AN AGRO-ECOLOGICAL STUDY OF ARRHENATHERUM ELATIUS

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ABSTRACT

The perennial grass, *Arrhenatherum elatius* has two extreme varieties: Onion Couch, a form which produces bulbous swollen internodes, and Tall Oat-grass which is non-bulbous. The Onion Couch variety is a weed of arable land on medium textured soils whilst the Tall Oat-grass is not. The work reported in this thesis describes the factors responsible for the success of one of the varieties as an arable weed, and gives an assessment of its weedy attributes and some measures for its effective control.

The approach adopted to study the agro-ecology of the species consisted mainly of two stages. In the first stage, surveys and experiments were performed in which comparative studies of the distribution, morphology, competitive status, regenerative capacity of both varieties were investigated to determine which attributes make the Onion Couch variety a successful weed of arable land.

In the second stage of the work, complimentary experiments and field observations were carried out to examine the factors governing the regrowth of the vegetative propagules of Onion Couch and the manner in which they affect crop yield in naturally occurring infestations. The population growth characteristics and an assessment of the measures for control under different management regimes were also highlighted with the help of a structured simulation model.

Finally, the ecological status of Onion Couch as a weed of arable land was assessed in the light of the results obtained from experiments, observations and the simulations.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Arrhenatherum elatius

Arrhenatherum elatius (L.) Beauv. ex J. and C. Presl, or the common Tall Oat-grass is a perennial grass of hedgerows and some grasslands. On account of its tufted habit, tall growth form, rapid establishment, and attainment of full development within a year after seeding it is sometimes used for leys of short duration, and particularly, for hay production. The internodes at the base of the stems of Tall Oat-grass are often thickened or slightly bulbous. A variety of A. elatius var. bulbosum (Willd.) Spenner (A.tuberosum (Gilib.) F.W. Schult) or 'Onion Couch' produces internodes which are extremely thickened, forming chains of bulbs. These bulbs are an efficient means of propagation in arable fields, where it can be a troublesome weed. The two varieties of Arrhenatherum are not found together in nature; Onion Couch succeeds as an arable weed, where it propagates vegetatively and thrives under arable systems, whereas Tall Oat-grass is prevalent in grassland of mesotrophic or neutral soils. The two varieties of Arrhenatherum can, however, interbreed freely and it has been shown (Jenkin, 1931) that Onion Couch is an extreme member of a complete series in Arrhenatherum, ranging from non-bulbous to extremly bulbous forms.

Related ecological forms, either within one species or between closely related species, have often provided interesting material for comparative studies, especially in investigating the adaptive significance of the life strategies of the forms (Cooper and Saeed, 1949; Sarukhan and Harper, 1973). It seems that the success of the two varieties of *Arrhenatherum* in their habitats depends on their reaction to the environmental factors operative in their respective habitats. The two varieties of *Arrhenatherum* provide interesting material to investigate the genetic and ecological basis of their morphological and physiological differences. It is of considerable interest not only from the purely ecological standpoint, in indicating the lines along which evolutionary changes may have taken place in adapting to their habitats, but also from the agricultural stand point, in exploring the efficiency of attributes which make Onion Couch a successful weed of arable land.

1.2 The rationale of agro-ecological studies

Variety and race formation is a common phenomenon in many species and is influenced by the amount and nature of genetic variation stored with in a species (Harlan, 1982). Pfitzenmeyer (1959) desribed *Arrhenatherum* as a species carrying with it a wealth of genetic variability and recommends that these genetic variations of the species should be carefully looked into by scientists and agriculturalists. In the present studies it was considered that the two varieties of *Arrhenatherum* representing the two extremes of genetic variability would provide good material to investigate the significance of genetic variation and adaptation. In addition, it has been recommended by several weed scientists (Ammon, 1979; Mortimer, 1985; Schreiber, 1982) that a thorough understanding of the biology of a species to be controlled is an essential ingredient of any control strategy. Since the two varieties of *Arrhenatherum* under study freely interbreed, it was considered essential that the work reported here should be based on investigations into the species as a whole, rather than restricting it to the variety which is a weed.

1.3 The agricultural significance of Arrhenatherum

Recent reports of the expansion of Arrhenatherum could become a matter of great concern for the agriculturalists; Onion Couch, like some other perennial grass weeds tends to increase under a reduced cultivation regime (Pierce, 1984). In addition, the expansion of Tall Oat-grass due to reduced grazing and increase in nutrient status due to fertilizer application and resultant runoff, has allowed Tall Oat-grass to grow and assume dominance, especially within areas