude for all forms of competition.

In tables 4.2 to 4.17, PS = pure stand, SC = shoot competition, RC = root competition, FC = full competition; H1, H2 and H3 = first, second and third harvests

Table 4.2. Effects of forms of competition on the mean dry matter yield of wheat (W) and wild oat (WO) at three harvests

Form of competition	Mean dry matter yield (g/plant) H1 W	H1 WO	H2 W	H2 WO	H3 W	H3 WO
PS	1.02	1.53	1.57	2.60	2.36	2.99
SC	0.63	0.80	0.90	1.30	1.12	1.65
RC	0.51	0.80	0.83	1.11	0.88	1.86
FC	0.55	0.85	0.72	1.27	1.05	1.78
LSD ($P < 0.05$, interaction)	0.16		0.21		NS	

Table 4.3. Effects of forms of competition on the relative yields of wheat (RYW) and wild oat (RYWO) calculated for yields of dry matter at three harvests

Form of competition	Relative yields (RYs) H1 RYW	H1 RYWO	H2 RYW	H2 RYWO	H3 RYW	H3 RYWO
SC	0.62	0.52	0.58	0.50	0.48	0.56
RC	0.50	0.53	0.53	0.43	0.37	0.62
FC	0.54	0.55	0.46	0.49	0.45	0.60
LSD ($P < 0.05$)	NS		NS		NS	

Table 4.4. Effects of forms of competition on mean relative yield totals (RYTs) of wheat (W) and wild oat (WO) calculated for shoot dry matter yields (g/plant) at 3 harvests

Treats	H1	H2	H3	Mean
SC	1.14	1.08	1.04	1.09
RC	1.02	0.96	0.99	0.99
FC	1.09	0.95	1.04	1.03
LSD ($P < 0.05$)	NS	0.06	NS	

Table 4.5. Effects of forms of competition on the aggressivity of wild oat towards wheat calculated for yields of shoot dry matter (g/plant) at 3 harvests

Treats	H1	H2	H3
SC	-0.05	-0.04	0.04
RC	0.03	-0.05	0.13
FC	0.01	0.02	0.08
LSD ($P < 0.05$)	NS	NS	NS

Relative Yields (RYs) and Relative Yield Totals (RYTs)

Relative yields (RYs) calculated for yields of dry matter of the two species showed that they did not differ significantly except at the third harvest where those of the weed were higher than the crop for all three forms of competition. Up to the 2nd harvest no clear trends in the competitive ability of either species at any one form of competition were shown. At the third harvest, it was shown that the competitive ability of the weed was greater than the crop and the RY of the latter under root competition (RC) was significantly reduced compared with shoot or full competition (Table 4.3).

Relative yield totals (RYTs) only differed at the 2nd harvest and values for root and full competition were significantly lower than for shoot competition (Table 4.4). In general values of mean RYTs either approximated to 1.0, as in the case of root competition or were slightly higher than 1.0.

Aggressivity of wild oat relative to wheat

The competitive ability of the two species did not differ at the three stages of growth or for the forms of competition (Table 4.5) i.e. aggressivity values of the weed relative to wheat did not significantly deviate from zero. However, the shoot competitive ability of the crop and its root competitive ability at the first and second harvest stages appeared to be greater than that of wild oat, i.e. aggressivity values of the weed were negative. Values for full competition at the three harvests and shoot and root competition at the third harvest were positive, indicating that the weed was the aggressor especially at later stages of growth and the higher value for root competitive ability may show that root effects were greater than those of the shoot, though the fact that it also exceeded the value for full competition is not easy to explain.

Nutrient concentrations

The nutrient concentrations in the crop for K and Ca were higher, whilst Mg concentration of the weed was significantly higher for almost all forms of competition. P concentrations in the species did not differ (Table 4.6).

Table 4.6. Effects of forms of competition on the nutrient concentration in wheat (W) and wild oat (WO) at the 2nd harvest

Forms of competition	Nutrient concentration (mMols/g DW of shoot) P		K		Ca		Mg	
	W	WO	W	WO	W	WO	W	WO
PS	0.17	0.16	0.35	0.29	0.83	0.55	0.21	0.30
SC	0.16	0.18	0.32	0.30	0.69	0.68	0.18	0.29
RC	0.19	0.15	0.34	0.23	0.92	0.60	0.19	0.26
FC	0.16	0.18	0.29	0.32	0.81	0.58	0.23	0.21
LSD ($P<0.05$ interaction)	NS		0.01		0.02		0.01	

Table 4.7. Effects of forms of competition on the relative yields of wheat (RYW) and wild oat (RYWO) calculated for nutrient yields (mMol/plant) at the 2nd harvest

Forms of competition	Relative yields (RYs) P		K		Ca		Mg	
	RYW	RYWO	RYW	RYWO	RYW	RYWO	RYW	RYWO
SC	0.59	0.61	0.58	0.47	0.54	0.53	0.53	0.58
RC	0.61	0.48	0.77	0.35	0.38	0.42	0.61	0.64
FC	0.64	0.49	0.70	0.40	0.40	0.61	0.58	0.56
LSD ($P<0.05$)	NS		0.08		0.12		0.08	

Table 4.8. Effects of forms of competition on the relative yield totals of wheat (W) and wild oat (WO) calculated for nutrient yields (mMol/plant) at the 2nd harvest

Treatments	Relative nutrient yield totals P	K	Ca	Mg	Mean
SC	1.11	1.07	1.14	1.07	1.10
RC	0.96	0.84	1.08	0.86	0.94
FC	0.95	0.89	0.96	0.84	0.91
LSD ($P < 0.05$)	NS	0.15	0.13	NS	

Table 4.9. Effects of forms of competition on aggressivity of wild towards wheat calculated for nutrient yields at the 2nd harvest

Treats	P	K	Ca	Mg
SC	-0.01	-0.01	0.10	-0.02
RC	-0.10	-0.07	-0.05	-0.06
FC	0.06	0.07	0.05	-0.08
LSD ($P < 0.05$)	0.09	0.10	0.09	NS

Relative yields (RY) and relative yield totals (RYTs)

RYs showed that shoot competitive ability of the species for P, Ca and Mg and root competitive ability for P and Ca were similar. The crop showed higher root competitive ability for the elements K and Mg. The RY of the crop for K was also higher under full competition than the weed, while the latter had higher RY for Ca. Both species showed similar competitive abilities for P and Mg under full competition (Table 4.7).

RYTs differed between the different forms of competition for K and Ca only (Table 4.8). RYTs were greater than 1.0, for P, K, Ca and Mg when shoot competition was operating. These did not approach unity in root or full competition.

The aggressivity of the weed towards the crop calculated for nutrient yields indicated that this differed between forms of competition (Table 4.9). Except under full competition, where the weed was the aggressor, the crop was competitively superior to the weed when shoot and root competitions were operating separately, i.e. deviations from zero were negative for the elements P, M, Ca and Mg.

(ii) Effects of Forms of competition on the re tive performance of wheat and barren brome

Dry weight (g/plant):-

Both species produced significantly greater amounts of shoot dry matter yield in pure stands than in mixtures where they were allowed to compete for aerial, underground or both resources at three stages of growth. At the first harvest yields of the two species competing under the three forms of competition did not differ significantly. Yields were different at the two later harvest and the yield of the crop was higher than the weed for all forms of competition (Table 4.10). The yield of barren brome under root competition was lower than for shoot or full competition at all three harvests.

Relative Yields (RYs) and Relative Yield Totals (RYTs)

RYs calculated for dry matter for wheat and barren brome for the three forms of competition gave higher values for the crop although this did not reach statistical significance at the first harvest (Table 4.11). The values of RY of the weed competing for soil resources were much lower than for shoot or full competition, indicating that the crop competed

Table 4.10. Effects of forms of competition on the relative yield totals of wheat (RYW) and barren brome (RYBB) calculated for dry matter yields at all 3 harvests

Forms of competition	Relative yields of species H1	H2	H3
SC	1.16	1.14	0.99
RC	0.95	1.04	0.85
FC	0.98	1.02	0.92
LSD ($P<0.05$)	0.18	NS	NS

Table 4.11. Effects of forms of competition on the aggressivity of wild oat towards wheat calculated for yields of shoot dry matter (g/plant) at 3 harvests

Forms of competition	Relative aggressivity of barren brome H1	H2	H3
SC	-0.06	-0.03	0.02
RC	-0.15	-0.13	-0.17
FC	-0.13	-0.05	-0.08
LSD ($P<0.05$)	NS	0.08	0.09

Table 4.12. Effects of forms of competition on the mean dry matter yields of wheat (W) and barren brome (BB) at three harvests

Forms of competition	Mean dry matter yield (g/plant) H1 W	H1 BB	H2 W	H2 BB	H3 W	H3 BB
PS	1.02	0.73	1.57	1.12	2.36	1.48
SC	0.64	0.37	0.94	0.61	1.11	0.76
RC	0.59	0.24	1.07	0.44	1.44	0.38
FC	0.62	0.27	0.88	0.52	1.25	0.57
LSD ($P < 0.05$, interaction)	NS		0.27		0.12	

Table 4.13. Effects of forms of competition on the mean relative yields (dry matter) of wheat (RYW) and barren brome (RYBB) at three harvests

Form of competition	Relative yields (RYs) H1 RYW	H1 RYBB	H2 RYW	H2 RYBB	H3 RYW	H3 RYBB
SC	0.63	0.51	0.60	0.54	0.47	0.51
RC	0.63	0.33	0.65	0.39	0.59	0.26
FC	0.61	0.36	0.56	0.46	0.53	0.39
LSD ($P < 0.05$ interaction)	NS		0.09		0.09	

Table 4.14. Effects of forms of competition on the nutrient concentrations of wheat (W) and barren brome (BB) at the 2nd harvest

Forms of competition	P		K		Ca		Mg	
	W	BB	W	BB	W	BB	W	BB
PS	0.17	0.16	0.35	0.44	0.83	1.13	0.21	0.28
SC	0.17	0.18	0.34	0.37	0.76	1.11	0.18	0.29
RC	0.16	0.19	0.39	0.38	0.49	1.21	0.20	0.33
FC	0.19	0.16	0.44	0.36	0.57	1.54	0.21	0.33
LSD ($P<0.05$ interaction)	NS		0.06		0.19		NS	

Table 4.15. Effects of forms of competition on the relative yields of wheat (RYW) and barren brome (RYBB) calculated for nutrient yields (mMol/plant) at the 2nd harvest

Forms of competition	P		K		Ca		Mg	
	RYW	RYBB	RYW	RYBB	RYW	RYBB	RYW	RYBB
SC	0.59	0.61	0.58	0.47	0.54	0.53	0.53	0.58
RC	0.61	0.48	0.77	0.35	0.38	0.42	0.61	0.49
FC	0.64	0.49	0.70	0.40	0.40	0.61	0.58	0.56
LSD ($P<0.05$ interaction)	0.13		0.08		0.12		NS	

strongly for these resources.

RYTs for shoot competition were greater than 1.0 except at harvest 3. For root and full competition they were less than 1.0 at the first and third harvests (Table 4.12).

Aggressivity of barren brome relative to wheat

Values for relative aggressivity of the weed towards the crop calculated for dry matter at the three harvests showed that the weed was a weaker competitor than the crop i.e. deviations from zero were negative (Table 4.13). The deviations differed between forms of competition at the 2nd and 3rd harvest only.

Nutrient concentrations:-

P and Mg concentrations did not differ significantly between and within species for the different forms of competition, although values in general were higher for the weed, especially for Ca and Mg. Interactions were different for K and Ca concentrations. The crop contained the highest tissue concentration for K when the species competed fully. The weed had higher K concentration in pure stands and under the other modes of competition it was either similar to or less than the crop. Ca concentrations, however, showed higher values for the weed for all modes of competition (Table 4.14).

Relative Yields (RYs) and Relative Yield Totals (RYTs)

RYs calculated for contents of P, K and Mg were greater for the crop for all forms of competition (Table 4.15). Interactions were significant except for Mg. RYs for Ca were similar except for full competition, where it was higher for the weed.

RYTs did not differ between forms of competition for any nutrient (Table 4.16). Values were slightly greater than unity except for Ca under root competition, thus probably implying competitive interactions between the species.

Aggressivity of barren brome relative to wheat

Values for the relative aggressivity of the weed towards the crop suggested that the latter was more competitive than the weed for P, K, Ca and Mg, but deviations from zero were significant only for P (Table 4.17). The fact that the values for the four elements and for all forms

Table 4.16 Effects of forms of competition on the relative yield totals of wheat and barren brome calculated for yields of dry matter at the 2nd harvest

Forms of competition	P	K	Ca	Mg
SC	1.21	1.09	1.07	1.11
RC	1.08	1.12	0.80	1.10
FC	1.18	1.10	1.01	1.14
LSD ($P < 0.05$)	NS	NS	NS	NS

Table 4.17 Effects of forms of competition on the relative aggressivity of barren brome towards wheat calculated for nutrient yields at the 2nd harvest

Forms of competition	Relative aggressivity of barren brome			
	P	K	Ca	Mg
SC	0.01	0.07	-0.01	0.02
RC	-0.02	-0.17	0.02	-0.06
FC	-0.08	-0.16	0.11	-0.01
LSD ($P < 0.05$)	0.05	NS	NS	NS

of competition were negative implies that the weed was the weaker competitor.

8.6 Discussion

Plants compete for both aerial resources (mainly light) and soil resources (various mineral nutrients and water) and it is likely that competition normally occurs for several of these resources simultaneously (Donald, 1963). The effects of competition for aerial resources (i.e. shoot competition) and the effects of competition for soil resources (i.e. root competition) were also first separated by the technique devised by this author. A number of other investigators have used modifications of Donald's technique to study the nature of competition between various plant species (e.g. Snaydon, 1971; Eagles, 1972; Remison and Snaydon, 1980; Snaydon and Howe, 1986; Johnson, 1987; Qasem, 1987). Generally the effects of root competition have been found to be greater than shoot competition. This was also true in the present experiments.

The competitive abilities of the two weeds relative to the crop competing for aerial or soil resources or both were assessed using the quantity of dry matter produced (g/plant), tissue nutrient concentrations, relative yields (RYs) and relative yield totals (RYTs) calculated for yields of dry matter and nutrient contents (de Wit, 1960; de Wit and Van den Burgh, 1965; Hall, 1974a and b). The relative competitive abilities of both weeds were also assessed as the aggressivity of an individual weed against the crop (McGilchrist and Trenbata, 1971). Analysis of variance were carried out on values of dry matter, nutrient concentrations, RYs, RYTs and aggressivity. Where negative values for aggressivity were produced, exceedingly high coefficients of variation were encountered due partially to small grand mean. Kempson (personal communication) indicated that if some data were negative the value of the coefficient of variation is not meaningful.

(i) Effects of forms of competition on the relative competitive ability of wheat and wild oat

Wild oat was the more competitive as shown by its aggressivity relative to wheat, relative yields and shoot dry matter yields, especially at later stages of growth. The greater competitive ability of wild oat relative to wheat was also noted in the previous competition

experiments (see Section III) and this is also in general agreement with the results of Martin and Field (1987, 1988). The greater competitive ability of the weed appeared to be predominantly due to the greater root competitive ability as shown by the greater value for aggressivity under root competition than shoot competition at the third harvest. The increase in the relative yield of wild oat and the decrease in the relative yield of the crop, especially under root competition, also indicate the greater competitive ability of the weed. At early stages of growth relative yields were close to 0.5 and values for aggressivity also did not deviate significantly from zero for any form of competition, indicating similar competitive abilities of the two species both for light and underground resources. Although deviations for values of RYs and aggressivity at the third harvest were greater than at harvests 1 and 2 for the weed for all forms of competition, these also did not reach statistical significance. It seems likely that the ability of the weed to compete for growth resources, especially those of the soil, increases with the period of competition and it could well be that if all the harvests had been rather later the effects would have been more obvious.

Differences in the growth and development of the root systems of wild oat and other cereals have been reported (Pavlychencko, 1937, 1940). He found that wild oat had three or fewer seminal roots, while wheat had four or five. At an early stage the weed may be suppressed by some cereals. However, at later stages the weed produces prolific roots which enable it to compete for nutrients more efficiently than the crop.

The different forms of competition had no significant effect on the relative yield total. Except at the 2nd harvest, RYTs did not deviate from unity (Table 4.4). This indicates a proportionate increase in the relative yield of one of the speices being matched by a decrease in the relative yield of the other under all forms of competition. This suggests that the two species compete for the same resources. At the 2nd harvest the RYT of the species in shoot competition was significantly greater than for root and/or full competition. The RYT for shoot competition also was greater than unity, suggesting that the species may or may not have competed for light, while RYT was less than 1.0, for root and full competition, which can indicate mutual antagonism, or reduced growth as the result of intense competition for resources.

Both species appeared to have absorbed similar quantities of P under

all forms of competition. However, K and Ca uptake of the crop was higher than the weed, and the latter had higher concentrations of Mg under all except the full competition (Table 4.6) where the crop was higher. Greater competitive ability of the crop for limiting K has also been found in experiment 3 of this section.

In wild oat the relative yields suggested that the magnitude of shoot competition was greater than root competition. The effects of full competition were not always additive, and the effects of roots or shoots were sometimes greater than the effects of full competition. Similar observations have been made by many investigators e.g. Martin and Field (1984); Wilson (1988). Nutrient concentration in pure stands also differed within species.

Relative yields calculated for nutrient yields showed that the competitive abilities of the two species were similar for phosphorus. The crop showed higher competitive ability for K for all forms of competition. The species differed for Ca but only for full competition where the weed was higher. The RY for the weed for Mg was also similar to the crop, except under root competition, where that of the crop was greater, indicating that below ground competition may determine the competitive ability of the species.

The RYTs for K and Ca differed between forms of competition, while they remained similar for P and Mg. RYTs for shoot competition were greater than, while those for root and full competition were less than unity, except for Ca in root competition, indicating the importance of root and/or full competition for mineral resources.

The aggressivity of the weed relative to the crop showed the crop to be more competitive for all the elements under shoot and root competition at early stages. Under full competition the weed was the aggressor species except in the case of Mg.

The results in general suggest that the crop may be more successful in competition than the weed particularly at early stages of growth. Although the absolute shoot yields of the weed were always greater than the crop shoot competition of the former was slightly less than that of the latter up to the second harvest. Its ability to compete for below ground resources was also shown by greater relative yields and relative aggressivity. A high initial root growth rate in wheat leading to a

larger root system may be attributed to a greater embryo size and initial reserves of the crop. An initial faster growth of the roots of the crop might lead to earlier competition with the weed for nutrients, and this could be reflected in shoot growth and subsequent shading effects. This did not appear to have happened with wild oat, because by the third harvest relative yields and relative aggressivities of the weed were greater than zero for all forms of competition, suggesting greater competitive ability of the weed at later stages of growth. Pavlychenko (1937, 1940) found that the slower initial growth rate of the wild oat root was to a large extent responsible for its initial weakness in competition with cereals. Martin and Field (1987), however, found that wild oat was more competitive than wheat over a period extending to 90 days when the two species were sown simultaneously. They reported that the greater competitive ability of the weed was due largely to its greater root competitive ability; shoot competitive abilities being similar to each other. In the present experiment although the crop showed strong competitive ability under shoot and root competition at early stages of growth and the weed later, differences were not statistically significant. Throughout the three harvest periods, the weed was also more competitive than the crop as judged by its values for aggressivity under full competition, which were positive for dry matter yields and for P, K and Ca (Tables 4.5 and 4.9).

(ii) Effects of forms of competition on the relative performance of wheat and barren brome

The results for the dry matter yields and the values for relative yields and aggressivity (Tables 4.11 and 4.13) showed that the crop was more competitive than the weed at the second and third harvests. Root competition usually affected the balance between wheat and barren brome more than shoot competition. In come cases the competitive ability of roots, shoots and full competition were similar. Other workers have reached similar conclusions (e.g. Donald, 1958; King, 1971; Snaydon, 1971; Remison and Snaydon, 1980b; Snaydon and Harris, 1981; Martin and Snaydon, 1982; Wilson and Newman, 1987; Martin and Field, 1987, 1988). Wilson (1988) made a survey on the relative importance of shoot and root competition. He reported that in 70% of such studies found in literature, root competition had a greater effect than shoot competition, while in 30% the reverse was true. He also found that in the crop/weed

experiments surveyed, the crop had the higher shoot competitive ability in eleven cases out of fifteen, higher root competitive ability in eleven cases and higher full (shoot and root) competitive ability in ten cases.

In the present experiments the weed appeared to have performed better under shoot competition than under root competition despite the fact that reduction in nutrient supply to shoots caused by severe root competition would lower the efficiency of the shoot and thus its ability to compete for light. This was not expected because the weed usually grew shorter than or similar height to the crop. It may thus be that barren brome is tolerant to some shading. It is noteworthy that the plant has become an important weed in relatively recent years, having previously been found in hedgerows and waysides, where shade tolerance may be important. This may also explain the presence of the weed in some tall growing field crops e.g. oilseed rape (Brassica rapa). In the present experiments the weed never grew tall enough to interfere with the light supply of the other species and must therefore have been affected by competition for light by both species.

Nutrient concentrations also differed within and between both species and forms of competition. Both species contained similar concentrations of P and Mg, under all forms of competition, although those of the weed were slightly higher. The crop had a higher concentration of K under full competition, the weed having the higher in pure stands, suggesting that the weed is a poorer competitor than the crop for this element. Higher concentrations and better competitive abilities for K in wheat were reported in Section I, and the previous section. Barren brome also contained higher concentrations of Ca than wheat under all forms of competition. The weed also contained slightly higher concentrations of Mg, particularly under root and full competition. Higher concentrations of both mineral elements in the weed were also reported in earlier sections, and may indicate higher requirement as well as greater competitive ability.

Relative yields for the contents of the elements P, K, Ca and Mg also showed the differences between the species except for Mg (Table 4.15). The crop had higher relative yields for P and K under root and full competition. Shoot competitive abilities of both species did not differ significantly except in respect of K. Under full competition the competitive ability of the weed was greater than the crop for Ca.

Relative yield totals for P, K, Ca and Mg did not differ significantly between forms of competition for any nutrient and the values were greater than 1.0 under all forms of competition, except for Ca under root competition. This implies both competitive and non-competitive interference. At half the optimum Long Ashton nutrient levels, competition for Ca may be expected considering the normal high requirement for it. At such levels the species probably also compete for other nutrient(s) e.g. N, which may be at levels less than the combined demands of both species.

The aggressivity values of barren brome relative to wheat (Table 4.17) calculated for contents of P, K, Ca and Mg, however, showed that the crop was the aggressor in competition under all forms of competition except for Ca, under root and full competition and P under shoot competition. Deviations from zero were significant only for P contents for the different forms of competition.

RYs for yields of dry matter and nutrient contents under root and full competition generally gave higher values than the expected 0.50 for wheat, and lower values for the weed. Under shoot competition RY values of both species were in general greater than expected, although those of the crop were slightly higher, again suggesting an element of non-competitive interference.

Johnson (1987) studied the effects of shoot and full competition and the interactions with N and P levels between winter wheat and blackgrass. He reported that the RYs for yield of dry matter and nutrient contents suggested that the separation of the root systems of the two species was more beneficial to wheat than to blackgrass. Under full competition both species showed higher values of RYz than the expected. He also found RYTs greater than 1.0, and suggested a partial avoidance of competition. He concluded that the occurrence of RYT $>$ 1.0 could not be attributed to a nutrient or group of nutrients being potentially available to only one species (as in symbiotic N-fixation) and that the results could be partly explained as a time-course effect in which full competition only developed slowly.

The greater competitive ability of wheat with this weed, expecially under root and full competition, may be due to araid root growth and profuse tillering as a result of the larger embryo than that of barren brome. This advantage appears to have overcome even the effect of the

weed's having been sown up to 5-6 days earlier. The crop could have exploited the soil more rapidly and therefore gained a larger share of the nutrient than the weed. The effect of root competition of the crop on the weed increased with time and at the third harvest the relative yield of the weed for yield of dry matter was reduced to half of the expected value of 0.50.

Relative yields for P and K contents of the crop were significantly higher under root and full competition, except for Ca, where the weed was more competitive than the crop under full competition. The effects of root or shoot competition on the relative yields for dry matter and nutrient contents of the species were either similar to or greater than full competition, indicating non-additive effects of the two components. In the case of absolute dry matter yields the aggressor species (wheat) never attained a yield equal to that in pure stands giving a clear indication of the effect of the weed on the crop under either form of competition. Nutrient concentrations in the crop were, however, significantly higher in mixtures for K and slightly higher for P especially under full competition. The weed showed higher Ca concentration under root and full competition than in pure stands and also slightly higher Mg under both forms of competition. When the species compete only above ground direct competition for these nutrients is not expected, although competition within plants of each species may occur. Donald (1958) stated that shoot competition would probably influence the size of the root system and its ability to extract nutrients and this may account for the apparent effect of shoot competition upon chemical composition.

Root competition in these experiments and in those carried out by other workers e.g. Snaydon and Howe, 1986; Snaydon, 1971, is usually more important than shoot competition in determining competitive ability, the intensity of competition and resource use. The experiments were carried out in pots under glasshouse conditions as in the present experiments. More realistic results and more widely applicable conclusions might be reached if such experiments were also to be carried out under field conditions. Such experiments can be performed using the methods of Snaydon and Howe (1986); Cook and Ratcliffe (1984) using additive or replacement series, or both models. Variations in the level of nutrient(s) in such experiments would further reveal the nature of competition between component species.

That the effects of root competition may be greater than those of shoot competition, is confirmed by the present results. The fact that RYTs were less than 1.0, under root and full competition and greater than 1.0 under shoot competition at the first harvest may indicate that intense competition may have occurred earlier under root competition. Similar observations were made by Milthorpe (1961) and Snaydon (1971). The smaller effects of shoot competition on both species may also be due to the shorter period of growth. Several investigators have concluded that the importance of shoot competition, relative to root competition increases with time (e.g. Aspinal, 1960; Martin and Field, 1984).

8.6 Results

Experiment 4.2 The responses of wheat (W), wild oat (WO) and barren brome (BB) to root restriction at three stages of growth

The effects of root restriction on the three species were assessed by considering a number of growth variates and nutrient contents. At the second harvest only shoot dry weights were recorded and the analyses of results showed similarities to those of the first and third harvests. Thus the data for yields of dry matter at that harvest are not presented.

For almost all variates the main effects (i.e. pot size and species) differed significantly. Where analyses showed significant interactions the LSDs for interactions were used to compare treatment means.

The results are discussed in relation to the species' ability to grow and extract their nutrient requirements from the soil under conditions of imposed stress.

(a) Shoot dry weight (g/plant)

The species responded similarly to root restriction. As the size of pots was reduced the decline in the dry matter yield was very similar for each. This was shown by the non-significant interactions for dry matter at three harvests and root dry weight at the third harvest (Tables 4.18 and 4.19). The percentage reductions in shoot dry weights between the largest and the smallest pots were 86, 71, 91 and 90, 89 and 92 at the first and third harvests for wheat, wild oat and barren brome respectively.

In Tables 4.18 to 4.23 pot sizes 1-4 are in decreasing order of soil volume

Table 4.18. Effects of root restriction on some growth variates of wheat (W), wild oat (WO) and barren brome (BB) at the first harvest

Pot size	Shoot dry weight(g/plant)			Root dry weight(g/plant)			Root/shoot ratio			Total root length (m/plant)		
	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB
1	2.14	2.12	2.11	0.72	0.61	0.53	0.34	0.29	0.27	526.3	291.8	451.4
2	1.53	1.29	0.95	0.65	0.46	0.39	0.43	0.36	0.41	258.7	230.9	457.4
3	0.92	0.86	0.72	0.49	0.31	0.37	0.54	0.36	0.52	153.0	142.5	288.7
4	0.31	0.41	0.20	0.16	0.17	0.16	0.51	0.43	0.84	52.0	57.4	76.0
LSD ($P<0.05$, interaction)	NS			0.08			0.09			75.11		

Table 4.19. Effects of root restriction on some growth variates of wheat (W), wild oat (WO) and barren brome (BB) at the third harvest

Pot size	Shoot dry weight(g/plant)			Root dry weight(g/plant)			Root/shoot ratio			Total root length (m/plant)		
	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB
1	3.96	4.61	3.64	1.96	1.56	2.11	0.50	0.34	0.58	954.4	714.3	1356.1
2	1.86	2.70	1.69	1.19	0.91	1.11	0.64	0.34	0.65	495.5	336.3	660.7
3	1.25	1.69	1.05	0.77	0.62	0.76	0.61	0.37	0.74	153.5	250.5	503.1
4	0.39	0.51	0.30	0.24	0.28	0.21	0.61	0.59	0.68	65.2	100.6	75.9
LSD ($P<0.05$, interaction)	NS			NS			0.09			93.93		

Table 4.20 Effects of root restriction on the total nutrient contents in shoots of wheat (W), wild oat (WO) and barren brome (BB) at the first harvest

	Total nutrient contents (mMol/plant)											
Pot	P			K			Ca			Mg		
size	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB
1	0.44	0.42	0.35	2.26	2.33	1.87	0.14	0.25	0.73	0.08	0.10	0.08
2	0.30	0.29	0.18	1.53	1.37	0.99	0.09	0.19	0.38	0.05	0.07	0.04
3	0.18	0.14	0.12	0.90	0.87	0.82	0.07	0.14	0.29	0.03	0.04	0.03
4	0.04	0.06	0.04	0.25	0.43	0.21	0.05	0.06	0.11	0.01	0.02	0.01
LSD	0.05			0.23			0.04			NS		
($P < 0.05$, interaction)												

Table 4.21 Effects of root restrictions on the total nutrient contents in roots of wheat (W), wild oat (WO) and barren brome (BB) at the first harvest

	Total nutrient contents (mMol/plant)											
Pot	P			K			Ca			Mg		
size	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB
1	0.16	0.12	0.09	0.20	0.08	0.11	0.21	0.31	0.16	0.012	0.010	0.012
2	0.11	0.06	0.07	0.20	0.05	0.10	0.13	0.16	0.10	0.009	0.006	0.008
3	0.08	0.04	0.07	0.16	0.04	0.12	0.11	0.07	0.09	0.009	0.004	0.009
4	0.03	0.02	0.03	0.08	0.03	0.07	0.03	0.04	0.03	0.003	0.003	0.004
LSD	0.02			0.03			0.03			0.002		
($P < 0.05$, interaction)												

Table 4.22. Effects of root restrictions on the total shoot nutrient contents in roots of wheat (W), wild oat (WO) and barren brome (BB) at the third harvest

	Total nutrient contents (mMol/plant)											
Pot	P			K			Ca			Mg		
size	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB
1	1.54	.155	.132	4.08	7.87	5.12	0.53	0.83	1.30	0.13	0.29	0.21
2	0.55	0.77	0.52	1.51	3.05	2.02	0.28	0.35	0.68	0.05	0.11	0.09
3	0.35	0.46	0.32	0.98	1.71	1.22	0.23	0.26	0.44	0.04	0.08	0.06
4	0.10	0.13	0.07	0.29	0.49	0.30	0.11	0.10	0.15	0.01	0.02	0.02
LSD		0.12			0.42			0.08			0.02	
($P \leq 0.05$, interaction)												

Table 4.23. Effects of root restriction on the total root nutrient contents in roots of wheat (W), wild oat (WO) and barren brome (BB) at the third harvest

	Total nutrient contents (mMol/plant)											
Pot	P			K			Ca			Mg		
size	W	WO	BB	W	WO	BB	W	WO	BB	W	WO	BB
1	0.63	0.58	0.74	0.72	0.22	0.54	0.52	0.60	0.54	0.025	0.026	0.037
2	0.39	0.20	0.36	0.45	0.08	0.28	0.29	0.27	0.26	0.015	0.011	0.019
3	0.23	0.16	0.28	0.27	0.07	0.27	0.15	0.17	0.20	0.009	0.006	0.017
4	0.07	0.06	0.07	0.09	0.02	0.06	0.05	0.08	0.06	0.003	0.003	0.004
LSD		0.06			0.06			NS			0.005	
($P < 0.05$, interaction)												

(b) Root dry weight (g/plant)

The species differed in root dry weight and, especially at harvest 1, this was shown by the significance of the interactions (Table 4.17). The crop produced the greatest root dry matter at all pot sizes except the smallest, where all species were similar. The weeds only differed in the largest pot, values for wild oat being greater than barren brome. In the other pots values for wild oat also were slightly higher than for barren brome. At the third harvest, however, the species produced similar amounts in all pot sizes (Table 4.19). At both harvests root dry weights within species were dramatically reduced by reductions in the size of pots.

(c) Root/shoot ratio

At harvests 1 and 2, the ratio increased in all species as the size of the pots was reduced. Barren brome had the highest ratio in almost all pot sizes and both harvests, the value being about twice that of the other species in the smallest pot at the first harvest (Tables 4.18 and 4.19). Root/shoot ratios were greater at harvests 3 than 1, and at the third harvest ratios within species in general tended to remain similar.

(d) Total root length (m/plant)

At both harvests the species differed in root length in all pot sizes except the smallest (Table 4.18 and 4.19). Barren brome produced the longest roots except in the largest pot at harvest 1 where the crop produced similar lengths. At the first harvest wheat and wild oat produced similar lengths of root except at the largest pot size where that of the crop was greater. At the third harvest the crop had more roots in pots 1 and 2 and the weed in 3. Although barren brome had the longest root system it had the smallest root dry matter, again reflecting the finer roots of the weed. Although results are not presented here, the intensity of roots (i.e. gm dry weight or m/unit volume of soil) also showed that this weed had the greatest values except in the smallest pots, again suggesting the ability of the weed to explore a greater volume of soil, a feature which could be important under field conditions.

(e) Shoot nutrient concentrations (mMol/g DW)

P: Interaction for P concentrations were not significant at either

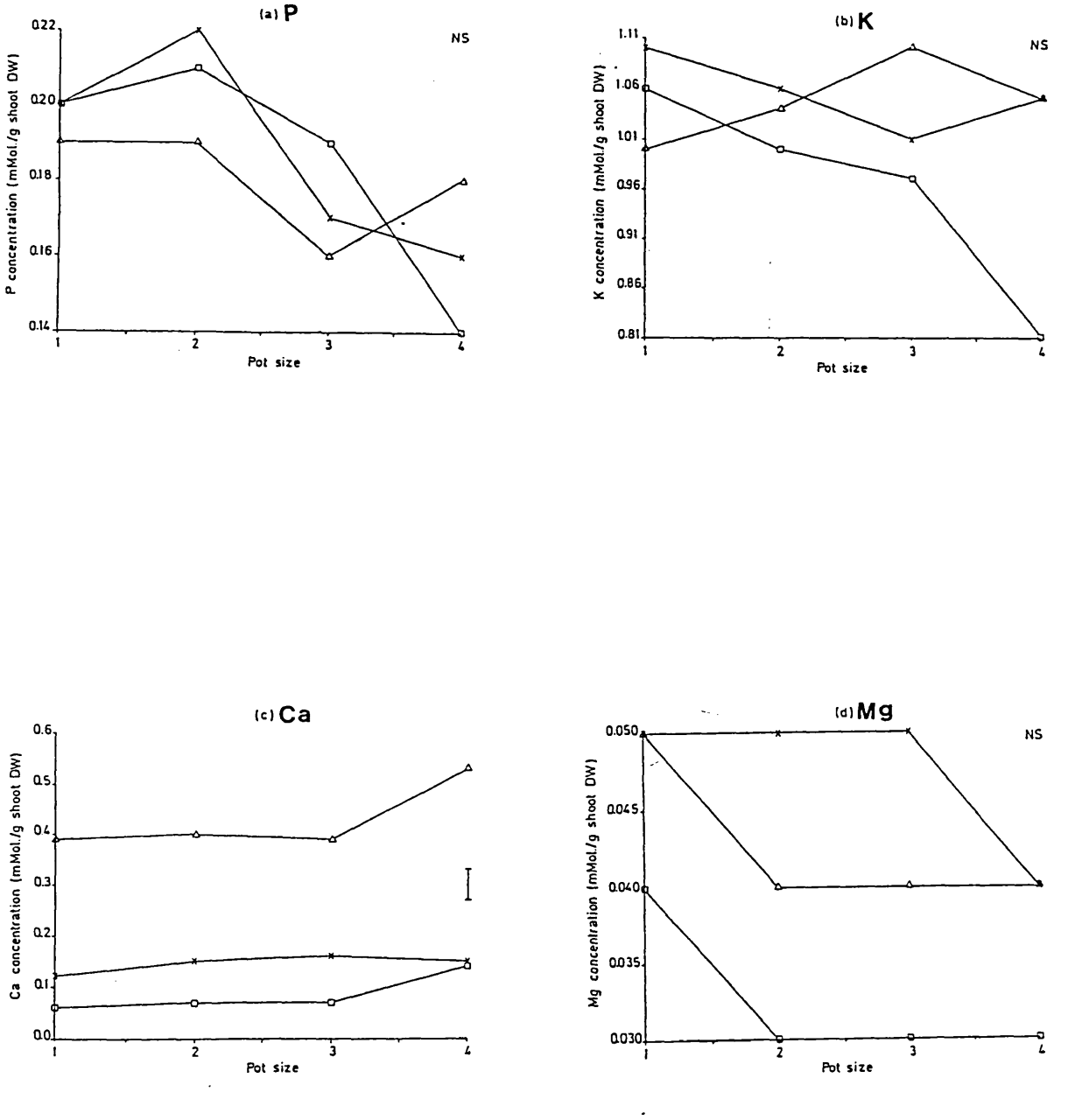


Figure 4.1 (a–d) Effects of root restriction on shoot nutrient concentrations (mMol./g DW) in wheat (□), wild oat (✕) and barren brome (△) at the first harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

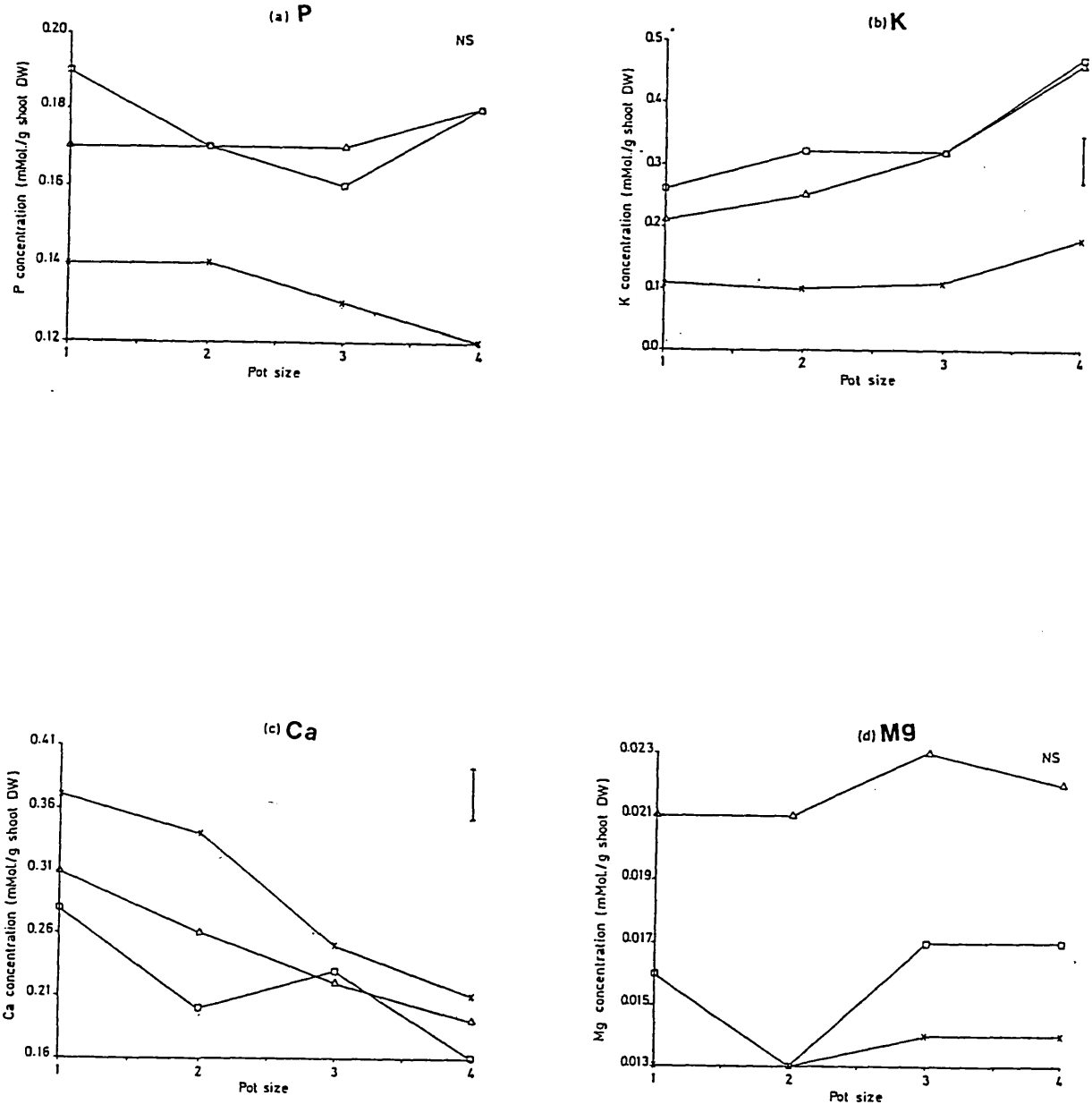


Figure 4.2 (a–d) Effects of root restriction on the root nutrient concentrations (mMol /g DW) in wheat (□), wild oat (×) and barren brome (Δ) at the first harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

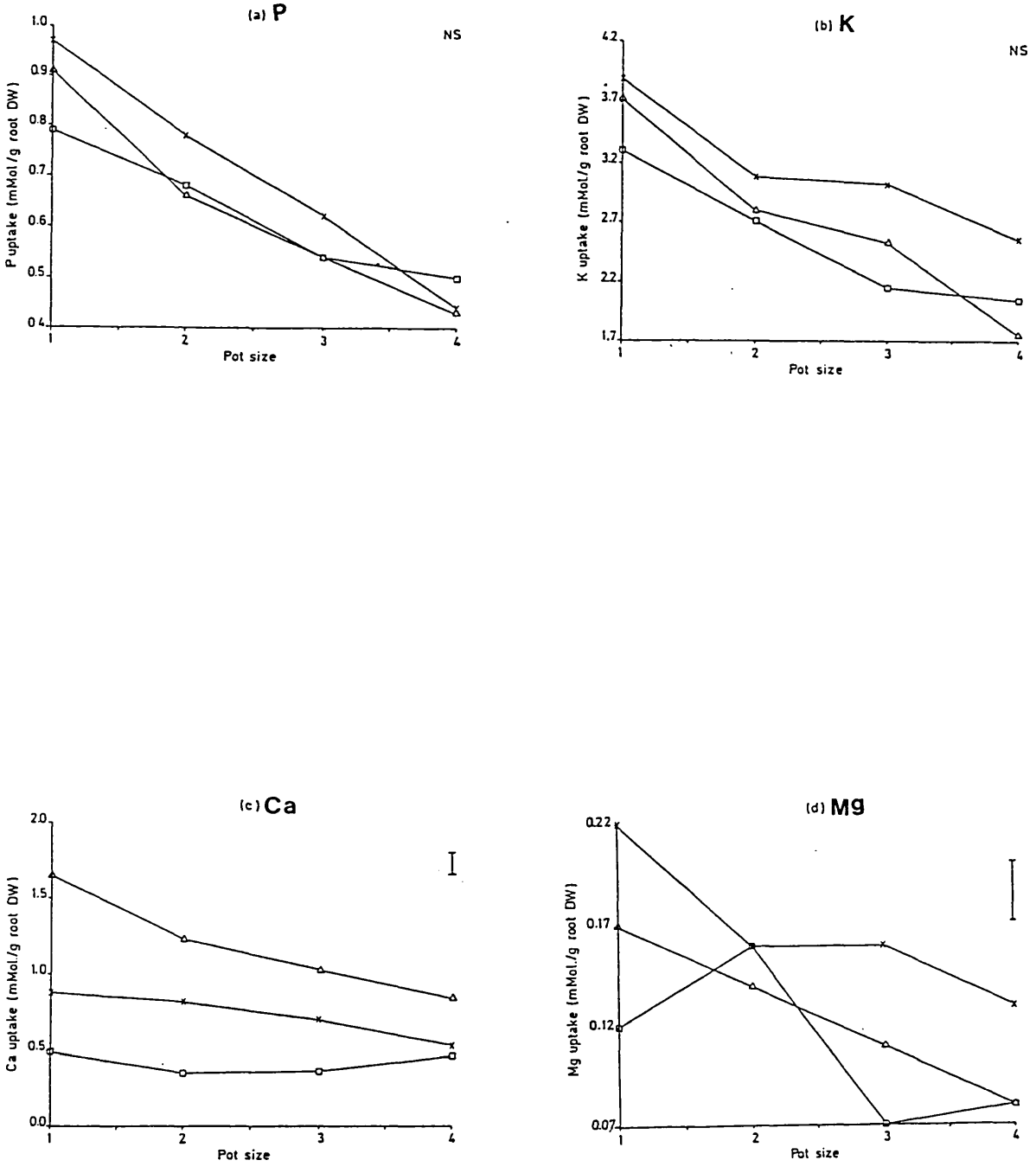


Figure 4.3 (a–d) Effects of root restriction on the nutrient uptake efficiency (mMol /g root DW) in wheat (□), wild oat (X) and barren brome (Δ) at the first harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

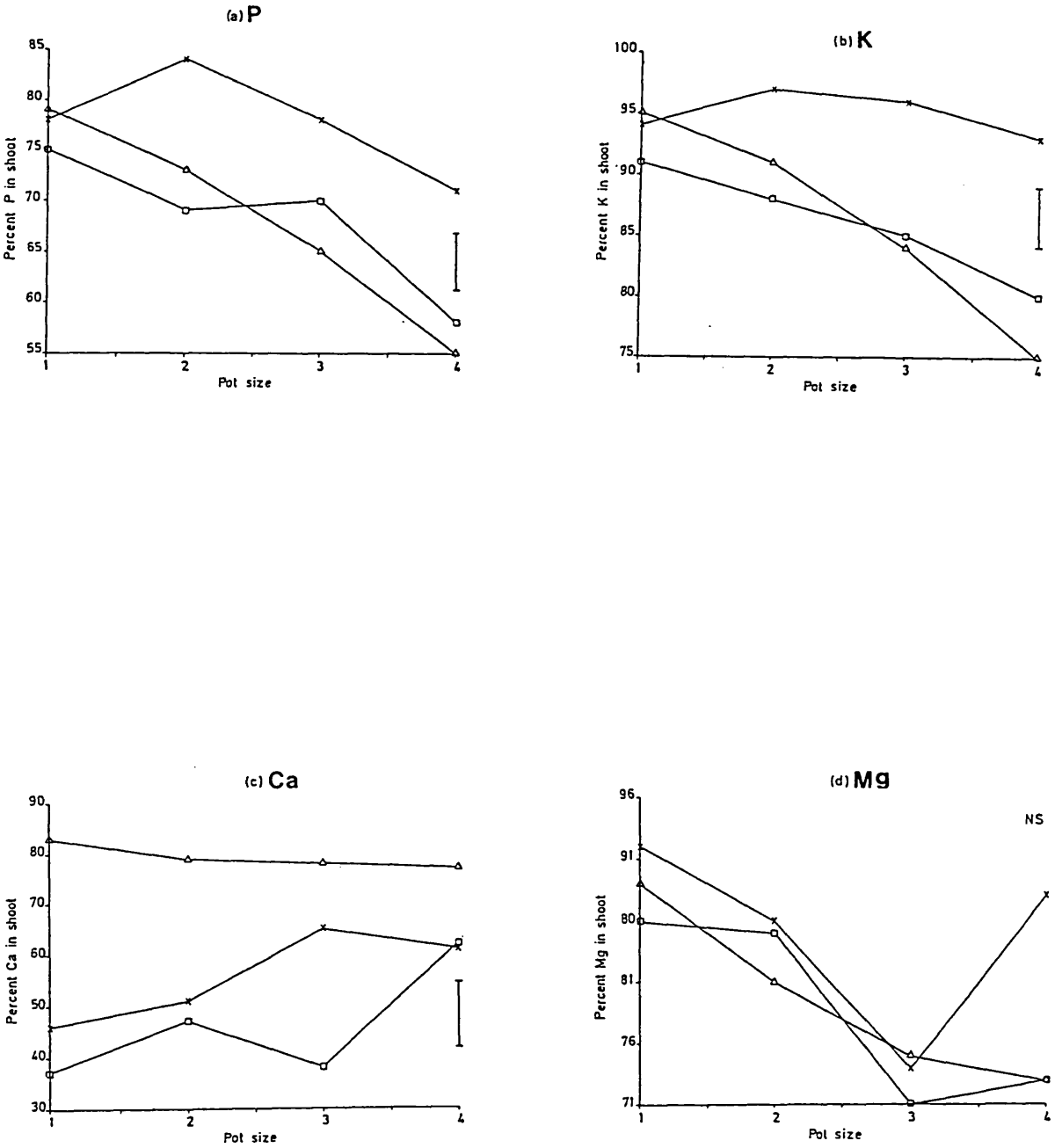


Figure 4.4 (a–d) Effects of root restriction on the distribution of nutrients between shoots and roots of wheat (□), wild oat (X) and barren brome (Δ) at the first harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

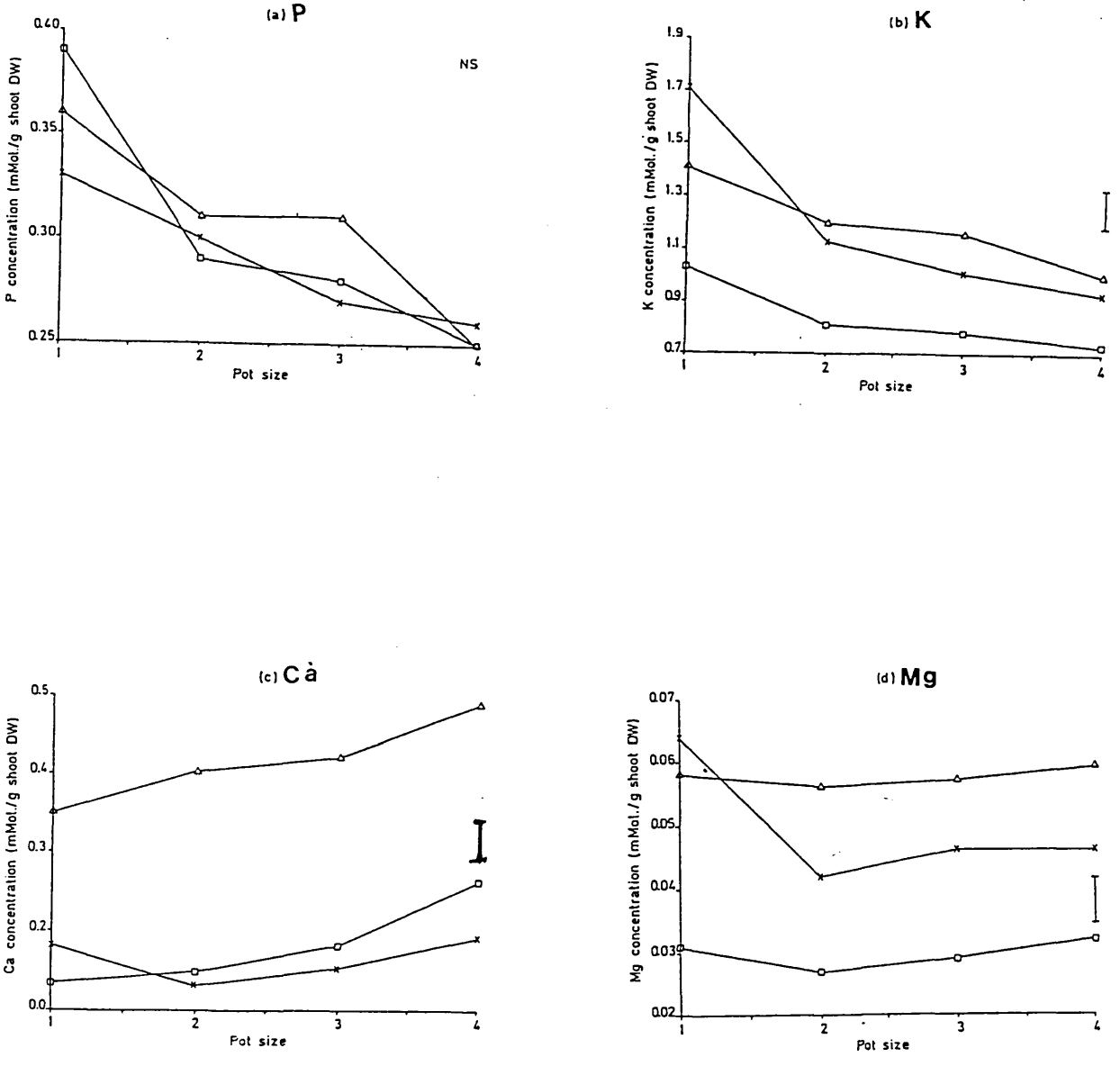


Figure 4.5 (a–d) Effects of root restriction on the shoot concentrations (mMol./g DW) of wheat (□), wild oat (×) and barren brome (Δ) at the third harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

harvest, although concentration generally fell in all species as pot size decreased (Figs. 4.1a and 4.5a). There was significant difference between pot sizes, but not between species at both stages.

K: At the first harvest interaction for K concentrations were not significant. The species differed for mean K concentrations though pot size did not appear to influence K uptake. By the third harvest main effects and their interactions were significant (Fig. 4.1b and 4.5b). All three species had their highest K concentrations in the largest pot and the weeds exceeded the crop in all pots. Wild oat contained more K than barren brome at pot size 1; the reverse being true in the third pot size. Barren brome also had slightly higher K in pot sizes 2 and 3.

Ca: Ca concentration in the weeds, especially in barren brome, was higher than in the crop for all treatments at the first harvest. At the third harvest again barren brome contained the highest concentrations. In the largest pot size wild oat was higher than the crop; the reverse being true at the smallest pot size. In all the species Ca concentration increased with a decrease in pot size (Figs. 4.1c and 4.5c).

Mg: At the third harvest Mg concentrations in the weeds were also higher than the crop and barren brome had the highest concentration in all pots except the largest where it was similar to wild oat (Fig. 4.5d). At the first harvest interactions were not significant, but the means for the main effects of species also showed that the weeds had higher concentrations than the crop.

(f) Total nutrient contents in shoots (mMol/g plant)

P: The total P content in the species differed. Barren brome contained the smallest quantity at both harvests and all pot sizes except for the smallest where species were all similar (Tables 4.20 and 4.21). Wild oat and the crop contained similar amounts of P at both harvests and all pot sizes except pot 2 and the third harvest where the weed was significantly higher. In other soil volumes wild oat was also higher in total P, although not significantly so. In all species total P declined with reduction in pot size.

K: At both harvests species differed in K content (Tables 4.20 and 4.22). At the first harvest wheat and wild oat had similar quantities at all pot sizes and barren brome was similar to both species at pot sizes 3 and 4 only. At the third harvest shoot contents for wild oad were the

Table 4.24. Effects of root restriction and P level on dry matter production of wheat (W), wild oat (WO) and barren brome (BB)

(a) First harvest

	Shoot dry weight (g/plant)						
	L1			L2			
Pot size	W	WO	BB	W	WO	BB	Mean
1	2.65	2.85	3.18	2.50	3.21	3.04	2.91
2	1.80	2.22	1.99	1.63	2.12	1.61	1.90
3	1.39	1.52	1.36	1.19	1.22	1.17	1.31
Mean	1.95	2.20	2.18	1.77	2.18	1.94	

(b) Second harvest

	Shoot dry weight (g/plant)						
	L1			L2			
Pot size	W	WO	BB	W	WO	BB	Mean
1	5.84	7.73	5.01	4.97	6.00	4.77	5.72
2	3.05	4.75	3.22	2.86	3.85	2.39	3.35
3	1.98	2.90	1.33	2.13	2.25	1.06	1.94
Mean	3.62	5.13	3.19	3.32	4.03	2.74	

Table 4.24. contd.

(c) Third harvest

Pot size	Shoot dry weight (g/plant) L1 W	L1 WO	L1 BB	L2 W	L2 WO	L2 BB	Mean
1	8.81	13.33	8.25	8.59	11.59	7.10	9.61
2	7.03	8.43	5.75	5.39	7.79	5.15	6.59
3	5.56	6.58	4.68	4.06	5.81	3.75	5.07
Mean	7.13	9.45	6.23	6.01	8.41	5.33	

	LSD ($P < 0.05$) First harvest	Second harvest	Third harvest
PL	0.15	0.31	0.53
PS	0.18	0.37	0.64
SP	0.18	0.37	0.64
PL.PS	NS	NS	NS
PL.SP	NS	NS	NS
SV.SP	0.31	NS	1.11
PL.PS.SP	NS	NS	NS

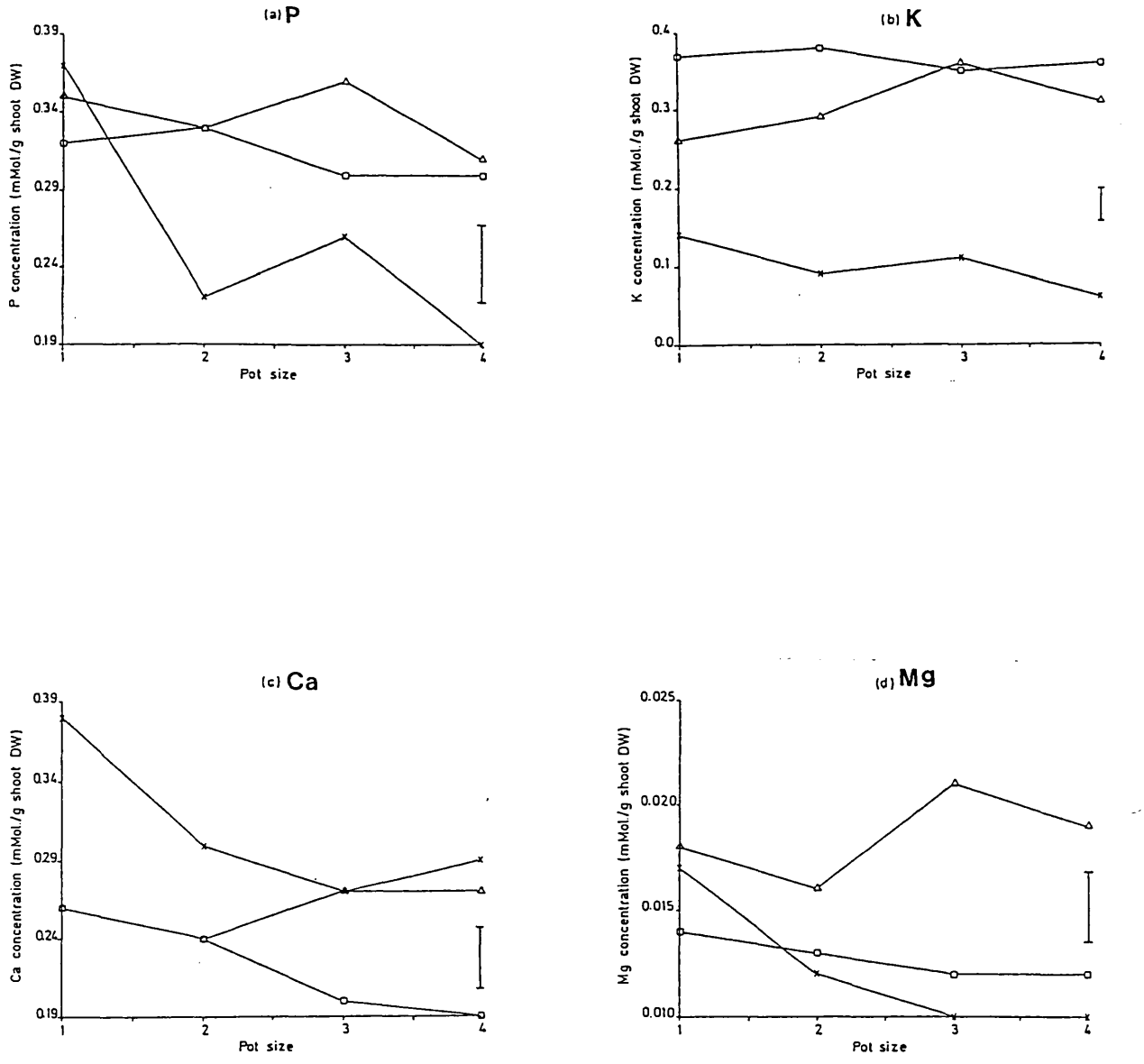


Figure 4.6 (a–d) Effects of root restriction on the root nutrient concentrations in wheat (□), wild oat (×) and barren brome (△) at the third harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

highest, except in the smallest pots where species were all similar. Barren brome also exceeded the crop in pots 1 and 2 at the third harvest.

Ca: Total Ca in the shoots was clearly higher in the weeds. Barren brome had a greater content than the crop in all pots and both harvests (Table 4.20 and 4.22).

Mg: At the first harvest interactions were not significant although the main effects indicated differences between species and soil volumes. At the final harvest, however, interactions were significant and suggested that the weeds contained higher amounts of Mg in their shoots than the crop except in the smallest pots where the species were similar (Table 4.22). In all species the content decreased with pot size.

(g) Nutrient uptake efficiencies (mMol/g root DW)

P and K: In all the three species uptake efficiency decreased with increasing root restriction. Interaction" for these nutrients did not differ significantly, however, the weeds, especially wild oat, showed slightly higher uptake efficiencies (Figs. 4.3a and b). At the third harvest species differed significantly (Fig. 4.7a and b) and in all species efficiency decreased with decreasing soil volume.

Ca and Mg: The weeds showed clearly higher efficiencies than the crop. Wild oat was more efficient in the uptake efficiency of Mg in all pot sizes except 2; Ca uptake was higher for barren brome in all pots (Fig. 4.3c and d, and Fig 4.7c and d). At both harvests efficiency decreased with decreasing soil volume generally.

(h) Nutrient distribution (percentage of nutrient in the shoot)

The weeds, especially wild oat, had higher percentages of nutrients in their shoots than the crop. In general percentage translocated to the shoots decreased as root restriction increased (Figs. 4.4a, b, c and d). The only exception was found in the crop and wild oat where the proportion of Ca translocated to the shoot generally increased with increasing root restriction. At the third harvest species did not differ significantly for any of the nutrient except Ca (Figs. 4.8a, b, c and d). Shoot nutrients decreased with decreasing soil volume; again the exception was for Ca in the crop.

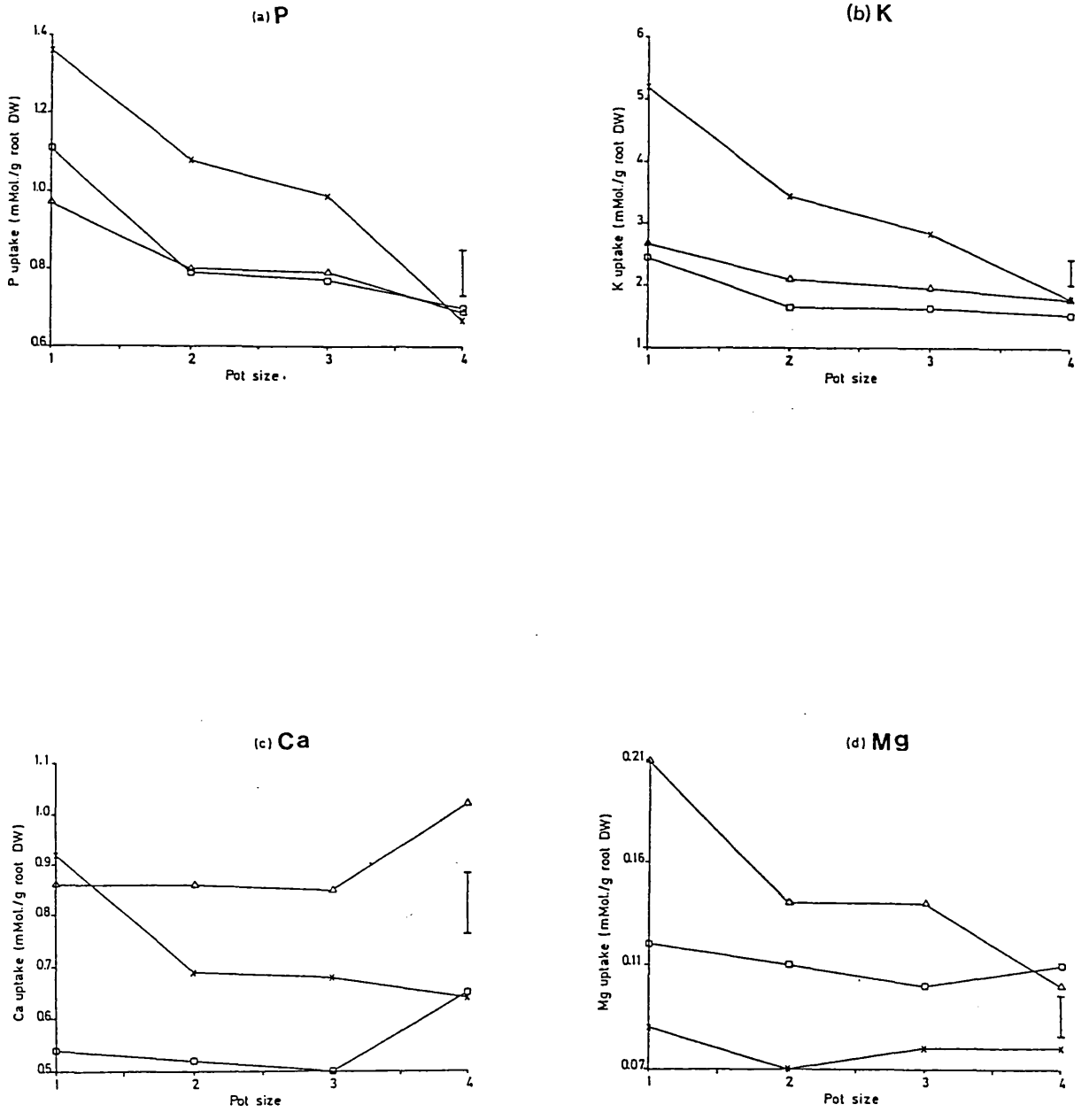


Figure 4.7 (a–d) Effects of root restriction on the nutrient uptake efficiency (mMol /g root DW) in wheat (□), wild oat (✗) and barren brome (△) at the third harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

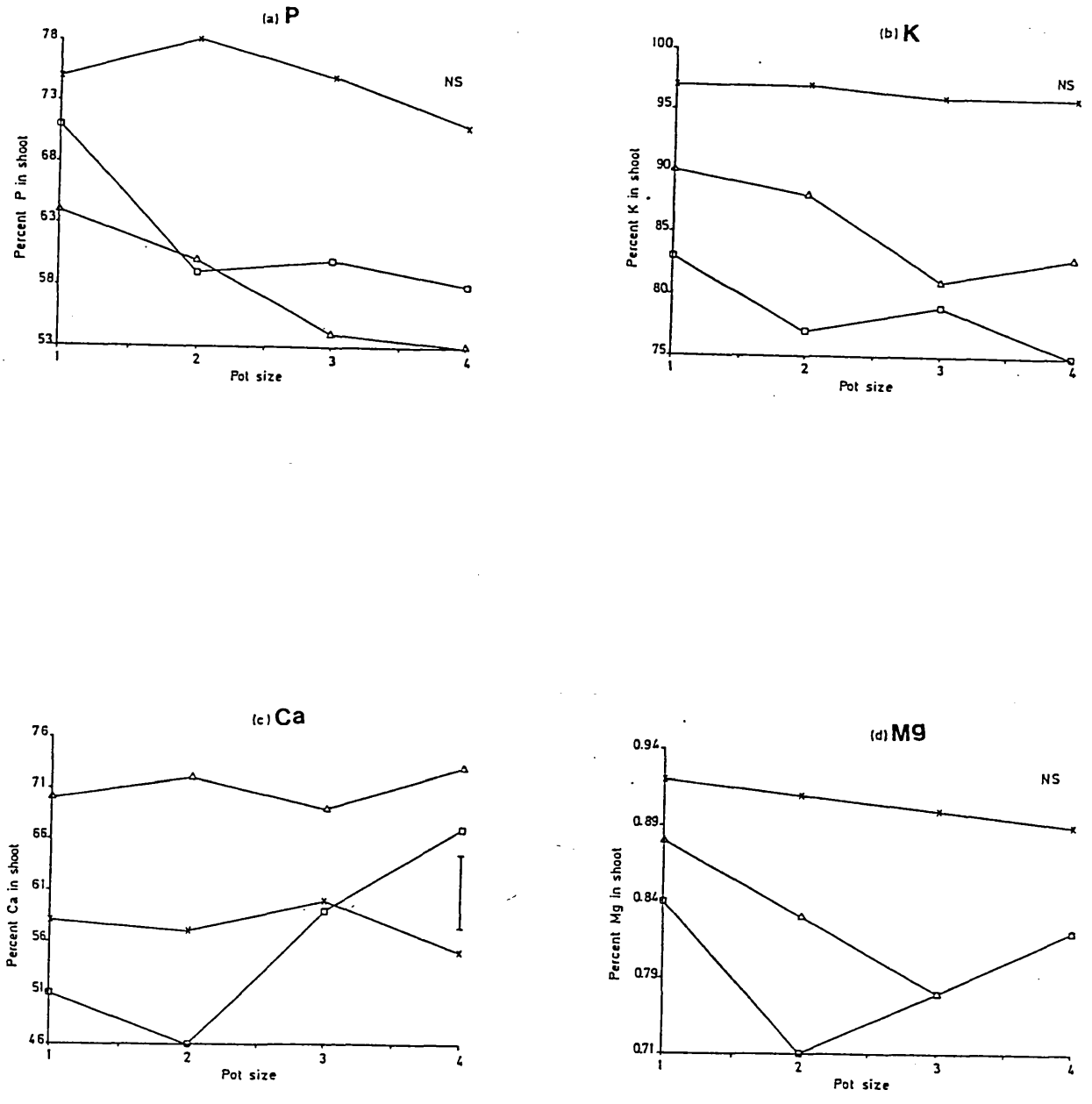


Figure 4.8 (a-d) Effects of root restriciton on the distribution of nutrients between shoots and roots of wheat (□), wild oat (✕) and barren brome (Δ) at the third harvest

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

(a) Root nutrient concentration (mMol/g DW)

P: At the first harvest interactions were not significant and the size of pots did not appear to influence the uptake of the nutrient. At the third harvest these were significant and barren brome was higher than wild oat in all soil volumes except the largest where the latter was higher. Wild oat was similar to the crop except in pot size 3, where it was higher (Figs. 4.2a and 4.6a). Wild oat was the species most affected by soil volume.

K: At the first harvest the crop had higher K concentrations than either weed and in all species concentration in the roots increased with decrease in pot size. At the final harvest the concentration within wheat appeared not to be influenced by pot size. This increased in barren brome with decrease in pot size, whilst in wild oat it decreased (Figs. 4.2b and 4.6b).

Ca: Differences between species were clear at both harvests and for all pot sizes. The weeds, especially wild oat, had higher Ca concentrations than the crop (Figs. 4.4c and 4.8c). Concentration generally decreased with decreasing pot size.

Mg: At the first harvest concentration remained constant in all pots sizes for all species. At the third harvest Mg was greater in barren brome for all pot sizes except the largest, where it was similar to wild oat. The concentration in barren brome also increased generally with decrease in pot size, whilst that of wheat remained constant and wild oat decreased.

(b) Root total nutrient contents (mMol/g DW)

P: At both harvests the root contents differed for all pots sizes except the smallest. At the first harvest wheat and wild oat contained higher amounts than barren brome and the crop was also higher than wild oat. At the third harvest barren brome had the highest amounts in the largest pot, and was also greater than wild oat in the other pot sizes except the smallest. It had similar amounts towheat in post 2, 3 and 4 (Tables 4.21 and 4.23).

K: At both harvests wheat contained the greatest amount and wild the smallest for all pot sizes.

Ca: The species differed in Ca root contents at the first stage of

harvest (Table 4.21). Wheat and wild oat had greater quantities than barren brome except at the smallest where all were similar. At the third pot size the weeds also did not differ in Ca content. At the third harvest, interactions were not significant and the species did not differ for the various soil volumes.

Mg: At both harvests species differed for total Mg. Mg content decreased with decreasing soil volume at both harvests (Tables 4.21 and 4.23). Barren brome had the greatest amounts in pots 1 and 2 at the third harvest. At the first harvest, wild oat had the smallest amounts and wheat and barren brome were similar. At the smallest pot all species were similar.

8.7 Discussion

The results clearly showed that reduction in the volume of soil gave parallel reductions in root and shoot production. The reduction in shoot dry matter at all three harvests indicated that barren brome was the species most affected by reduction in the volume of soil. Wild oat showed less reduction both in shoot and root dry weight production than the other species. At the first harvest root dry weight was most affected in the crop whilst at the third harvest both wheat and barren brome were more affected than wild oat, suggesting the likelihood of the earlier commencement of the effects of root competition in the crop.

In all three species increases in root/shoot ratios were noted as pot size was reduced and values were greater at harvest 3 than 1. In general barren brome had the highest root/shoot ratio, and wild oat the lowest at these harvests. At both harvests the ratios in wheat and especially wild oat tended not to change dramatically perhaps indicating rigid control of top growth by the root systems as opposed to barren brome which produce more roots at the expense of shoots. In both species, especially the crop, the ratio decreased significantly with increasing soil volume, indicating that both species can produce an increased top growth without a corresponding increase in root development if roots are grown in a sufficient volume of soil. The lower root/shoot ratios in wild oat than in other species, particularly barren brome, may show that the possibility of mutual competition between its roots may have begun later than barren brome and hence it was able to produce a greater proportion of shoots than roots. The generally greater reduction

in the growth of barren brome, unlike in wild oat in smaller pots (3 and 4), and its higher root/shoot ratio and longer roots suggest the probability of greater competition in the weed. Qasem (1987) carried out similar experiments with tomato, fat hen, and groundsel to see if physical restriction of the roots had more effect on one species than the other. He reported that groundsel, which had a smaller and less dense root system than the other species was the least affected by root restriction, although all species showed reduced growth in smaller pots. Cornforth (1968) also reported that the decreases in the volume of soil available to plants growing in pots decreased the yields of oats, ryegrass, kale and tomato and decreased the intensity of rooting and root yields. Other investigators making similar observations on different plant species were Armiger et al. (1958) and Stevenson (1967).

Barren brome had the longest and the finest and thus the most dense roots at both stages of growth and in all pots except the smallest. Reduction in the length of roots with pot size was once again smaller in wild oat than the other species.

The results thus point to the fact that plant performance would be greatly limited if the available space in which the roots grow is restricted. The magnitude of responses clearly suggested that the species are different. Wild oat would, for these results, be expected to grow more normally in soils which may be marginal with respect to the availability of growth resources. In such marginal conditions in arable fields where wheat is grown, the weed might be expected to grow more normally than the crop and outcompete the latter for the resources available and might eventually reduce the yield of the crop significantly. This ability of the weed to perform better than either species under root restriction could be related to its ability to produce more dry matter when nutrients are deliberately limited. Experiments in Section 1, where the availability of the major nutrients was reduced indicated that this weed was less sensitive to lower levels of P and K than the other species. The production of finer and denser roots and higher root/shoot ratios in media where nutrient availability is limiting has been shown to be characteristics of barren brome elsewhere in this thesis. These effects also occur with root restriction treatments. The large effect of root restriction appears due partly to root intra-specific competition in the smaller pots. Although all three species produced higher root/shoot ratios in smaller pots (sizes 3 and 4), that

of barren brome was the greatest. This may have significant survival value in the field, where nutrients may be deficient. Under such circumstances the advantage of having a larger root system in proportion to the size of the shoot may lie in the ability to explore a greater effective volume of soil containing immobile elements such as phosphorus.

The main component of competitiveness is the ability of a species to grow more vigorously than others in mixtures. Rapidly expanding leaf canopies and root systems then make greater use of resources essential for growth. In earlier experiments both in competition and pure stands, barren brome showed higher concentrations for some of the major nutrients (e.g. P, Ca and Mg), but it was the least efficient species in utilizing these nutrients. Other experiments in which both population density and nutrient concentrations were varied also showed that although the weed produced a higher root/shoot ratio, it was the subordinate species in competition. The finer and denser root system of the weed may also increase the ability to extract moisture from low levels in the soil. Experiments on water stress effects were not carried out, but it might be rewarding to do so. Froud-Williams et al. (1980) attributed the success of barren brome as a weed to dry autumns such as that of 1976 and to the establishment of winter cereals by minimum cultivation, a practice which was becoming popular at that time.

The shoot and root nutrient concentrations and contents of the species were affected differently by root restriction treatments and both were generally higher for the weeds. Bray (1954) stated that the quantity of nutrients taken up depends on their accessibility to roots, which related to their mobility in the soil. He noted that mobile nutrients are taken from the total volume of soil containing roots whereas immobile nutrients are absorbed only from a thin layer around the roots; supply of an immobile nutrient thus depends on the surface area of the root system. Wiersum (1962) supported the view that the proportion of the total supply of nutrients used depends on both the mobility of nutrient ions on the intensity of roots in the soil.

In the present experiments, nutrient uptake and the growth of the species were both affected by available soil volume. Decrease in the volume of soil increased the intensity of roots and at greater restrictions intra-specific competition reduced the dry matter yields, especially that of barren brome. The concentration of nutrients in

shoots and root in general also followed plant growth responses, except at the early harvest, where the crop and barren brome showed significant increase in K and a slight increase in P and Ca root concentrations. Shoot concentrations remained similar except for Ca, which significantly increased in wheat and barren brome in the smallest pot. Total nutrient contents were also reduced. It is probable that the growth of the plants was reduced as a result of root competition due to greater root intensity in smaller pots. Reduction in the space available for root growth would certainly increase the likelihood of competition between the roots of the same species, especially in barren brome where root intensity was the highest, leading eventually to lower nutrient contents. Higher contents of P, Ca and Mg in the weeds and K in the crop generally observed in these experiments are in agreement with previous finding in competition and NFT and may show species specific requirements. Armiger et al. (1958) reported slightly higher percentages of P in alfalfa plants that were grown in smaller pots under greenhouse conditions. Cornforth (1968) found increases in the uptake of N and P in ryegrass when soil volume was increased, but not to the same extent. In smaller pots the increase in the concentration of P was higher than N, and he concluded that P uptake was correlated with root intensity but that of N was independent of the total volume of soil and intensity of roots. In the present experiments the significant increase in K in roots and Ca concentration in shoots in the crop and barren brome plants appeared to be due partially to intensity of roots. This agrees with the results of Larsen and Sutton (1963), and Baker and Woodruff (1962) who found that plants absorb more P per unit volume of soil when grown in small than large volumes of soil.

In the studies of Qasem referred to above, higher shoot concentrations of N, P, K and Mg in the weeds were noted whilst the crop showed higher Ca, although these differences commonly varied with degree of root restriction. Groundsel gave higher concentrations of P and Mg and the roots of this species being the least affected by severe root restriction. He also reported a general trend of decrease in the nutrient contents of shoots and roots as root restriction was increased. The decline in the contents of the nutrient elements as root restriction increased also reflects the lower total amount of nutrient available in smaller pots.

The nutrient uptake efficiencies (mMol/g DW of roots) in the three species also differed for different pot sizes. At the first harvest

uptake efficiencies for P and K did not differ significantly. The weeds were more efficient in taking up Ca and Mg at the first harvest, but by the third harvest they were more efficient in taking up all the elements. In all species uptake efficiency decreased with more severe restriction of the roots. The significant increase in K with root restriction in all species and the slight increase in P and Mg observed at the first harvest in smaller pots does not appear to be due to uptake efficiency of the roots, because this in general decreased as root restriction was increased. The effect may be due to temporary storage before translocation to the shoots. In larger volumes of soil mobile elements like K, Ca and Mg may be extracted from the whole volume of soil. Competition in larger soil volumes would also be expected to be less because of the greater quantity of nutrients present. Baker and Woodruff (1962) noted that plants absorbed more P in small than in large volumes, but Cornforth (1968) reported increases in P concentrations in large volumes when this element was added. The reverse was true with N and he concluded that it is more important to apply a mobile nutrient than an immobile nutrient when soil volume is restricted. Later in this section (experiment 4.3), the additions of P appeared to compensate for a small volume of soil as similar plant concentrations were found in both large and small pots used.

The partitioning of nutrients between shoots and roots indicated that all three species translocated more nutrients to shoots and this proportion was significantly higher at greater volumes of soil. Within species, wild oat generally had higher percentages of all the nutrients in its shoots, except for Ca which was greater in barren brome. In all species the proportion of nutrients in the shoots increased with decrease in root restriction, except for K in wild oat and Mg in all the species which were unaffected by root restriction. The weeds which showed higher concentrations for some elements, also showed higher proportions of these in shoots e.g. Ca in barren brome. It may be that the weed's efficiency in taking up and translocating the nutrient(s) is greater in the case of those for which they have higher requirements. The greater accumulation of P, K, and Mg in wild oat and Ca in barren brome in their shoots in larger pots, especially at the third harvest may also indicate a higher requirement in the weeds and/or more efficient root systems. The crop accumulated similar P to wild oat in the largest pots. It was similar to the weeds for all elements in the smallest pot except for K which was

higher in wild oat. Higher P accumulation in the crop than in barren brome in large volumes of soil is also in agreement with earlier observation in water culture, and may reflect its higher requirement for the element. In some situations it is of course not possible to rule out 'luxury consumption'.

Decreasing pot size led to a trend of decrease in shoot proportions of some nutrients, e.g. P and Mg in all three species; K in wheat and barren brome and Ca in the latter. This may again suggest increasing intraspecific root competition. The higher percentages of K and Ca in the shoots of wild oat and barren brome at both harvests and all soil volumes may give some indication of an attribute relating to their respective ecological habitat in which efficiency in translocating nutrients to the shoots may have developed. Such efficiency is likely to lead to better growth of above ground parts and to effective competition for light. The ability of these weeds to maintain higher shoot K and Ca percentages in all soil volumes, and their higher efficiencies of uptake per unit weight of root emphasise the existence of differential responses from the crop, as reported elsewhere for various experiments.

Although the weeds were more efficient than the crop in taking up Mg/unit of root dry weight they did not differ in the proportions translocated to shoots. The higher efficiency of the weeds in absorbing this nutrient is also in agreement with earlier observations in the responses of the species to levels of the element in water culture experiments (Section 1).

Experiment 4.3 The responses of wheat (W), A. fatua and barren brome to root restriction and P level

8.8 Results

Shoot dry weight (g/plant)

At all harvests the effects of the main treatments were significant. The expected reduction of yield with pot size was clear. Interactions between species and pot size were significant at only the first and third harvests (Table 4.24). The non-significant interaction between P level and soil volume at all harvests showed that the extra P applied had probably reduced the effect of the smaller volume of soil; although in general per plant dry matter yield decreased as the volume of soil was

Table 4.25. Effects of root restriction and P level on the total nutrient contents of wheat (W), wild oat (WO) and barren brome (BB)

(a) Total P (mMol/plant)

Soil volume	L1 W	L1 WO	L1 BB	L2 W	L2 WO	L2 BB	Mean
1	0.29	0.35	0.32	0.24	0.36	0.29	0.31
2	0.20	0.21	0.17	0.16	0.18	0.15	0.18
3	0.14	0.16	0.13	0.11	0.11	0.08	0.12
Mean	0.21	0.24	0.21	0.17	0.22	0.17	

(b) Total K (mMol/plant)

Soil volume	L1 W	L1 WO	L1 BB	L2 W	L2 WO	L2 BB	Mean
1	1.84	2.04	1.89	1.84	2.66	1.95	2.04
2	1.30	1.37	1.29	1.37	1.36	1.33	1.34
3	1.13	1.09	0.76	0.96	1.19	0.84	1.00
Mean	1.42	1.50	1.31	1.39	1.74	1.37	

(c) Total Ca (mMol/plant)

Soil volume	L1 W	L1 WO	L1 BB	L2 W	L2 WO	L2 BB	Mean
1	0.63	10.56	1.03	0.55	10.71	1.01	0.75
2	0.41	0.38	0.60	0.33	0.38	0.55	0.41
3	0.28	0.31	0.45	0.27	0.24	0.35	0.32
Mean	0.44	0.42	0.69	0.38	0.44	0.64	

Table 4.25. contd.

(d) Total Mg (mMol/plant)

Soil volume	L1 W	L1 WO	L1 BB	L2 W	L2 WO	L2 BB	Mean
1	0.19	10.28	0.29	0.20	10.27	0.30	0.26
2	0.13	0.21	0.17	0.10	0.17	0.15	0.16
3	0.10	0.13	0.13	0.07	0.10	0.10	0.11
Mean	0.14	0.21	0.20	0.12	0.18	0.18	

LSD ($P < 0.05$)

	P	K		Ca*	Mg
PL	0.016	0.090	P	0.030	0.01
PS	0.020	0.11		0.03	0.02
SP	0.020	0.11		0.03	0.02
PL.PS	NS	NS		0.05	0.02
PL.SP	NS	NS		0.05	NS
PS.SP	0.034	0.20		0.06	0.03
PL.PS.SP	NS	NS		0.08	NS

reduced in all species and irrespective of P level. Reductions varied between and within species and P levels, though not significantly at any one harvest. At the first harvest, the yield of barren brome appeared to be more reduced at higher P but under greater restriction and at the lower P level both weeds were more reduced than the crop. At the 2nd harvest the weeds were again more reduced than the crop. At the third harvest, the yield of the weeds was more reduced than the crop at high P level, but at the lower P that of wheat and wild oat appeared to be more reduced than barren brome. At this stage percentage decrease in dry matter yields of wheat, wild oat and barren brome at phosphorus level 1 and 2 were 37, 51, 43 and 53, 50 and 47% respectively. Generally, dry matter yield reductions with greater root restriction were higher at the deficient P at all harvests. The reduction in the yield of barren brome appeared to increase with time, i.e. the mean yield reductions at the three harvests were 40%, 25% and 50% for harvests 1, 2 and 3 respectively.

Nutrient concentration (mMol/g DW)

P: Interactions between species and the other main treatments failed to reach significance. At the higher P, the concentration of P in the three species decreased slightly or remained similar when soil volume was reduced, but at the deficient level concentration generally tended to decrease in all species (Fig. 4.9a). This suggested that intra-specific competition amongst roots increased with reduction in soil volume and P level.

K: All interactions approached statistical significance. In wheat and wild oat concentration appeared to increase with decrease in soil volume and increased in all species at the deficient P level. The crop and wild oat had higher K concentration than barren brome (Fig. 4.9b). The increase in K concentration in all the three species as soil volume decreased reflected decreased plant size but may also imply that the nutrient may be removed more fully from small volumes of soil than from large.

Ca: Main treatments and the interaction between these were significant (Fig. 4.9c) and barren brome had the highest mean concentration in all pot sizes and both P levels. Ca concentration decreased slightly with decrease in volume; except in barren brome which increased in the smallest pot at the higher P.

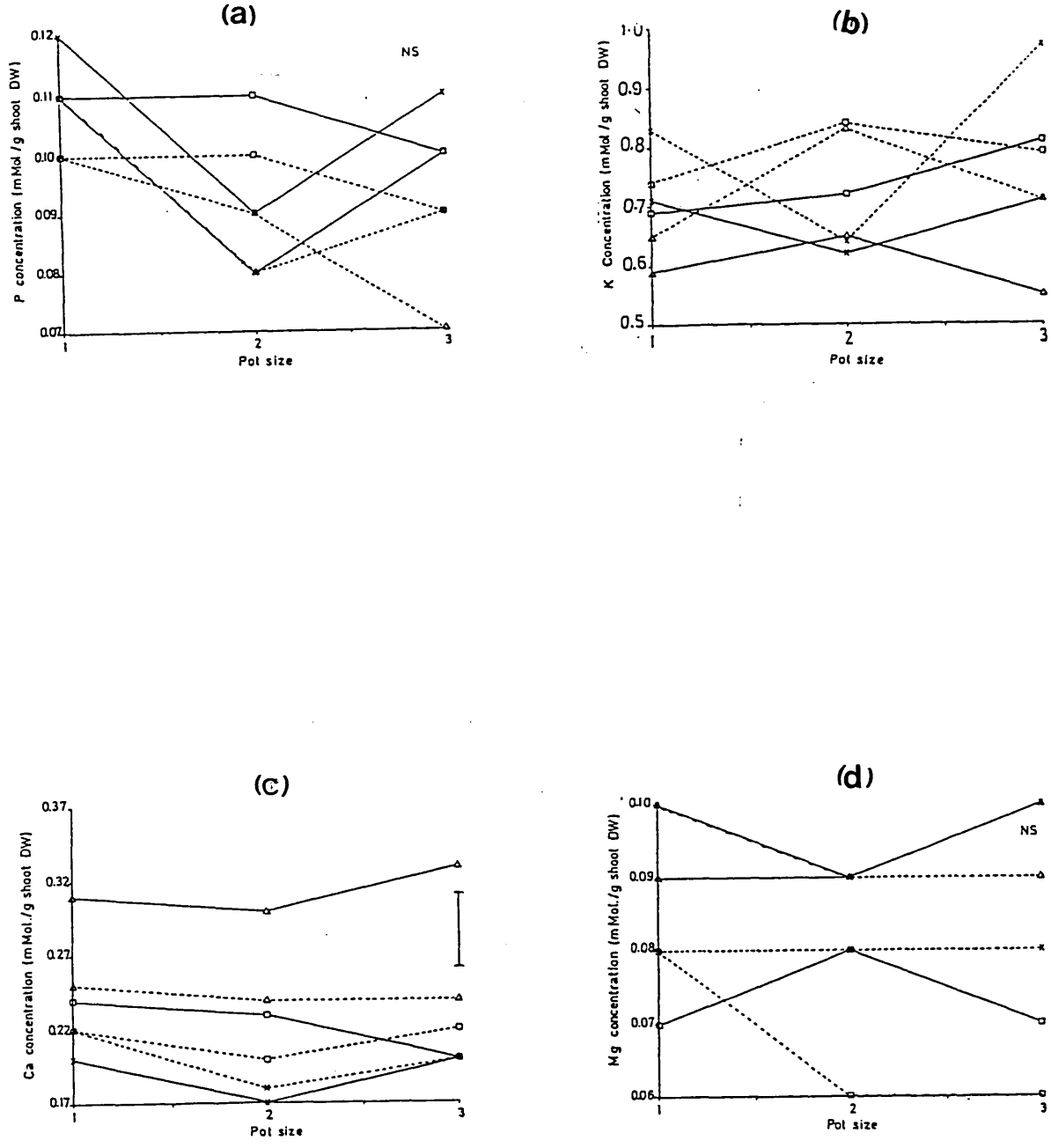


Figure 4.9 (a–d) Effects of root restriction and phosphorus level on the nutrient concentrations (mMol /g DW) in wheat (□), wild oat (X) and barren brome (△)

Vertical bars represent LSD at the 5% level of probability

NS = no significant differences

□ Wheat
X W.Oat
△ B.brome
—— L1
----- L2

Mg: Only the main effects were significant. The weeds appeared to show higher concentrations than the crop (Fig. 4.9d). Mg concentration in all three species was unaffected by soil volume and P level.

Total nutrient contents

P: Most interactions just failed to reach statistical significance; however, total contents in all species showed reductions with soil volume as shown by the significant interaction between soil volume and species (Table 4.25a). Wild oat contained higher amounts, whilst wheat and barren brome were similar.

K: The results were similar to those for P content; and wild oat also had higher amounts at both P levels. Wheat and barren brome had similar amounts at the deficient level, but at the higher level, the crop accumulated more K than barren brome (Table 4.25b).

Ca: The results were similar to those for Ca concentration i.e. all main effects and their interactions were significant (Table 4.25c). The amount of Ca accumulated decreased as soil volume was reduced. At all volumes and P levels barren brome had higher total Ca, whilst wheat and wild oat were similar at higher P, the latter having more Ca at the deficient level.

Mg: although the three-way interaction between P levels, soil volume and species were not significant those between P level and soil volume and species and soil volume were (Table 4.25d). Mg contents in all species decreased as the volume of soil was reduced. In all species contents were higher at higher P level than at the lower concentrations.

8.9. Discussion

In general the responses of the three species to root restriction were similar to those reported for the previous experiment (Experiment 2). Reductions in shoot dry matter yield as a result of root restriction were greater in the weeds, especially barren brome in the earlier harvests. Interactions between phosphorus levesl and soil volumes failed to reach statistical significance at any harvest (Table 4.24). This suggested that the addition of a higher level of P to smaller pots could have narrowed the differences between and within the yields of the species. The similarities within and between species at all harvests, as

shown by the non-significant interactions for phosphorus level, soil volume and species, indicated that although yield was reduced generally by reduction in both P level and soil volume, effects were not significant for any one species. One or more hypotheses may be put forward to explain these results:

(a) That the effects of root competition resulting from severe root restriction may be partially or fully reduced by adding a higher level of phosphorus to smaller pots.

(b) That an immobile element like phosphorus may be easily extracted from smaller than larger volumes of soil at low levels and hence decrease the effects of root restriction. The plants only take up a part of any nutrient in the soil. It has been found that the nutrient absorption depends on the accessibility of the nutrient to the roots and its mobility in the soil (e.g. Bray, 1954; Wiersum, 1962). Cornforth (1968) studied how the volume of soil available to roots influences yields, responses to added P and N and their uptake by tomato, oats and kale. He reported that increasing soil volume increased the yields of tops and roots and decreased both the uptake of nutrients per litre of soil and the concentration of roots in the soil. He also found that P increased yields of the three species more when added to a large than to small volumes of soil, and N increased yields of oats and tomatoes more when applied to small volumes. In the present experiments, although the application of more P to large and small volumes of soil increased yield in all the species the increase was not statistically significant compared with yields from smaller and larger pot sizes to which ten times less P was added. Irrespective of the P level added the yields of the three species declined with the volume of soil used, the weeds, especially barren brome, being more reduced than wheat at harvests 1 and 2. At the third harvest, the yield of wil oat appeared more reduced than barren brome. This may be because root growth in this weed is initially slower and becomes vigorous at latter stages of growth (Pavlychenko, 1937, 1940). Hence root competition in the weed may have begun later than in either of the other species. The ability of the crop to produce more dry matter than the weeds at smaller soil volumes implies less competition between its roots as a result of a lower root/shoot ratio. In the previous experiment wheat showed a lower root/shoot ratio than the weeds, especially barren brome under several levels of root restriction.

The results for shoot nutrient concentration showed that the main effects were significant, whilst interactions were not, for the nutrients determined. The only exception was Ca (Fig. 4.9a-d). The results for shoot contents were similar to those for shoot concentration (Table 4.25a-d).

In general species tissue nutrient concentrations were independent of total soil volume used except for K which increased with increasing restriction and decrease in P level. Wheat had higher concentration of P and K than barren brome. The crop had higher concentration of K than wild oat at higher P and a similar concentration at the lower level. The weeds, especially barren brome had higher concentrations of Ca and Mg. These results were similar to those reported for various experiments elsewhere in the thesis.

Total nutrient contents generally decreased with increasing root restriction. The weeds usually had a higher content than the crop especially for Ca which was significantly higher in barren brome.

The total amount of nutrients in the plant expressed on the basis of a unit volume of soil in which it was growing increased with with greater root restriction. This implies that proportionately more nutrients are taken up from smaller volumes of soil than from large. These results agree with those of Larsen and Sutton (1963) and Baker and Woodruff (1962).

Cornforth (1968) also found that plants absorb more P per unit volume of soil when grown in small than in large volumes, but the uptake of N decreased with increasing volume. He correlated the higher uptake of P with root intensity in smaller soil volumes, although responses of oat and tomatoes in terms of increased yields was higher when P was added to a larger volume of soil. The opposite was true with N and the responses to P were greater with than without added N. In the present study although the addition of P to large volumes increased dry matter yields, this was not significant. The addition of P also had similar effects on its contents and concentrations as on its dry matter production. Contents and concentrations of the other nutrients also appeared to be independent of P levels, though these tended to depend on the volume of soil used. The addition of P at levels differing ten-fold to both small and large volumes did not appear to have any influence on either dry matter or nutrient yields. This suggests that in smaller

volumes P may be easily available to plant roots and the lowest quantity applied may have not been small enough to cause reduction in the yields of the species.

Root restriction obviously affected the growth of all three species but differently; the most reduced species being barren brome, especially at early stages of growth (harvests 1 and 2). This may be due partially to greater root competition. By the third harvest the effect of root restriction on the weed was reduced and it hence produced more shoot. The greater production of shoots at later stages may be a change in the competitive strategy of the weed in response to this treatment. As reported elsewhere the weed's competitiveness was enhanced by its production of dense roots. Under root restriction conditions competitiveness is unlikely to be affected by this factor directly but the additional root growth may have enhanced shoot growth and enabled the plant to compete better for above ground resources. Wild oat also increased its shoot production at the third harvest. At all stages the crop produced either greater than or similar amounts of shoots to the weeds and this may imply tolerance to greater restriction of roots, especially at the higher available phosphorus, than both weed species.

Experiment 4.4 Root growth, development and depth distribution of species at different stages of growth

8.10 Results

Root dry weight distribution

The data for each species were analysed separately. Combined analyses were also done, but LSD for the separate analyses were used to compare root production within species. In all species the density of roots decreased with depth (Table 4.26). At the first harvest wheat and barren brome had similar distribtuion of roots although the total root dry weight was lightly greater for the weed. Approximately 50% of the total roots produced in these species were localized in the top 0-20 cm of the soil. The comparable figure for wild oat was 46%. At this stage the weeds tended to increase density of their roots at the deepest layer.

At the second harvest wheat and wild oat had 47% of their roots in the top 0-20 cm, the figure for barren brome being about 55%. Root

Table 4.25 Mean root dry weights (g) and percentage distribution in the soil profile (in parentheses) of wheat (W), wild oat (WO) and barren brome (BB) at the first harvest

Depth (cm)	W	WO	BB
0-10	0.34 (32)	0.28 (25)	0.39 (32)
10-20	0.21 (19)	0.23 (21)	0.23 (19)
20-30	0.19 (18)	0.17 (16)	0.21 (17)
30-40	0.18 (17)	0.20 (18)	0.18 (15)
40-50	0.16 (15)	0.22 (20)	0.21 (17)
LSD (P<0.05)	0.035	0.05	0.083

Table 4.27. Mean root dry weight (g) and percentage distribution in the soil profile (in parentheses) of wheat (W), wild oat (WO) and barren brome (BB) at the 2nd harvest

Depth (cm)	W	WO	BB
0-10	0.85 (28)	1.12 (25)	1.28 (33)
10-20	0.59 (19)	0.97 (22)	0.84 (22)
20-30	0.50 (16)	0.58 (13)	0.61 (16)
30-40	0.48 (16)	0.86 (20)	0.48 (13)
40-50	0.63 (21)	0.84 (19)	0.61 (16)
LSD (P<0.05)	0.15	0.22	0.25

(a) Wild oat

(b) Wheat

(c) Barren brome



Plate 4.1a-c Root systems of the three species grown for 3 months in deep metal boxes filled with compost mixtures. Clear differences in root density and penetration are visible

production in the crop was significantly less between 20 and 40 cm than in deepest layer. The same was true of wild oat where the amount produced in the deepest soil layers was much greater than in the other species. In barren brome, root dry weight production was also reduced with depth, but the reduction was significant only between 30-40 cm. In all soil layers, except the top 0-10 cm, where barren brome produced the greatest amount of root dry weight, wild oat had greater quantities (Table 4.27). The crop produced smaller than or similar amounts of root to barren brome. All species had their lowest weights between 20-30 cm.

Root length distribution

In terms of the total root length barren brome had the longest and thus the densest roots in the top-most layers of the soil profile (Table 4.28). Wheat also produced the greatest proportion of its root length between 0-20 cm, whilst for wild oat this proportion occurred in the depth between 40-50 cm. In terms of percentage distributions wheat and barren brome had 33 and 31% respectively in the top 0-10 cm of the soil; wild oat having 17% only at this depth. At 40-50 cm this weed had 30% of its total root length, suggesting that it exploits deeper layers of the soil more than the other species. In wheat the length of root in the soil layers 20-30, 30-40 and 40-50 did not differ significantly. In wild oat there was less root length between 30-40 cm, but this increased significantly in the deepest layer. Similar trends were found in barren brome, but the total length in the lowest layer was much smaller than at the surface. For all species the lengths of root produced between 30-40 cm were the smallest. Percentage distributions of wheat and barren brome were also similar in the deepest layer.

When the three species were grown in deep metal boxes (Exp 4.4b) for up to four months differences in the depth of rooting and distribution of their roots were observed (Plate 4.1). Wild oat gave the appearance of having denser roots in both shallow and deeper layers of the soil than either of the other species. Roots and shoots of the weed species were recovered and measurements of length (m/plant) and dry weights showed clear differences between them. These differences agreed with earlier observations in this section and section 1. Measurements of root length again showed longer, finer and thus denser roots for barren brome than wild oat. The latter produced heavier roots and shoots than barren brome. The total length of root in barren brome amounted to about 41,000

Table 4.28. Mean total root length (m) and percentage distribution in the soil profile (in parentheses) of wheat (W), wild oat (WO) and barren brome (BB) at the 2nd harvest

Depth (cm)	W	WO	BB
0-10	459 (33)	390 (17)	562 (31)
10-20	313 (23)	375 (17)	438 (24)
20-30	219 (16)	461 (21)	327 (18)
30-40	180 (13)	342 (15)	191 (11)
40-50	216 (16)	682 (30)	296 (16)
LSD (P<0.05)	79.6	101.9	74.5

m/plant and that of wild oat to about 29,500 m/plant. The shoot dry weights for barren brome and wild oat were 40.35 and 50.44 g/plant respectively and root dry weights 5.65 and 8.8 g/plant respectively. These variates were not recorded for the crop but visual observations suggested that the roots were not as dense as either weed, implying less surface area of roots/unit volume of soil.

8.11. Discussion

Differences in the distribution of roots of the three species at various depths were noted at the two stages of growth. At both stages the distribution in wheat and barren brome was similar for root dry weights and total lengths. In both species more than 50% of the root system was found in the top 0-20 cm of the soil profile. Although the two species showed similarities in percentage distributions at various depths, they differed in the amount and total length of roots produced at different depths and stages of growth. Barren brome had greater root dry weights and longer and thus denser roots especially between 0-30 cm. The distribution in wild oat was different and these differences were more obvious at the later stages of growth, where the weed produced more roots in the deeper layers (30-50) than the other species. This agrees with the report of Ellern et al. (1976). They studied the root distributions in Avena fatua and Avena strigosa both in pure and mixture stands using radioactive $^{14}CO_2$ which was supplied to the shoot system of A. fatua. They found that the root systems differed markedly in their distributions with depths in the soil, and at two stages of growth they reported higher percentage of total root weight for wild oat at lower depths (20-40 cm) than at 0-20 cm. Such striking differences between plant species in the relative distribution of their roots at different depths may have significant importance in their ecological relationships. Fitter (1976) stated that the competitive efficiency of species under low fertility levels depends on their ability to absorb nutrients and distribute their root systems more effectively in the soil. The ability of species to spread their roots vertically and/or horizontally in the soil in response to limiting conditions of growth resources (nutrients and moisture) vary from species to species. Under such conditions those species which are able to produce more spreadidng roots, capable of exploring greater volumes of soil, may have the advantage of absorbing limiting growth resources of the soil to a greater extent than those possessing shallow

and less spreading roots. In the associations between crops and weeds, numerous investigators have attributed the greater competitive abilities of the latter to the extensiveness of their root systems (e.g. Chambers and Holm, 1965; Adapetu and Akapa, 1977; Qasem, 1987). The existence of stable equilibria in homogeneous environments in natural conditions has also been attributed to differences inn the rooting abilities of species in deeper soil layers, because the species partially avoid competition by exploring different layers of the soil. Although the nutrient content of the soil in deeper layers is low, deep rooting populations can draw on the supply of nutrients present in such layers. Such differences in component species in competition in open field experimetns as opposed to pot experiments have resulted in non-competitive types of inter-relationshipe (Harper, 1977). When crop and weed species differing in rooting abilities compete both in pots and field conditions contradictory conclusions may be drawn. Some investigators in the past have, therefore, questioned the relevance of pot competition experiments in determining competitive abilities between species (Trenbath, 1970; Berendse, 1979). Trenbath and Harper (1973) grew Avena strigosa, Avena fatua, Avena sativa and Avena ludoviciana in pure stands and in all possible mixtures. They found values of RYT much greater than 1.0 when the species A. fatua and A. strigosa competed together in deep soil. When the species were grown in competition on shallow soil they found RYT values which approached unity, suggesting competition in the latter and avoidance in the former situations. In an attempt to extend De Wit's competition theory to plant populations having different rooting depths, Berendse (1979) predicted RYTs to be greater than 1.0, and the relative crowding coefficient of a deep rooting population with respect to a shallow rooting one to decrease with increasing frequency of the deep rooting plants. In 1981 and 1982, he conducted pot and field competition experiments between Anthoxanthum odoratum L. - a species with roots confined to the upper soil layer and Plantago laceolata L. - a deep rooting species. The experiments was divided into one series where different rooting depths were possible and another where gauze with a narrow mesh width prevented differences in rooting depths. In the first series he observed the predicted frequency dependence of the relative crowding coefficient, whereas in the series with gauze, the relative crowding coefficient was independent of plant frequency. He concluded that in such mixtures the deep rooting species has been forced to utilize the nutrients from deeper soil layers. In the presence of a shallow

rooting species, like wheat and/or barren brome, the nutrient available to wild oat in the upper layer may be reduced. This may enhance nutrient uptake of the weed from deeper soils and produce more roots and shoots than the other species. The ability of deep rooted species to take up localized growth resources such as N and P at some places relative to others in the soil environments has been demonstrated (e.g. Drew and Saker, 1978). In greater soil volumes, as in the deep boxes (Exp. 4.4b) and the large pots (Exp. 4.2) wild oat produced the greatest amoungs of roots as well as shoots, as the greater growth of the former usually leads to enhanced growth of the latter.

In situations where nutrients and/or moisture are the major factors limiting the growth of two competing species, the ability to increase root density in deeper soil layers could be a character of great importance. Wild oat, having this ability, may exploit growth resources which inaccessible to wheat and barren brome and thus under field conditions results are likely to favour this weed over either species. On the contrary, the ability of wild oat to exploit nutrients at greater depths may leave the other species a greater opportunity of extracting such resources in the top soil layers, and the result would be less intensive competition with the crop and barren brome. In situations where competition may become intense, wheat and barren brome should have a greater competitive ability sufficient to compensate for the extra nutrients exploited by wild oat. The fact that wild oat root production increased in the upper-most layer with time, puts the weed in a favourable situation of competing for resources occurring in both shallow and deeper layers. Berendse's results, to which reference has already been made, showed RYT values exceeding unity in mixtures between the shallow and deep rooting species. There were achieved in treatments both with and without gauze and in fertilized and non-fertilized plants. He suggested the presence of a mechanism other than deep rooting causing RYT values greater than 1.0. Competition experiments in the field with the crop and wild oat and the latter with barren brome may also lead to values of RYT greater than unity being found, since root distributions in these species suggest the exploitation of different soil horizons by their root systems.

In the present investigations, replacement series experiments in pots with varying nutrient levels (Section 3) generally indicated that wild oat had higher relative yields than either species, the lowest being

for barren brome. This species however, had nutrient concentrations greater than or similar to both other species. RYTs greater or smaller than 1.0 have also been found in competition between wild oat and barren brome or wheat and wild oat, suggesting both competitive and non-competitive interference. RCCs of wild oat with respect to either species also suggested this weed to be generally more competitive. Since these relationships were not determined in field experiments, it would be deisrable to know how the observed differences in depth rooting of the species in cylinders under glasshouse conditions compare with those which may be obtained in the field as root densities in the field are known to change with depth (Andrew and Newman, 1976).

The results of the present experiments showed that the density of roots (length per 10 cm soil profile) was greater for barren brome than either of the other species especially in the top 0-20 cms. This also resulted in greater total length over the entire profile. Most of the available nutrients are found in the surface regions of the soil and a surface rooting species would be expected to take up these nutrients. Hence both wheat and barren brome may be expect3d to compete better than wild oat for nutrients near the surface and this was the case especially with barren brome in competition with wild oat in pot experiments. The higher nutrient concentrations reported elsewhere (Sections 1 and 3) in barren brome than in wheat may also be because root density in the weed was greater than the crop. Barren brome would thus have an advantage in absorbing immobile nutrients from shallow soils whilst wild oat may explore a large volume of soil and extract both mobile and immobile nutrients from deeper soil layers.

When the species were grown in deep metal boxes, distribution of the root systems confirmed that wild oat roots were denser at deeper layers than wheat or barren brome. Barren brome again had about 1.4 times longer roots than wild oat, although root and shoot dry weights were greater for wild oat. Pavlychenko (1937) investigated the development of roots of wheat and wild oat with and without competition. He reported that wild oat grown as separate plants without competition developed about 89.0 kilometers of root and when grown in 15 cm rows with 18-20 plants/30 cm of row they each had 978 m of root. Davis et al. (1967) also studied the spatial extents of root systems of a number of weeds grown without competition under favourable moisture conditions. At maturing he reported root profile areas varying from 5.20 m^2 for pigweed

(Amaranthus retroflexus L.) to 17.92 m^2 for cocklebur (Xanthium pennsylvanicum Waller).

Differences within and between species have been reported for root branching, distribution patterns, surface area, hair density, dry weight and volume (Barley, 1970; Gerloff, 1976) and the uptake of soil resources, especially P and K appeared to be related to one or more of these characteristics of the root system (Hackett, 1968; Newman, 1966; Newman and Andrews, 1973; Evans, 1977).

Differences in root density and ability to root to greater depths at early stages showed that the weeds have different configuration of the root systems than the crop. Wheat, with a low rooting density, is likely to be susceptible to deficiency of less mobile nutrients, as rooting density has an important influence on the rate at which the soil is depleted and thus on the intensity of competition. Several authors have also pointed out that the early growth pattern in a root system has a permanent effect on the future vigour and distribution of roots (Yorke and Sagar, 1970; May et al., 1975). Qasem (1987) studied the distribution of the roots of tomato, fathen and groundsel and reported differences in the amount of root produced and distribution at various soil depths. He found higher percentages of roots in the top 0-10 cm in tomato and groundsel, with roots of fathen predominating in the deeper layers of the soil and showed that these differences were particularly marked at early stages of growth. Using the wide range of tracers available (chiefly radioisotopes) a number of investigators have attempted to study patterns of nutrient uptake and the distribution of roots of species both in pure stands and mixtures. For example, Tarawali (1987) studied root lengths and spread in wheat and Alopecurus myosuroides visually in the field, and in the glasshouse using ^{32}P. In the field the roots of the crop tended to be more deeply distributed than those of A. myosuroides, but they were more or less similar in their lateral spread. In his glasshouse experiments using an autoradiographic method, he found evidence suggesting that roots of the weed were probably more active in P uptake and perhaps more densely distributed than those of the crop.

Information on the ability of some species to change growth patterns of their roots and hence relocate zones of active absorption has been reported (Drew, 1975; Hackett, 1972). Goodman and Collison (1982) have

also shown, using ^{32}P, that the major zones of P uptake by Lolium perenne were deeper in the presence of clover than when the grass was grown in monoculture. In the present studies, the ability of wild oat to produce more roots in deeper soil layers may be the main reason for its relative better performance in competition with the crop or barren brome. Higher nutrient concentrations (e.g. Ca and Mg) found in barren brome may result from the activity of its dense roots, though other root factors such as uptake mechanisms could be involved. Deeper penetration in wild oat may be compensatel for in barren brome by its ability to absorb immobile nutrients from the soil, since plants require higher root densities for phosphate uptaken than for nitrate or water. The large differences, especially in the nutrient contents of the species, observed in competition and water culture experiments may not only indicate efficiency in the mechanisms of absorption and translocation, but also in the effective exploitation of larger volumes of soil due to a large or finely branched root system. Van Noordwijk (1983) demonstrated the requirement for a dense root system when the abundance of soil resources decreases or as the resistance to movement in the soil or into the root increases. According to Troughton (1974) a large root system would only be an advantage if it enables the plant to have access to a larger quantity of water, e.g. by being deeper rooted; but in a limited volume of soil a large root system would be a disadvantage, because the water would be exhausted sooner. In the present experiments water was maintained at a level intended to be non-limiting throughout.

8.12. Conclusion

A number of points which are in general agreement with observations made in previous sections emerged from experiments reported in this section. Separation of root and shoot effects showed that competition for underground resources was generally greater than for those above ground (mainly light). Dry matter and nutrient yields, and values for relative yields and aggressivity calculated for the three species and for the different forms of competition showed that the order of competitive ability tends to be wild oat wheat barren brome.

Studies on root restriction indicated that wild oat was generally tolerant to such treatment, especially at early stages of growth. Barren brome produced higher root/shoot ratios, denser roots and contained

higher or similar concentrations of P, K, Ca and Mg than the other species. It was the species most affected by reduction in soil volume, presumably as the result of increased root competition.

When levels of P were varied at all pot sizes, there was no significant difference between and within species for yields of dry matter and P and K contents. Interactions between species, pot size and P level were not significant (Tables 4.23 and 4.24). This suggested that, since roots are more densely packed in smaller than larger pots, the available low P may be more fully extracted to maintain similar growth to plants in larger volumes of soil where some of the nutrient would be inaccessible to roots due to its immobility. Higher root density in smaller pots would, however, result in intense root competition for low P and the addition of the element at a higher level might have reduced competition and increased growth. Generally root restriction was more important than the level of P in dictating the growth of species. The present study was clearly a preliminary one and further investigations in this area could be rewarding as they might lead to a better understanding of root competition and the competitive ability of species growing in association.

Studies on the distribution and growth of root at various depths along the soil profile showed differences between species. Wheat and barren brome generally showed similar root distributions and occupied the top soil layer (0-30 cm). Wild oat was capable of producing a greater quantity of roots at greater depths than the other species, implying ability to extract growth resources from these depths, which could be an advantage in competition under field conditions. The total length of roots in the uppermost layer (0-10 cm) was greatest for barren brome, perhaps enabling the species to extract nutrients effectively from this part of the soil profile.

9. GENERAL CONCLUSIONS

The project started with the hypothesis that weeds by nature of their evolutionary background may be expected to show greater efficiency of nutrient uptake and/or utilization, particularly at low levels of these resources, than cultivated crops. The main objective of this work was therefore, to look for evidence of differences and similarities between wheat, wild oat and barren brome both in pure stands and mixtures at varying levels of nutrients.

The responses of the species to variations in the levels of five major elements clearly showed that they differed in terms of dry matter production, root growth and morphology, total N, P, K, Ca and Mg contents and concentrations and in the efficiency of uptake and utilization. The weeds, particularly barren brome, were more efficient in taking up and concentrating these mineral elements than the crop. In this laboratory similar investigations were carried out involving various crop and weed species and similar conclusions were reached by Tarawali (1983), Johnson (1987) and Qasem (1987). It may be worthwhile to carry out further such experiments under both glasshouse and field conditions to determine specific nutrient requirements of crops and associated weeds. This may lead to the application of appropeiate fertilizer regimes so as to favour the crop. Benefits from such studies could be reductions in the population of weed species and consequential crop losses, decreased fertilizer costs and perhaps decreased need for herbicides. Even modest savings could be valuable as the cost of such inputs increases.

The depletion studies were of a preliminary type and ion uptake kinetic parameters could not be determined for reasons which are discussed. This needs to be followed up because uptake studies using whole plants in NFT would provide several advantages (see Section II) includidng the fact that results might reflect the normal activities of growth and development of plants in the field. The determination of kinetic values (Vmax and Km) might help to clarify why weeds in general are more efficient in the uptake and accumulation of nutrients, especially under limiting conditions. Studies using radio-active tracers such as ^{32}P and ^{86}Rb could be used additionally to substantiate results in these areas of investigation.

The competitive inter-relationships between the weeds and the crop

generally showed the particular aggressiveness of wild oat towards both wheat and barren brome. This was demonstrated by the ability of the weed to produce a greater amount of total dry matter and by its large root system growing at greater depth in the soil. The total amount of nutrients taken up by this weed usually exceeded the other species. It was also as efficient as the crop in taking and utilizing nutrients. A noteworthy observation was that wild oat is less sensitive than the other plants to variations in the levels of P, K and Mg. This suggests that under competitive situations with wheat in heavy soils where these nutrients could be limiting the crop would undoubtedly suffer from an association with the weed. The superior ability of barren brome to take up and accumulate nutrients both in pure and mixture stands may well be related to its ability to produce a finer and denser root system than the other species. The crop usually showed higher efficiency of uptake and concentration of K than either weed under lower levels of the element and at higher levels 'luxury consumption' was noted. In general tissue nutrient concentrations, total contents and their relative crowding coefficients and their products indicated that there was competition for P, K, Ca and Mg between the crop and the weeds. For all the three species competition for underground resources appeared to be more important than those above ground (light) showing the importance of differences in root production.

The competition experiments reported in this thesis were carried out in pots under glasshouse conditions and the conclusions made may or may not reflect those which would be obtained under field conditions. It would be helpful to conduct such experiments in the field especially because the results reported here clearly indicate differences between the species in the production of roots at various depths. Moreover, in pots root growth is physically impeded and under these conditions intra-specific root competition could be greater than inter-specific competition.

There are various aspects of this work which need to be pursued.

(1) Studies relating to root growth and distribution and their relationships to the efficiency of nutrient uptake both in competition and pure stands under field conditions using ratio-active tracers.

(2) The use of foliar fertilization as a means of alleviating below ground competition.

(3) Further studies on the kinetics of ion uptake.

(4) Further parallel studies comparing long-established weeds (comparable to wild oat) with those which have become established more recently (comparable to barren brome).

(5) The relationship between nutritional interactions and weed control strategies and perhaps other forms of interactions such as allelopathy.

It is clear from the studies reported that no one set of generalizations relating to the nutritional relationships between a particular crop and different weeds which compete with it is likely to be valid. There is therefore a need for detailed studies of the nutritional interaction between species growing in competition such as those reported here.

REFERENCES

ADEPETU, J.A., and AKAPA, L.K. (1977). Root growth and nutrient uptake characteristics of some cowpea varieties. Agronomy Journal 69: 940-943.

ALDRICH, R.J. (1984). Weed-crop Ecology. Principles in weed management. Breton Publishers, Massachusetts, U.S.A. pp. 1-13.

ALKAMPER, J. (1973). The Fertilization of Teff. Soil and water management and mechanization. Journal of the Association for the Advancement of Agricultural Science in Africa. 1: 56-65.

ALKAMPER, J. PESSIOS, E. and LONG, D. (1979). The influence of fertilizers on the development and nutrient uptake of various weeds in maize. In: Proceedings of the EWRS symposium - The influence of different factors on the development and control of weeds. Mainz, Germany. pp. 181-192.

ALLEN, S.E., GRIMSHAW, H.M. and ROWLAND, A.P. (1986). In: Methods in plant ecology. (Ed. by P.D. MOORE and S.B. CHAPMAN). Blackwell Scientific Publications, Oxford. pp. 285-344.

ANDREW, R.H. (1966). A technique for measuring root volume in vivo. Crop Science, 6: 384-386.

ANGHINONI, I., BALIGAR, V.C. and BARBER, S.A. (1981). Growth and uptake rates of P, K, Ca and Mg in wheat. Journal of Plant Nutrition 3 (6): 923-933.

ANON., (1967). Report Drayton Experimental Husbandry Farm for 1967, pp. 11-15.

ANON., (1981). Barren Brome. Ministry of Agriculture, Fisheries and Food. Leaflet 777.

ANTONOVICS, J., BRADSHAW, A.D. and TURNER, R.G. (1971). Heavy metal tolerance in plants. Advances in Ecological Research. 7: 1-85.

ANTONOVICS, J., LOVETT, J. and BRADSHAW, A. D. (1967). The evolution of adaptation to nutritional factors in populations of herbage plants. In: Isotopes in plant nutrition and physiology. International Atomic Agency, Vienna.

A. O. A. C. (1984). Official Methods of Analysis of the Association of Official Analytical Chemists. 14th edition (1984).

ARMIGER, W. H., DEAN, L. A., MASON, D. D., and KOCH, E. J. (1958). Effect of size and type of pot on relative precision yields, and nutrient uptake in greenhouse fertilizer experiments. Agronomy Journal, 50: 244-247.

ASHER, C. J. and OZANNE, P. G. (1967). Growth and potassium content of plants in solution cultures maintained at constant potassium concentrations. Soil Science, 103 (3): 155-161.

ASPINAL, D. and MILTHORPE, F. L. (1959). An analysis of competition between barley and white Persicaria. I. The effects on growth. Annals of Applied Biology. 47: 156-172.

ATKINSON, D. (1973). Some general effects of phosphorus deficiency on growth and development. New Phytologist, 72: 101-111.

ATWELL, B. J., VEERKAMP, M. T., STUIVER, BEP, C. E. E., KUIPER, P. J. C. (1980). The uptake of phosphate by Carex species from oligotrophic to eutrophic swamp habitats. Physiologia Plantarum, 49: 487-494.

AUSTIN, M. P., FRESCO, L. F. M., NICHOLLS, A. O., GROVES, R. H., and KAYE, P. E. (1988). Competition and relative yield: Estimation and interpretation at different densities and under various nutrient concentrations using Silybum marianum and Cirsium vulgare. Journal of Ecology, 76: 157-171.

AYALA, F. J. (1971). Competition between species frequency dependence: Science, 171: 820-824.

BAAN HOFMAN, T. and ENNIK, G.C. (1980). Investigation into plant characters affecting the competitive ability of perennial ryegrass (Lolium perenne L.). Netherlands Journal of Agricultural Science, 28: 97-109.

BAANHOFMAN, T. and ENNIK, G.C. (1982). The effect of root mass of perennial ryegrass (Lolium perenne L.) on the competitive ability with respect to couchgrass (Elytrigia repens (L.) Desv.). Netherlands Journal of Agricultural Science, 30: 275-283.

BAKER, D.A. and HALL, J.L. (1973). Pinocytosis, ATP-ase and ion uptake by plant cells. New Phytologist, 72: 1281-1291.

BAKER, D.E., JARRELL, A.E., MARSHALL, L.E. and THOMAS, W.I. (1970). Phosphorus uptake from soil by corn hybrids selected for high and low phosphorus accumulation. Agronomy Journal, 62: 103-106.

BAKER, E., DALE and WOODRUFF, C.M. (1962). Influence of volume of soil per plant upon growth and uptake of phosphorus by corn from soils treated with different amounts of phosphor us. Soil Science 94: 409-412.

BAKER, H.G. (1974). The evolution of weeds. Annual Review of Ecology and Systematics, 5: 1-24.

BAKHUIS, J.A. and KLETER, H.J. (1965). Some effects of associated growth on grass and clover under field conditions. Netherlands Journal of Agricultural Science, 13: 280-310.

BANTING, J.D. (1962). The dormancy behavior of Avena fatua L. in cultivated soil. Canadian Journal of Plant Science, 42: 22-39.

BARBER, S.A. (1979). Growth requirement for nutrients in relation to demand at the root surface. In "The Soil-Root Interface" (J.L. Harley and R. Scott-Russell, eds.), pp. 5-20. Academic Press, London, and Orlando.

BARRETT, D.W. and CAMPBELL, N.A. (1973). An evaluation of the effect of competition between wheat and Wimmera ryegrass (Lolium rigidum) during early stages of growth. Australian Journal of Experimental Agriculture and Animal Husbandry, 13: 581-586.

BARROW, N.J. (1975). The response to phosphate of two annual pastures species. II. The specific rate of uptake of phosphate, its distribution and use for growth. Australian Journal of Agricultural Research, 26: 145-156.

BECERRIL-ROMAN, A.E. (1988). Nutrient uptake of Strawberry (Fragaria x ananassa Duch.) under different environmental conditions. Ph.D. Thesis, University of London.

BEGON, M., HARPER, J.L. and TOWNSEND, C.R. (1986). Individuals, Populations and Communities, Ecology. Blackwell Scientific Publications. pp. 199-288.

BEHRENDT, S., and HANF, M. (1979). Grass Weeds in Agriculture: Identification in the Flowerless State. BASF Aktiengesellschaft, Ludwingshafen. pp. 53-70.

BELL, A.R. and NALEWAJA, J.D. (1968a). Competitive effects of wild oats in flax. Weed Science, 16: 501-504.

BELL, A.R. and NALEWAJA, J.D. (1968b). Competition of wild oats in wheat and barley. Weed Science, 16: 505-508.

BERENDSE, F. (1979). Competition between plant populations with different rooting depths. I Theoretical considerations. Oecologia (Berl.) 43: 19-26.

BERENDSE, F. (1981). Competition between plant populations with different rooting depths. II Pot Experiments. Oecologia (Berl.) 48: 334-341.

BERENDSE, F. (1982). Competition between plant population with different rooting depths. III Field Experiments. Oecologia (Berl.) 53: 50-55.

BERGH, J.P. VAN DEN (1968). An Analysis of yields of grasses in mixed and pure stands. Verslagen van landbouwkundige onderzoekingen, 741: 1-71.

BHASKAR, A. and VYAS, K.G. (1988). Studies on competition between wheat and Chenopodium album L. Weed Research, 28: 53-58.

BIELESKI, R.L. (1973). Phosphate pools, phosphate transport and phosphate availability. Annual Reviews of Plant Physiology. 24: 225-252.

BLACK, C.C., CHEN, T.M. and BROWN, R.H. (1969). Biochemical basis for plant competition. Weed Science, 17: 338-344.

BLACKMAN, G.E. and TEMPLEMAN, W.G. (1938). The nature of competition between cereal crops and annual weeds. Journal of Agricultural Science, 28: 247-271.

BLACKSHAW, R.E., STOBER, E.H. and STURKO, A.W.R. (1981). Effects of seeding dates and densities on green foxtail (Setaria viridis (L.) Beauv.). Weed Science, 29: 212-217.

BLEASDALE, J.K.A. (1960). Studies on plant competition. In: The Biology of weeds (ed. J.L. Harper). Blackwell Scientific Publications, Oxford, 256 pp.

BOGGIE, R. and KNIGHT, A.H. (1960). Studies of root development in a grass sward growing on deep peat using radioactive tracers. Journal of the British Grassland Society, 15: 133-136.

BÖHM, W. (1979). Methods of studying root systems, Springer-Verlag. Berlin, Heidelberg.

BOWEN, G.D. and ROVIRA, A.D. (1971). Relationship between root morphology and nutrient uptake. In: Recent Advances in Plant Nutrition. 1: 293-305, (Ed. R.M. Samish).

BRADSHAW, A.D. (1965). Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics: 13: 115-155.

BRADSHAW, A.D., LODGE, R.W., JOWETT, D. and CHADWICK, M.J. (1958). Experimental investigations into the mineral nutrition of several grass species. I. Calcium level. Journal of Ecology, 46: 749-757.

BRADSHAW, A.D., LODGE, R.W., JOWETT, D. and CHADWICK, M.J. (1960a). Experimental investigations into the mineral nutrition of several grass species. II. Ca and pH. Journal of Ecology, 48: 143-50.

BRADSHAW, A.D., CHADWICK, M.J., JOWETT, D., LODGE, and SNAYDON, R.W. (1960b). Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. Journal of Ecology, 48: 631-637.

BRADSHAW, A.D., CHADWICK, M.J., JOWETT, D., SNAYDON, R.W. (1964). Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. Journal of Ecology, 52: 665-676.

BRADSHAW, A.D., and SNAYDON, R.W. (1959). Population differentiation within plant species in response to soil factors. Nature, London, 183: 129-130.

BRAY, R.H. (1954). A nutrient mobility concept of soil-plant relationships. Soil Science, 78: 9-22.

BREEZE, V.G., CANAWAY, R.J., WILD, A., HOPPER, M.J., and JONES, L.H.P. (1982). The uptake of phosphate by plants from flowing nutrient solution. I. Control of phosphate concentration in solution. Journal of Experimental Botany, 33: 183-189.

BRENCHLEY, W.E. (1920). Weeds of farm land. Longmans Green and Co., London, 239 pp.

BREWSTER, J.L. and TINKER, P.B. (1972). Nutrient flow rates in roots. Soils and Fertilizer, 35: 355-359.

BROAD, P.D. (1952). The occurrence of weed seeds in samples submitted for testing by the O.S.T.S. Journal of the National Institute of Agricultural Botany, 6: 275-286.

BROWN, L.H. and COCHEMÉ, J. (1970). Agrometeorology Survey of the Highlands of East Africa. Nature and Resources, UNESCO, 6(3), 2-10.

BUDD, E.G. (1981). Survey, dormancy and life cycle of Bromus sterilis (Sterile brome) in cereals, with particular reference to spring barley. Journal of the National Institute for Agricultural Botany, 15: 430-439.

BUNTING, A.H. (1960). Some reflections on the ecology of weeds. In: Harper, J.L. (Ed.). The Biology of Weeds. British Ecological Society Symposium No. 1. Blackwell Scientific Publications, Oxford. pp. 11-26.

CALDWELL, M.M. and RICHARDS, J.H. (1986). Competing root systems: Morphology and models of absorption. In: On the Economy of Plant Form and Function, (ed.) T.J. Givnish, Cambridge: Cambridge University Press. pp. 251-273.

CARTER, H.W., NORTON, H.W. and DUNGAN, G.H. (1957). Wheat and Cheat. Agronomy Journal, 49: 261-267.

CARTWRIGHT, W. (1972). The effects of phosphate deficiency on the kinetics of phosphate absorption by sterile excised barley roots and some factors affecting the ion uptake efficiency of roots. Communications in Soil Science and Plant Analysis. 3: 313-322.

CHADWICK, M.J. and OBEID, M. (1963). The response to variations in Nitrogen level of some weed species of the Sudan. Weed Research, 3: 230-241.

CHAMBERS, E.E. and HOLM, L.G. (1965). Phosphorus uptake as influenced by associated plants. Weeds, 13: 312-314.

CHANCELLOR, R.J. (1969). Competition between wild oats and cereals. 3e Colloque de Biologie Mauvaises Herbes Grignon, 10 pp.

CHANCELLOR, R.J. (1976). Growth and development of wild oat plants. In: Wild Oats in World Agriculture (ed.) by D. Price Jones, Agricultural Research Council, London, 1976.

CHANCELLOR, R.J. and FROUD-WILLIAMS, R.J. (1984). A secondary survey of cereal weeds in central Southern England. Weed Research 24: 29-36.

CHANCELLOR, R.J. and PETERS, N.C.B. (1972). Germination periodicity, plant survival, and seed production in populations of Avena fatua, growing in spring barley. Proceedings of the 11th British Weed Control Conference, 218-225.

CHANCELLOR, R.J. and PETERS, C.B. (1974). The time of onset of competition between wild oats (Avena fatua L.) and spring cereals. Weed Research, 14: 197-202.

CHANCELLOR, R.J. and PETERS, C.B. (1976). Competition between wild oats and crops. In: Wild oats in World Agriculture. Ed. D. Price Jones, London) pp. 99-112.

CHAPIN, F.S. III. (1980). The mineral nutrition of wild plants. Annual Reviews of Ecology and Systematics, 11: 233-260.

CHAPIN, F.S. III. (1983). Adaptation of selected trees and grasses to low availability of phosphorus. In: Genetic Aspects of Plant Nutrition, Developments in Plant and Soil Sciences, Ed. M.R. Sarić and B.C. Loughman) 8: 217-221.

CHESTNUTT, D.M.B., BARTHOLOMEW, P.W. and BINNIE, R.C. (1980). The interaction of perennial rye-grass and timothy in mixtures and their reaction to clover and nitrogen in cut swards. Grass and Forage Science, 35: 281-286.

CHRISTIE, E.K. and MOORBY, J. (1975). Physiological responses of semi-arid grasses. I. The influence of phosphorus supply on growth and phosphorus absorption. Australian Journal of Agricultural Research. 26: 423-436.

CLAASSEN, N. and BARBER, S.A. (1974). A method for characterizing the relation between nutrient concentration and flux into roots of intact plants. Plant Physiology, 54: 564-568.

CLAASSEN, N. and BARBER, S.A. (1976). Simulation model for nutrient uptake from soil by a growing plant root system. Agronomy Journal, 68: 961-964.

CLAPHAM, A.R., TUTIN, T.G., and WARBURG, E.F. (1981). Excursion flora of the British Isles. Cambridge University Press, 3rd Edn. 499 pp.

CLARK, R.B. (1975). Differential magnesium efficiency in corn inbreds. I. Dry matter yields and mineral element composition. Soil Science Society of America: Proceedings, 39: 488-491.

CLARK, R.B. (1978). Differential response of inbred maize to Zn. Agronomy Journal, 70: 1057-1060.

CLARK, R.B. (1983). Plant genotype differences in the uptake, translocation, accumulation, and use of mineral elements required for growth. In: Genetic Aspects of Plant Nutrition. Development in Plant and Soil Sciences, (Ed. by M.R. Sarić and B.C. Loughman). 8: 49-71.

CLARKSON, D.T. (1967). Phosphorus supply and growth rates in species of Agrostis L. Journal of Ecology, 55: 707-731.

CLARKSON, D.T. (1985). Factors affecting mineral nutrient acquisition by plants. Annual Review of Plant Physiology, 36: 77-115.

CLEMENT, C.R., HOPPER, M.J. CANAWAY, R.J., and JONES, L.H.P. (1974). A system for measuring the uptake of ions by plants from flowing solutions of controlled composition. Journal of Experimental Botany, 25 (84): 81-99.

CLEMENTS, F.E. and GOLDSMITH, G.W. (1924). The phytometer method in ecology. Carnegie Institute, Washington, Publication No. 35b, 1-106.

CLEMENTS, F.E., WEAVER, J.E., and HANSON, H. (1929). Plant Competition - an analysis of community function. Carnegie Institute, Washington. Publication No. 398.

CONNOLLY, J. (1986). On difficulties with replacement series methodology in mixture experiments. Journal of Applied Ecology, 23: 125-137.

COOK, S.J. and RATCLIFFE, D. (1984). A study of the effects of root and shoot competition on the growth of green Panic (Panicum maxinim var. Tricholglume). Seedlings in an existing grassland using root exclusion tubes. Journal of Applied Ecology, 21: 971-982.

COOPER, A.C. (1978). The ABC of NFT. Grower Books, London. 181 pp.

CORNFORTH, I.S. (1968). Relationships between soil volume used by roots and nutrient accessibility. Journal of Soil Science, 19 (2): 291-301.

COUSENS, R. (1985). A simple model relating yield loss to weed density. Annals of Applied Biology, 107: 239-252.

COUSENS, R., FIRBANK, L.G., MORTIMER, A.M. and SMITH, R.G.R. (1988). Variability in the relationship between crop yield and weed density for winter wheat and Bromus sterilis. Journal of Applied Ecology, 25: 1033-1044.

CROSSLEY, G.K. and BRADSHAW, A.D. (1968). Differences in response to mineral nutrients of populations of ryegrass, Lolium perenne L., and orchard grass, Dactylis glomerata L. Crop Science, 8: 383-387.

CUSSANS, G.W. (1976). Population Studies. In: Wild oats in World Agriculture Ed. D. Price Jones. Agricultural Research Council, London. pp. 119-125.

DAVIES, M.S. and SNAYDON, R.W. (1973a). Physiological differences among populations of Anthoxanthum odoratum L. collected from the Park Grass experiment, Rothamsted. 1. Response to Ca. Journal of Applied Ecology, 10: 33-45.

DAVIES, M.S. and SNAYDON, R.W. (1973b). Physiological differences among populations of Anthoxanthum odoratum L. collected from the Park Grass experiment, Rothamsted. II. Response to Al. Journal of Applied Ecology, 10: 47-55.

DAVIES, M.S. and SNAYDON, R.W. (1974). Physiological differences among populations of Anthoxanthum odoratum L. collected from the Park Grass experiment, Rothamsted. III. Response to P. Journal of Applied Ecology, 11: 699-707.

DAVIS, R.G., JOHNSON, W.C., and WOOD, F.O. (1967). Weed root profiles. Agronomy Journal 59: 555-556.

DAWSON, J.H. (1964). Competition in irrigated field beans and annual weeds. Weeds, 12: 206-208.

DE TURK, E.E., HOLBERT, J.R. and HOWK, B.W. (1933). Chemical Transformations of phosphorus in the growing corn plant, with results on two first-generation crosses. Journal of Agricultural Research, 46: 121-141.

DEW, D.A. (1972). An index of competition for estimating crop loss due to weeds. Canadian Journal of Plant Science, 52: 921-927.

DONALD, C. M. (1958). The interaction of competition for light and nutrients. Australian Journal of Agricultural Research, 9: 421-435.

DONALD, C. M. (1963). Competition among crop and pasture plants. Advances in Agronomy, 15: 1-118.

DRAKE, M., VENGRIS, J. and COLBY, W. G. (1954). Cation-exchange capacity of plant roots. Soil Science, 72: 139-147.

DREW, M. C. (1979). Properties of roots which influence rates of absorption. In: The soil-root interface. Eds. J. L. Harley and R. S. Russell. Academic Press, London, pp. 21-38.

DREW, M. C. and SAKER, L. R. (1975). Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increase in lateral root growth and rates of nitrate uptake. Journal of Experimental Botany, 26: 79-90.

DREW, M. C. and SAKER, L. R. (1978). Nutrient supply and the growth of the seminal root system in barley. III. Compensatory increases in growth of lateral roots and in rates of phosphate in response to a localized supply of phosphate. Journal of Experimental Botany, 29: 435-451.

DREW, M. C., SAKER, L. R., BARBER, S. A. and JENKINS, W. (1984). Changes in the kinetics of phosphate and potassium absorption in nutrient-deficient barley roots measured by a solution-depletion technique. Planta, 160: 490-499.

DUNLOP, J., GLASS, A. D. M. and TOMKINS, B. D. (1979). The regulation of K+ uptake by ryegrass and white clover roots in relation to their competition for potassium. New Phytologist, 83: 365-370.

DUNLOP, P. J. and TOMKINS, B. (1976). Genotypic differences in potassium translocation in rye-grass. In: Transport and Transfer Processes in Plants. Eds. I. F. Wardlaw and J. B. Passioura. Academic Press, New York. pp. 145-152.

EAGLES, C.F. (1972). Competition for light and nutrients between natural populations of Dactylis glomerata. Journal of Applied Ecology, 9: 141-151.

EAVIS, B.W. and TAYLOR, H.M. (1979). Transpiration of Soybeans as related to leaf area, root length and soil water content. Journal of Agronomy, 71: 441-445.

EDWARDS, D.G. (1970). Phosphate absorption and long-distance trans port in wheat seedlings. Australian Journal of Biological Science, 23: 255-264.

EDWARDS, J.H. and BARBER, S.A. (1976). Phosphorus uptake rate of soybean roots as influenced by plant age, root trimming and solution P concentration. Agronomy Journal, 68: 973-976

ELLERN, S.J., HARPER, JOHN L. and SAGAR, G.R. (1970). A comparative study of the distribution of the roots of Avena fatua and Avena strigosa in mixed stands using a 14C-labelling technique. Journal of Ecology, 58: 865-868.

ELLIOTT, J.G., CHURCH, B.M., HARVEY, J.J., HOLROYD, J., HULLS, R.H. and WATERSON, H.A. (1979). Survey of the presence and methods of control of wild oat, blackgrass and couch grass in the United Kingdom during 1977. Journal of Agricultural Science, Cambridge, 92: 617-634.

ENNIK, G.C. and BAAN HOFMAN, T. (1983). Variation in root mass of ryegrass types and its ecological consequences. Netherlands Journal of Agricultural Science, 31: 325-334.

EPSTEIN, E. (1966). Dual pattern of ion absorption by plant cells and by plants. Nature, 212: 1324-1327.

EPSTEIN, E. (1972). Mineral Nutrition of Plants: Principles and Perspectives. John Wiley and Sons, Inc. New York, London, Sydney, Toronto. pp. 346.

EPSTEIN, E. and HAGEN, C.E. (1952). A kinetic study of the absorption of alkali cations by barley roots. Plant Physiology 27: 457-474.

EPSTEIN, E. and HENDRICKS, S.B. (1956). Uptake and transport of mineral nutrients in plant roots. Proceedings of the International Conference on Peaceful Uses of Atomic Energy, 12: 98-102. United Nations, Geneva.

EPSTEIN, E. and JEFFERIES, R.L. (1964). The genetic basis of selective ion transport in plants. Annual Review of Plant Physiology, 15: 169-184.

EPSTEIN, E., RAINS, D.W., and EZZAM, O.E. (1963). Resolution of dual mechanisms of potassium absorption by barley roots. Plant Physiology: 49: 684-692.

EVANS, H. (1938). Studies on the absorbing surface of sugar-cane root systems. 1. Method of study with some preliminary results. Annals of Botany 2: 159-182.

EVANS, P.S. (1977). Comparative root morphology of some pasture grasses and clovers. New Zealand Journal of Agricultural Research, 20: 331-335.

FAGERIA, N.K. (1973). Uptake of nutrients by rice plants from dilute solutions. Doctoral thesis, Catholic University, Louvain, Belgium.

FAGERIA, N.K. (1974). Kinetics of phosphate absorption by intact rice plants. Australian Journal of Agricultural Research, 25: 395-400.

FIRBANK, L.G. and WATKINSON, A.R. (1985). On the analysis of competition within two-species mixtures of plants. Journal of Applied Ecology, 22: 503-519.

FITTER, A.H. (1976). Effects of nutrient supply and competition from species on root growth of Lolium perenne L. in soil. Plant and Soil, 45: 177-189.

FITTER, A.H. and BRADSHAW, A.D. (1974). Root penetration of Lolium perenne on colliery shale in response to reclamation treatments. Journal of Applied Ecology, 11: 609-616.

FITTER, A.H. and HAY, R.K.M. (1987). Environmental Physiology of Plants. Academic Press, London. 2nd Edn. 423 pp.

FLEMING, G.F., YOUNG, F.L. and OGG, G.A. (1988). Competitive relationships among winter wheat (Triticum aestivum), jointed goatgrass (Aegilops cylindrica) and downey brome (Bromus tectorum). Weed Science, 36: 479-486.

FONTES, P.C.R., BARBER, S.A. and WILCOX, G.E. (1986). Prediction of phosphorus uptake by two tomato cultivars growing under insufficient and sufficient phosphorus soil conditions using a mechanistic mathematical model. Plant and Soil, 94: 87-97.

FOWLER, D.B. and GUSTA, V. (1982). Fall growth and cold acclimation of winter wheat and rye differentially fertilized with phosphorus. Agronomy Journal, 74: 539-540.

FOY, C.D. and BARBER, S.A. (1958). Magnesium absorption and utilization by two inbred lines of corn. Soil Science Society of America Proceedings, 22: 57-62.

FRANKOW-LINDBERG, B.E. (1985). Effect of couchgrass on competition between timothy and red clover. Journal of Applied Ecology, 21: 245-254.

FREY, K.J. (1959). Yield components in oats. II. The effects of nitrogen fertilization. Agronomy Journal, 51: 605-608.

FROUD-WILLIAMS, R.J. (1981). Germination behaviour of Bromus species and Alopecurus myosuroides. Association of Applied Biologists Conference: Grass weeds in cereals in the United Kingdom. pp. 31-40.

FROUD-WILLIAMS, R.J. (1983). The influence of straw disposal and cultivation regime on the population dynamics of Bromus sterilis. Annals of Applied Biology, 103: 139-148.

FROUD-WILLIAMS, R.J. and CHANCELLOR, R.J. (1982). A survey of grass weeds in cereals in central Southern England. Weed Research, 22: 163-171.

FROUD-WILLIAMS, R.J., POLLARD, F. and RICHARDSON, W.G. (1980). Barren brome: A threat to winter cereals? Weed Research Organization, Eighth Report 1978-1979. pp. 43-51.

GABLEMAN, W.H., and GERLOFF, G.C. (1982). The search for an interpretation of genetic controls that enhance plant growth under deficiency levels of a macro nutrient. In: Genetic Aspects of Plant Nutrition (Ed. M.R. Saric and B.C. Loughman). Proceedings of the first International Symposium on Genetic Aspects of Plant Nutrition, Belgrade.

GEBRESELASSIE, A. (1985). Control of growth and development of Tef (E. tef (2ucc.) Trotter) and Niger-seed (Guizotia abyssinica class.) by daylength, temperature and plant growth regulators. Ph.D. Thesis, Wye College, University of London.

GERLOFF, G.C. (1963). Comparative mineral nutrition of plants. Annual Review of Plant Physiology. 14: 107-124.

GERLOFF, G.C. (1977). Plant efficiencies in the use of nitrogen, phosphorus and potassium. In: Wright, M.J. (Ed.). Plant adaptation to mineral stress in problem soils. Cornell University Agricultural Experiment Station, Ithaca, New York, pp. 161-173.

GLASS, A. D. M. and PERLEY, J. E. (1980). Varietal differences in potassium uptake of barley. Plant Physiology, 65: 160-164.

GLASS, A. D. M., SIDDIQUI, M. Y. and GILES, K. I. (1981). Correlation between potassium uptake and hydrogen efflux in barley varieties: a potential screening method for the isolation of nutrient efficient lines. Plant Physiology, 68: 457-459.

GLAUNINGER, J. and HOLZNER, W. (1982). Interference between weeds and crops: A review of literature. pp. 149-159. In: Biology and ecology of weeds. Geobotany 2. Ed. W. HOLZNER and M. NUMATA. Junk Publishers, The Hague.

GOLDBERG, D. E. and FLEETWOOD, L. (1987). Competitive effect and response in four annual plants. Journal of Ecology; 75: 1131-1143.

GOLDENBERG, D. E. and WERNER, P. A. (1983). Equivalence of competitors in plant communities: A null hypothesis and a field experimental approach. American Journal of Botany, 70: 1098-1104.

GOOCH, S. M. S. (1963). The occurrence of weed seeds in samples tested by the official seed testing station, 1960-1. Journal of the National Institute of Agricultural Botany. 9: 353-371.

GOODMAN, P. J. and COLLISON, M. (1982). Varietal differences in uptake of ^{32}P labelled phosphate in clover plus ryegrass swards and monocultures. Annals of Applied Biology, 100: 559-565.

GORSLINE, G. W., THOMAS, W. I. and BAKER, D. E. (1964). Evidence of inheritance of differential accumulation of calcium, magnesium and potassium by maize. Crop Science, 1: 155-156.

GRAY, G. R. (1981). Aspects of the ecology of barren brome (Bromus sterilis L.). D. Phil. Thesis, University of Oxford.

GREGORY, F.G. and CROWTHER, F. (1928). A physiological study of varietal differences in plants. Part 1. A study of the comparative yields of barley varieties with different manurings. Annals of Botany, 42: 757-770.

GREGORY, P.J., CRAWFORD, D.V. and MCGOWAN, M. (1979). Nutrient relations of winter wheat. 1. Accumulation and distribution of Na, K, Ca, Mg, P, S and N. Journal of Agricultural Science, Cambridge, 93: 485-494.

GRIME, J.P. and CURTIS, A.V. (1976). The interaction of drought and mineral nutrients stress in calcareous grassland. Journal of Ecology, 64: 976-998.

GRIME, J.P. and HUNT, R. (1975). Relative growth rate: its range and adaptive significance in a local flora. Journal of Ecology, 63: 393-422.

GRIME, J.P. and JARVIS, B.C. (1975). Shade avoidance and shade tolerance in flowering plants. II. Effects of light on the germination of species of contrasted ecology. In: Light as an Ecological Factor. pp. 525-532. (Ed. by N. Bainbridge, G.O. Evans, and O. Rackman). Blackwell Scientific Publications, Oxford.

GWYNNE, D. and MURRAY, R.B. (1985). Weed Biology and Control in Agriculture and Horticulture. Batsford Academic and Educational, London, pp. 120-121.

HACKETT, C. (1968). A study of the root system of barley. I. Effects of nutrition on two varieties. New Phytologist, 67: 287-300.

HAGEN, C.E. and HOPKINS, H.T. (1955). Ionic species in orthophosphate absorption by barley roots. Plant Physiology, 30: 193-199.

HAIZEL, K.A. and HARPER, J.L. (1973). The effects of density and the timing of removal on interference between barley, white mustard and wild oats. Journal of Applied Ecology, 10: 23-31.

HALL, R.L. (1974a). An analysis of the nature of interference between plants of different species. I. Concepts and extension of de Wit analysis to examine effects. Australian Journal of Agricultural Research, 25: 739-747.

HALL, R.L. (1974b). An analysis of the nature of interference between plants of different species. II. Nutrient relations in a Nandi Setaria and Greenleaf Desmodium association with particular reference to potassium. Australian Journal of Agricultural Research, 25: 749-756.

HANNAH, L.H. (1964). Wild oat competition in wheat and flax. Proceedings of the 20th North Central Weed Control Conference, pp. 481-485.

HARLAN, J.R. (1965). The possible role of weed races in the evolution of cultivated plants. Euphytica, 14: 173-176.

HARLAN, J.R. and DE WIT, J.M.J. (1965). Some thoughts about weeds. Economic Botany, 19: 10-24.

HARPER, F. (1983). Principles of Arable Crop Production. Granada, London. pp. 198-229.

HARPER, J.L. (1961). Approaches to the study of plant competition In: Mechanisms in Biological Competition. Ed. F.L. Milthorpe). Symposium of the Society for Experimental Biology No. 15. Cambridge University Press, 1-39.

HARPER, J.L. (1964). The individual in the population. Journal of Ecology, 52: 149-158.

HARPER, J.L. (1977). Population Biology of Plants. Academic Press, London. 892 pp.

HARPER, J.L. and MCNAUGHTON, I.H. (1962). The comparative biology of closely related species living in the same area. VII. Interference between individuals in pure and mixed populations of papaver species. New Phytologist, 61: 175-188.

HARTMAN, R.W. and ALLARD, R.W. (1964). Effect of nutrient and moisture levels on the competitive ability in barley (Hordeum vulgare L.). Crop Science, 4: 424-426.

HARVEY, P.H. (1939). Hereditary variation in plant nutrition. Genetics, 24: 437-461.

HAWTON, D. (1980). Temperature effects of Eleusine indica and Setaria anceps grown in association. Weed Research, 20: 261-266.

HAY, J.R. and CUMMING, B.G. (1959). A method for inducing dormancy in wild oats (Avena fatua L.). Weeds, 7: 34-40.

HAYES, R.J., and GOH, K.M. (1978). Ammonium and nitrate nutrition of plants. Biological Reviews, 53: 465-510.

HEWITT, E.J. and SMITH, T.A. (1975). Plant Mineral Nutrition. The English Universities Press Ltd., London. 298 pp.

HILL, T.A. (1977). The Biology of Weeds. Studies in Biology No. 79. Edward Arnold, London. 64 pp.

HILL, J. and SHIMAMOTO, Y. (1973). Methods of analysing competition with special reference to herbage plants. I. Establishment. Journal of Agricultural Science (Cambridge), 81: 77-89.

HILLS, F.J., SALISBURY, R.L., ULRICH, A. and SIPITANOS, K.M. (1970). Effects of phosphorus on nitrate in sugar beet (Beta vulgaris L.). Agronomy Journal, 62: 91-92.

HILTON, J.R. (1982). An unusual effect of the far-red absorbing form of phytochrome: photoinhibition of seed germination in Bromus sterilis. Planta, 155: 524-528.

HILTON, J.R. (1984). The influence of temperature and moisture status on the photoinhibition of seed germination in Bromus sterilis L. by the far-red absorbing form of phytochrome. New Phytologist, 97: 369-374.

HOAGLAND, D.R. (1944). Lectures on Inorganic Nutrition of Plants. Chemica Botanica Company, Waltham.

HOAGLAND, D.R. and BROYER, T.C. (1936). General nature of the process of salt accumulation by roots with description of experimental methods. Plant Physiology, 11: 471-507.

HOENER, I.R. and DE TURK, E.E. (1938). Journal of the American Society for Agronomy, 30: 232-243.

HOLROYD, J. (1964a). The emergence and growth of Avena fatua from different depths in the soil. Proceedings of the 7th British Weed Control Conference, pp. 621-627.

HOLZNER, W. (1982). Concepts, categories and characteristics of weeds. In: Biology and Ecology of Weeds, Geobotany 2. (ed) W. Holzner and M. Numata. Junk Publishers, The Hague. 461 pp.

HOVELAND, C.S., BUCHANAN, G.A. and HARRIS, M.C. (1976). Response of species to soil phosphorus and potassium. Weed Science, 24(2): 194-201.

HOWARD, D.D. and ADAMS, F. (1965). Calcium requirement for penetration of sub-soils by primary cotton roots. Proceedings of the Soil Science of America, 29: 558-561.

HULBERT, L.C. (1955). Ecological Studies of Bromus tectsum and other annual brome grasses. Ecological Monographs, 37: 181-213.

HUNT, R. (1978). Plant Growth Analysis. Studies in Biology, No. 96. Edward Arnold, London. 67 pp.

HUNT, R. and BURNETT, J.A. (1973). The effects of light intensity and external potassium uptake in perennial ryegrass (Lolium perenne L.). Annals of Botany, London, 37: 519-537.

ISLAM, A. K. M. C., ASHER, C. J. and EDWARD, D. G. (1987). Response of plants to calcium concentration in flowing solution culture with chloride or sulphate as the counter-ion. Plant and Soil, 98: 377-395.

IVENS, G. W. and MLOWE, F. (1980). A Study of competition between gorse (Ulex europeanus L.) and perennial ryegrass (Lolium perenne L.) by means of replacement series experiments. Weed Research, 20: 181-191.

JACKMAN, R. H. (1965). The uptake of rubidium by roots of some graminaceous and leguminous plants. New Zealand Journal of Agricultural Research, 8: 763-777.

JAGER, A. de (1979). Localized stimulation of root growth and phosphate uptake in Zea mays L, resulting from restricted phosphate supply. In: J. L. Harley and R. S. Russell (eds.): The Soil Root Interface. Academic Press, London, pp391-403.

JEFFERIES, R. L., LAYCOCK, D., STEWART, G. R., and SIMS, A. P. (1969). The properties of mechanisms involved in uptake and utilization of calcium and potassium by plants in relation to an understanding of plant distribution. In: Ecological Aspects of the Mineral Nutrition of Plants. (Ed. I. H. Rorison), Blackwell, Oxford pp. 281-307.

JEFFERIES, R. L. and PERKINS, N. (1977). The effects on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk, Journal of Ecology, 65: 867-882.

JENSEN, P. and PETTERSSON, S. (1980). Varietal variation in uptake and utilization of potassium (rubidium) in high-salt seedlings of barley. Physiologia Plantarum, 48: 411-415.

JOHNSON, S. D. (1987). Nutritional aspects of crop-weed interaction with special reference to the effects of phosphorus on the competition between winter wheat (Triticum aestivum L. cv. Avalon), and Blackgrass (Alopecurus myosuroides Huds). Ph. D. Thesis, University of London.

JOHNSTON, L. P. V. (1935). General preliminary studies on the physiology of delayed germination in Avena fatua. Canadian Journal of Research. C-O, 13: 283-300.

JOLLIFFE, A., MINJAS, A. N. and RUNECKLES, V. C. (1984). A Reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology, 21: 227-243.

JOWETT, D. (1959). Adaptation of a lead-tolerant population of Agrostis tenuis to low soil fertility. Nature, London, 184: 43.

JOWETT, D. (1964). Population studies on lead-tolerant Agrostis tenuis. Evolution, 18: 70-80.

KING, L. J. (1966). Weeds of the World. Biology and Control. Leonard Hill, London, Interscience, New York, pp. 1-24.

KIRA, T., OGAWA, H. and SAKAZAKI, N. (1953). Intraspecific competition among higher plants. 1. Competition - density - yield inter-relationships in regularly dispersed populations. Journal of the Institute of Polytechnique, Osaka City University, D. 4. 1-16.

KLINGMAN, C., GLENN, and ASHTON, M. FLOYD., (1975). Weed Science: Principles and Practices. Wiley-Interscience Publication, New York, pp. 1-55.

KNIGHT, R. (1960). The growth of Dactylis glomerata L. under spaced and sward conditions. Australian Journal of Agricultural Research, 11: 457-472.

KOCH, W. (1967). Competition between crop plants and weeds. 2. Effect of annual weeds on cereals. Weed Research, 7: 22-28.

LAFEVER, H. N. (1981). Genetic differences in plant responses to soil nutrient stress. Journal of Plant Nutrition, 4: 89-109.

LAFEVER, H. N., CAMPBELL, L. G. and FOY, C. D. (1977). Differential response of wheat cultivars to aluminium. Agronomy Journal, 69: 563-568.

LARSEN, S. and SUTTON, C. D. (1963). The influence of soil volume on the absorption of soil phosphorus by plants and on the determination of labile soil phosphorus. Plant and Soil, 18: 77-84.

LATIES, G. G. (1969). Dual mechanisms of salt uptake in relation to compartmentation and long-distance transport. Annual Review of Plant Physiology, 20: 89-116.

LAUCHLI, A. (1984). Mechanisms of nutrient fluxes at membranes of root surface and their regulation in the whole plant. In: Roots, Nutrient and Water Influx, and Plant Growth, Ed. S. A. Barber and D. R. Boulding. ASA Spec., Publication No. 49. Madison, Wisconsin: American Society of Agronomy.

LAWTON, K. and DAVIS, J. F. (1956). The effects of liming on the utilization of soil and fertilizer phosphorus by several crops grown on acid organic soil. Soil Science Society of America, Proceedings, 20: 665-668.

LEE, R. B. (1982). Selectivity and kinetics of ion uptake by barley plants following nutrient deficiency. Annals of Botany: 50: 429-449.

LINDGREN, D.T., GABELMAN, W.H. and GERLOFF, G.C. (1977). Variability of phosphorus uptake and translocation in Phaseolus vulgaris L. under phosphorus stress. Journal of the American Society for Horticultural Science, 102: 674-677.

LONERAGAN, J.F. and ASHER, C.J. (1967). Response of plants to phosphate concentration in solution culture. II. Rate of phosphate absorption and its relation to growth. Soil Science: 103: 311-318.

LONERAGAN, J.F., GLADSTONE, J.S. and SIMMONS, W.J. (1968). Mineral elements in temperate crop and pasture plants. II. Calcium. Australian Journal of Agricultural Research, 19: 353-364.

LONG, H.C. (1910). Common weeds of the farm and garden. pp. 451. Smith, Elder, and Co., London.

LÜTTGE, U. and HIGINBOTHAM, N. (1979). Transport in Plants. Springer, New York, Heidelberg, Berlin. 468 pp.

LÜTTGE, U. and PITMAN, M.G. (1976). Transport and energy. In: Encyclopedia of Plant Physiology, New Series, 2A, edited by U. Lüttge and M.G. Pitman, pp. 251-259. Berlin: Springer-Verlag.

LYNESS, A.S. (1936). Varietal differences in the phosphate feeding capacity of plants. Plant Physiology, 11: 665-688.

McBEATH, D.K., DEW, D.A. and FRIESEN, H.A. (1970). Competition between barley and wild oats as affected by nitrogen, barban and time of seeding. Canadian Journal of Plant Science, 50: 541-550.

MacDONALD, I.R., DEKOCK, P.C. and KNIGHT, A.H. (1960). Variations in the mineral content of storage tissue disks maintained in tap water. Physiologia Plantarum, 13: 76-89.

MacDUFF, J.H. and WILD, A. (1986). Effects of temperature on parameters of root growth relevant to nutrient uptake. Measurements on oil seed rape and barley grown in flowing nutrient solution. Plant and Soil, 94: 321-332.

McGILCHRIST, C.A. and TRENBATH, B.R. (1971). A revised analysis of plant competition experiments. Biometrics, 29: 659-671.

McGRAW, B. JAMES. (1985). Experimental ecology of Dryas octopetala ecotypes: relative response to competitors. New Phytologist, 100: 233-241.

MACK, R. and HARPER, J.L. (1977). Interference in dune annuals: spatial pattern and neighbourhood effects. Journal of Ecology, 65: 345-363.

MAHMOUD, A. and GRIME, J.P. (1976). An analysis of competitive ability in three perennial grasses. New Phytologist, 77: 431-435.

MARINOS, N.G. (1962). Studies on submicroscopic aspects of mineral deficiencies. 1. Calcium deficiency in the shoot apex of barley. American Journal of Botany, 49: 834-841.

MARSCHNER, H. (1986). Ion uptake mechanisms of individual cells and roots: short-distance transport. In: Mineral Nutrition of Higher Plants. Ed. H. Marschner. Academic Press London. pp. 7-69.

MARTIN, M.P.L.D. and FIELD, R.J. (1984). The nature of competition between perennial ryegrass and white clover. Grass and Forage Science, 39: 247-253.

MARTIN, M.P.L.D. and FIELD, R.J. (1987). Competition between vegetative plants of wild oat (Avena fatua L.) and wheat (Triticum aestivum L.). Weed Research, 27: 119-124.

MARTIN, M. P. L. D. and FIELD, R. J. (1988). Influence of time of emergence of wild oat on competition with wheat. Weed Research, 28: 111-116.

MARTIN, M. P. L. D. and SNAYDON, R. W. (1982). Root and shoot interactions between barley and field beans when intercropped. Journal of Applied Ecology, 19: 263-272.

MATHER, K. (1961). Competition and co-operation. In: Mechanisms in biological competition. Society for Experimental Biology, Symposium, 15: 264-281. Cambridge University Press, Cambridge

MAY, L. H., CHAPMAN, F. H. and ASPINALL, D. (1965). Quantitative studies of root development. 1. The influence of nutrient concentration. Australian Journal of Biological Sciences, 18: 25-35.

MEAD, R. and RILEY, J. (1981). A review of statistical ideas relevant to intercropping research. Journal of the Royal Statistical Society, A144 (4): 462-509.

MENGESHA, M. H. (1966). Chemical composition of Teff (Eragrostis tef) compared with that of wheat, barley and grain sorghum. Economic Botany, 20: 268-273.

MERSIE, W. and PARKER, C. (1983). Response of teff (Eragrostis tef (Zucc.) Trotter) to 2, 4-D and MCPA at various growth stages. Weed Research, 23: 53-59.

MILNE, A. (1961). Definition of competition among animals. In: Mechanisms in Biological Competition. Society for Experimental Biology Symposium, 15: 40-61. Cambridge University Press, Cambridge.

MILTHORPE, F. L. (1961). The nature of analysis of competition between plants of different species. In: Mechanisms in Biological Competition. Symposium of the Society for Experimental Biology, No. 15 (Ed. by F. L. Milthorpe), pp. 330-355). Cambridge University Press, Cambridge.

MINOTTI, P.L. (1977). Differential response of tomato and lamb-quarter seedlings to potassium level. Journal of American Society of Horticultural Science, 102: 646-648.

MOLBERG, E.S. and LEGGETT, H.M. (1955). Cultural methods for wild oat control. Research Reprints 12th N. Cent Weed Control Conference 76.

MORSE, R. and PALMER, R. (1925). British Weeds: Their identification and control. Benn. London. 207 pp.

MULLER, C.H. (1970). Photoxins on plant habitat variables. Recent Advances in Phytochemistry, 3: 106-121.

MULLINS, G.L. and EDWARDS, J.H. (1988). Root trimming influence on elongation, development, and potassium influx of corn roots. Agronomy Journal, 80: 91-94.

MULLINS, G.L. and EDWARDS, J.H. (1989). A Comparison of two methods for measuring potassium influx kinetics by intact corn seedlings. Journal of Plant Nutrition, 12 (4): 485-496.

NAYLOR, R.E.L. (1972). The nature and consequence of interference by Alope curus myosuroides Huds. on the growth of winter wheat. Weed Research, 12: 137-143.

NELSON, D.C. and NYLUND, R.E. (1962). Competition between peas grown for processing and weeds. Weeds, 10: 224-229.

NEWMAN, E.I. (1966). A method of estimating the total lenght of roots in a sample. Journal of Applied Ecology, 3: 139-145.

NEWMAN, E. and ANDREWS, R.E. (1973). Uptake of phosphorus and potassium in relation to root growth and root density. Plant and Soil, 38: 49-69.

NIELSEN, N.E. and BARBER, S.A. (1978). Differences among genotypes of corn in the kinetics of P uptake. Agronomy Journal, 70: 695-698.

NIELSEN, N.F. and SCHJØRRING, J.K. (1983). Efficiency and kinetics of phosphorus uptake from soil by various barley genotypes. In: Genetic Aspects of Plant Nutrition. Developments in Plant and Soil Sciences. Ed. by M.R. Sarić and B.C. Loughman. 8: 145-150.

NIETO, J. Jr. and STANIFORTH, D.W. (1961). Corn-foxtail competition under various production conditions. Agronomy Journal, 53: 1-5.

NISSEN, P. (1971). Uptake of sulfate by roots and leaf slices of barley: Mediated by single, multiphasic mechanisms. Physiologia Plantarum, 24: 315-324.

NISSEN, P. (1973a). Kinetics of ion uptake in high plants. Physiologia Plantarum, 28: 113-120.

NISSEN, P. (1980). Multiphasic uptake of potassium by barley roots of low and high potassium content: Separate sites for uptake and transitions. Physiologia Plantarum, 48: 193-200.

NISSEN, P. (1983). Validity of the multiphasic concept of ion absorption in plants. Physiologia Plantarum, 57: 47-56.

NOGGLE, J.C. and FRIED, M. (1960). A kinetic analysis of phosphate absorption by excised roots of millet, barley and alfalfa. Soil Science Society of America: Proceedings, 24: 33-35.

NOLAN, T. and CONNOLLY, J. (1977). Mixed stocking of sheep and steers - a review. Herbage Abstracts, 47 (11): 367-374.

NOORDWIJK, M. VAN. (1983). Functional interpretation of root densities in the field for nutrient and water uptake. In: Wurzeloekologie und ihre Nutzanwendung/Root Ecology and its practical application, International Symposium Gumpenstein, 1982. pp. 207-26. Austria: Bundesanstalt Gumpenstein, Irdning.

NYE, P.H. (1977). The rate-limiting step in plant nutrient absorption from soil. Soil Science: 123: 292-297.

NYE, P.H. and FOSTER, W.N.M. (1958). A study of the mechanism of soil phosphate uptake in relation to plant species. Plant and Soil, 9: 338-351.

NYE, P.H. and TINKER, P.B. (1977). Solute Movement in the Soil-Root System. University of California Press, Berkeley. 342 pp.

OBEID, M. (1965). Experimental models in the study of interference in plant populations. Ph.D. Thesis, University of Wales.

OERTLI, J.J. (1967). The salt absorption isotherm. Physiologia Plantarum, 20: 1014-1026.

OLSEN, C. (1952). The significance of concentration for the rate of absorption by higher plants in water culture. Physiologia Plantarum, 3: 152-164.

ORSON, J.H. (1981). The control of Bromus sterilis in cereals with herbicides. Association of Applied Biologists Conference: Grass weeds in cereals in the United Kingdom, pp. 291-298.

PANDEY, H.N., MISRA, K.C. and MUKHERJEE, K.L. (1971). Phosphate uptake and its incorporation in some crop plants and their associated weeds. Annals of Botany, 35: 367-372.

PATTERSON, R.P, GRUMES, D.L. and LATHWELL, D.J. (1972). Influence of root-zone temperature and P supply on total and inorganic P, free sugars, aconitate and soluble amino N in corn. Crop Science, 12: 227-230.

PAVLYCHENKO, T.K. (1937). Quantative studies of the entire root systems of weed and crop plants, under field conditions. Ecology, 18: 62-79.

PAVLYCHENKO, T.K. and HARRINGTON, J.B. (1934). Competitive efficiency of weeds and crops. Canadian Journal of Research, 10: 77-94.

PHILLIPS, J.W., BARKER, D.E. and CLAGETT, C.O. (1971). Kinetics of P absorption by excised roots and leaves in corn hybrids. Agronomy Journal, 63: 517-520.

POLLARD, F. (1982). Light induced dormancy in Bromus sterilis. Journal of Applied Ecology, 19: 563-568.

POLLARD, F. and RICHARDSON, W.G. (1981). Chemical control of Bromus sterilis in winter wheat and barley. Association of Applied Biologists Conference: Grass weeds in cereals in the United Kingdom, pp. 273-281.

POOLE, R.J. (1978). Energy coupling of membrane transport. Annual Review of Plant Physiology, 29: 437-460.

QASEM, J.R.S. (1987). Fat-hen (Chenopodium album L.) and Groundsel (Senecio vulgaris L.) interference with certain vegetable crops, with special reference to nutrition. Ph.D. Thesis, University of London.

RABIDEAU, G.S., WHALEY, W.G. and HEIMSCH, C. (1950). The absorption and distribution of radioactive phosphorus in two maize inbreds and their hybrids. American Journal of Botany, 37: 93-99.

RACZ, G.J., RENNIE, D.A. and HUTCHEON, W.L. (1964). The 32 P injection method for studying the root system of wheat. Canadian Journal of Science, 44: 100-108.

RAMAKRISHNAN, P.S. (1968). Nutritional requirements of edaphic ecotypes in Melilotus alba (medic.). I. pH, Ca, and P. New Phytologist, 67: 145-157.

RAMAKRISHNAN, P.S. (1969). Nutritional factors influencing the distribution of the calcareous and acidic populations in Hypericum perforatum L. Canadian Journal of Botany, 47: 175-181.

RAPER, C.D. Jr. and BARBER, S.A. (1970). Rooting systems of soybeans. I. Differences in root morphology among varieties. Agronomy Journal, 62: 581-84. II. Physiological effectiveness as nutrient absorption surfaces. Agronomy Journal, 62: 585-588.

REMISON, S.U. and SNAYDON, R.W. (1980). A comparison of root competition and shoot competition between Dactylis glomerata and Holcus lanatus. Grass and Forage Science, 35: 183-187.

RENNIE, J.C. (1974). Some effects of competition and density of plants on dry weight produced. Annals of Botany, 38: 1003-1012.

RHODES, I. (1968). The growth and development of some grass species under competitive stress. 3. The nature of competitive stress and characters associated with competitive ability during seedling growth. Journal of the British Grassland Society, 23: 330-335.

RICE, E.L. (1984). Allelopathy. 2nd edition; Academic Press, London. 422 pp.

ROBINSON, P.J. and JONES, R.K. (1972). Effect of phosphorus and sulphur fertilization on the growth and distribution of dry matter, N, P, and S in Townsville Stylo (Stylosanthes humilis). Australian Journal of Agricultural Research: 23: 633-640.

RORISON, I.H. (1968). The response to phosphorus of some ecologically distinct plant species. 1. Growth rates and phosphorus absorption. New Phytologist, 67: 913-923.

RUSSELL, E.W. (1973). Soil Conditions and Plant Growth. Longman, London, 849 pp.

SAKAI, K. (1961). Competitive ability in plants. Its inheritance and some related problems. In: Mechanisms in Biological Competition. Symposium of Experimental Biology, 15: 245-263, Cambridge University Press, Cambridge.

SARIĆ, M.R. (1981). Genetic Specificity in relation to plant mineral nutrition. Journal of Plant Nutrition. 3: 743-766.

SAYRE, J.D. (1955). Mineral nutrition of corn and corn improvement. Sprague, G.F. Ed. pp. 293-294. Academic Press, New York.

SCOTT, R.S. and LOWTHER, W.L. (1980). Competition between White Clover 'Grasslands Huia' and Lotus pedunculatus 'Grasslands maku'. 1. Shoot and Root Competition. New Zealand Journal of Agricultural Research, 23: 501-507.

SEXSMITH, J.J. and PITTMAN, U.J. (1963). Effects of nitrogen and phosphorus fertilization on wild oats. Weeds, 11, 99-101.

SEXSMITH, J.J. and RUSSELL, G.C. (1963). Effects of nitrogen and phosphorus fertilization on wild oats and spring wheat. Canadian Journal of Plant Science, 43: 64-69.

SHEA, P.F., GABLEMAN, W.H. and GERLOFF, G.C. (1967). The inheritance of efficiency in potassium utilization in snap beans, (Phaseolus vulgaris L.). Proceedings of the American Society for Horticultural Science, 91: 286-293.

SHENK, M.K. and BARBER, S.A. (1980). Potassium and phosphorus uptake by corn genotypes in the field as influenced by root characteristics. Plant and Soil, 54: 65-76.

SHOCK, C.C. and WILLIAMS, W.A. (1989). Sulfate uptake kinetics of three annual range species. Agronomy Journal, 76: 35-40.

SHUKLA, U.C. and HANS RAJA. (1974). Influence of genetic variability on zinc response in wheat (Triticum spp). Soil Science Society of America: Proceedings, 38: 477-479.

SIDDIQI, M. Y. and GLASS, A. D. M. (1981). Utilization Index: A modified approach to the estimation of comparison of nutrient uitilization efficiency in plants. Journal of Plant Nutrition, 4: 289-302.

SILBERBUSH, M. and BARBER, S. A. (1984). Phosphorus and potassium uptake of field-grown soybean cultivars predicted by a simulation model. Soil Science Society of America Journal, 48: 592-596.

SINGH, B. N. and SINGH, L. B. (1939). Relative absorption of nutrients by weeds of arable land. Soil Science, 47: 227-235.

SMITH, R. J. Jr. (1967). Weed competition in rice. Weed Science, pp. 252-255.

SMITH, S. N. (1934). Response of inbred lines and crosses in maize to variations of N and P supplied as nutrients. Journal of American Society for Agronomy, 26: 785-804.

SNAYDON, R. W. (1971). An analysis of competition between plants of Trifolium repens populations collected from contrasting soils. Journal of Applied Ecology, 8: 687-698.

SNAYDON, R. W. (1979). A new technique for studying plant interactions. Journal of Applied Ecology, 16: 281-286.

SNAYDON, R. W. and BRADSHAW, A. D. (1961). Differential response to calcium within the species Festuca ovina L. New Phytologist, 60: 219-234.

SNAYDON, R. W. and BRADSHAW, A. D. (1962). Differences between natural populations of Trifolium repens L. in response to mineral nutrients. I. Phosphate. Journal of Experimental Botany, 13: 422-434.

SNAYDON, R. W. and BRADSHAW, A. D. (1969). Difference between natural populations of Trifolium repens L. in response to mineral nutrients. II. Calcium, magnesium and potassium. Journal of Applied Ecology, 6: 185-202.

SNAYDON, R. W. and HOWE, C. D. (1986). Root and shoot competition between established Ryegrass and invading grass seedlings. Journal of Applied Ecology: 23: 667-674.

SPANSWICK, R. M. (1981). Electrogenic ion pumps. Annual Review of Plant Physiology, 32: 267-289.

SPITTERS, C. J. T. (1983). An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. Netherlands Journal of Agricultural Science, 31: 1-11.

STANIFORTH, D. W. and WEBER, C. R. (1956). Effects of annual weeds on the growth and yield of soybeans. Agronomy Journal, 48: 467-471.

STEVENSON, D. S. (1967). Effective soil volume and its importance to root and top growth of plants. Canadian Journal of Soil Science, 47: 163-174.

TARAWALI, G. (1983). Nutritional aspects of the competition between crops and weeds with special reference to winter wheat (Triticum aestivum L. cv. Kaydor) and blackgrass (Alopecurus myosuroides Huds.) Ph. D. Thesis, University of London.

TENNANT, D. (1975). A test of a modified line intersect method of estimating root length. Journal of Ecology, 63: 995-1001.

THIEN, S. J. and McFEE, W. W. (1972). Effects of N on P transport system in Zea mays L. Soil Science Society of America, Proceedings, 36: 617-620.

THOMAS, P. E. and ALLISON, J. C. S. (1975). Comparison between maize and Rottboellia exaltata. Journal of Agricultural Science (Cambridge) 84: 305-312.

THOMAS, V. J. (1970). A mathematical approach to fitting parameters in a competition model. Journal of Applied Ecology, 7: 487-496.

THOMPSON, K. and GRIME, J. P. (1979). Seasonal variations in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology, 67: 893-921.

THURSTON, J. M. (1951a). Some experiments and field observations on the germination of wild oat (Avena fatua and A. ludoviciana) seed in soil and the emergence of seedlings. Annals of Applied Biology, 38: 812-832.

THURSTON, J. M. (1951b). A comparison of the growth of wild oat and of cultivated oat in manganese-deficient soils. Annals of Applied Biology, 38: 289-302.

THURSTON, J. M. (1954). A survey of wild oats (Avena fatua and A. ludoviciana in England and Wales in 1951. Annals of Applied Biology, 41: 619-636.

THURSTON, J. M. (1956). Wild oats. Journal of Agricultural Society, 117: 43-52.

THURSTON, J. M. (1959). A comparative study of the growth of wild oats (Avena fatua L.) and A. ludoviciana Dur.) and of cultivated cereals with varied nitrogen supply. Annals of Applied Biology, 47: 716-739.

THURSTON, J. M. (1961). The effect of depth of burying and frequency of cultivation on survival and germination of seeds of wild oats (Avena fatua L.) and Avena ludoviciana Dur.). Weed Research, 1: 19-31.

THURSTON, J.M. (1963). Biology and Control of wild oats. Reprints of Rothamsted Experimental Station, 1962. pp. 236-253.

THURSTON, J.M. (1971). Reprints of the Rothamsted Experimental Station, 1970, pp. 115-116.

THURSTON, J.M. (1972). Reprints of the Rothamsted Experimental Station, 1971, 1: 104-105.

THURSTON, J.M. (1982). Wild Oats as successful weeds. In: Biology and Ecology of Weeds, Geobotany 2. pp. 191-199. (ed.) W. Holzner and M. Numata. Junk Publisher, The Hague.

THURSTON, J.M. and PHILLIPSON, A. (1976). Distribution. In: Wild Oats in World Agriculture. Ed. D. Price Jones. pp. 19-64. Agricultural Research Council, London.

TONKIN, J.H.B. and PHILLIPSON, A. (1973). The presence of weed seeds in cereal seed drills in England and Wales during Spring 1970. Journal of the National Institute of Agricultural Botany, 13: 1-8.

TORII, K. and LATIES, G.G. (1966). Dual mechanisms of ion uptake in relation to vacuolation in corn roots. Plant Physiology, 41: 863-870.

TRENBATH, B.R. and HARPER, J.L. (1973). Neighbour effects in the genus Avena. 1. Comparison of crop species. Journal of Applied Ecology, 10: 379-400.

TROUGHTON, A. (1974). In: Structure and Function of Primary Root Tissues, Ed. J. Kolek, pp. 153-64, Bratislava, Veda.

TROUGHTON, A. and WHITTINGTON, W.J. (1969). The significance of genetic variation in root systems. In: Root Growth, Ed. Whittington, W.J., Butterworths, London, pp. 296-313.

TURNER, R.G. (1969). Heavy metal tolerance in plants. Ecological aspects of the mineral nutrition of plants. Ed. I.H. Rorison. Blackwell Scientific Publications, Oxford and Edinburgh, 399-410.

VANKEUREN, R.W. (1961). An evaluation of orchard grass strains grown alone and with alfalfa. Crop Science, 1: 411-415.

VENGRIS, J., COLBY, W.G. and DRAKE, M. (1955). Plant nutrient competition between weeds and corn. Agronomy Journal, 47: 213-216.

VENGRIS, J., DRAKE, M., COLBY, W.G. and BART, J. (1953). Chemical composition of weeds and accompanying crop plants. Agronomy Journal, 45: 213-218.

VOSE, P.B. (1962). Nutritional response and shoot/root ratio as factors in the composition and yield of genotypes of perennial ryegrass, Lolium perenne. Annals of Botany, 26: 425-437.

VOSE, P.B. (1963). Varietal differences in plant nutrition. Herbage Abstracts, 33: 1-13.

VOSE, P.B. (1984). Effects of genetic factors on nutritional requirements of plants. In: Crop Breeding - a Contemporary Basis. Ed. P.B. Vose and S.G. Blixt. Pergamon Press, UK (Oxford). pp. 67-114.

WARNCKE, D.D. and BARBER, S.A. (1974). Root development and nutrient uptake by corn grown in solution culture. Agronomy Journal, 66: 514-516.

WEISS, M.G. (1943). Inheritance and physiology of efficiency in iron utilization in soybeans. Genetics, 28: 253-268.

WELBANK, P.J. (1962). A study of nitrogen and water factors in competition with Agropyron repens (L.). Beauv. Annals of Botany, N.S. 25: 116-137.

WELBANK, P.J. (1963). A comparison of competitive effects of some common weed species. Annals of Applied Biology, 51: 107-125.

WELLS, G.N. (1979). Annual weed competition in wheat crops: the effect of weed density and applied nitrogen. Weed Research, 19: 185-191.

WHITE, R.E. (1972). Studies on mineral ion absorption by plants. 1. The absorption and utilization of phosphates by Stylosanthes humilis, Phaseolus atropurpureus and Desmodium intortum. Plant and Soil, 36: 427-447.

WHYBREW, J.E. (1964). The survival of wild oats (Avena fatua) under continuous spring barley growing. Proceedings of the 7th British Weed Control Conference, pp. 614-620.

WHYBREW, J.E. (1969). Wheat without ploughing. Agriculture, 76: 497-501.

WIERSUM, L.K. (1962). Uptake of N and P in relation to soil structure and nutrient mobility. Plant and Soil, 16: 62-70.

WILD, A., WOODHOUSE, P.J. and HOPPER, M.J. (1979). A comparison between the uptake of potassium by plants from solutions of constant potassium concentration and during depletion. Journal of Experimental Botany, 30 (117): 697-704.

WILLEY, R.W. (1979). Intercropping - Its importance and research needs. I. Competition and yield advantages. Field Crop Abstracts, 32: 2-10.

WILLEY, R.W. and HEATH, S.B. (1969). The quantitative relationships between plant population and crop yield. Advances in Agronomy, 21: 281-321.

WILLEY, R.W. and RAO, M.R. (1980). A competitive ratio for quantifying competition between intercrops. Experimental Agriculture, 16: 117-125.

WILLIAMS, R.F. (1948). The effects of phosphorus supply on the rates of intake of phosphorus and nitrogen upon certain aspects of phosphorus metabolism in graminaceous plants. Australian Journal of Science Research, Series B. 1: 333-361.

WILSON, B.J. and CUSSANS, G.W. (1972). The effects of autumn cultivations on the emergence of Avena fatua seedlings. Proceedings of the 11th British Weed Control Conference, pp. 234-241.

WILSON, H.P. and COLE, R.H. (1966). Morning glory competition in soybeans. Weeds, 14: 49-51.

WILSON, J.B. (1988). Shoot competition and root competition. Journal of Applied Ecology, 25: 279-296.

WIT, C.T. de. (1960). On competition. Verslagen van landbouwkundige onderzoekingen, 66 (8): 1-82.

WIT, C.T. de and GOUDRIAAN, J. (1974). Simulation of Ecology Processes. Centre for Agricultural Publishing and Documentation, Wageningen.

WIT, C.T. de, TOW, P.G. and ENNIK, G.C. (1966). Competition between legumes and grasses. Verslagen van landbouwkundige onderzoekingen 687: 3-30.

WIT, C.T. de. and VAN DEN BERGH, J.P. (1965). Competition between herbage plants. Netherlands Journal of Agricultural Science, 13: 212-221.

WOODHOUSE, P.J., WILD, A. and CLEMENT, C.R. (1978). Rate of uptake of potassium by three crop species in relation to growth. Journal of Experimental Botany, 29: 885-894.

WRIGHT, A.J. (1981). The analysis of yield-density relationship in binary mixtures using inverse polynomials. Journal of Agricultural Science, 96: 561-567.

YORKE, J.S. and SAGAR, G.R. (1970). Distribution of secondary root growth potential in the root system of Pisum sativum. Canadian Journal of Botany, 48: 699-704.

ZIMDAHL, R.L. (1980). Weed-Crop Competition. A Review. International Plant Protection Centre, Oregon State University, Corvallis, Oregon. 196 pp.

ADDENDA

BROUWER, R. (1962). Distribution of dry matter in plant. Netherlands Journal of Agricultural Science **10**: 361-376.

EPSTEIN, E. and JEFFERIES, R.L. (1964). The genetic basis of selective ion transport in plants. Annual Reviews of Plant Physiology **15**: 169-184.

JEFFREY, D.W. (1964). The formation of polyphosphate in Bankissia ornata, an Australian heath plant. Australian Journal of Biological Science **17**: 875-854.

KOCK, W. and KOCHER, H. (1968). The significance of nutrient factor on the competition between crop plants and weeks. Z. Pflkrankh. Pflpath. pflschutz. (Sonderh. 4) 79-87.

PAWLIK, A. (1957). Investigations on the growth of some agricultural weeds in water culture with particular reference to the effect of boron. Diss. Landw. Hochsch. Hohenkeim. pp. 65.

SINYAGIN, I.I. (1966). Biological grouping of weeds according to their relations to mineral fertilizer. Agrokhimiya **3**(9): 11-17.

WEISE, A.F. (1968). Rate of weed root elongation. Weed Science **61**: 11-13.

WILLIAMSON, M.H. (1972). The Analysis of Biological Populations. Edward Arnold, London.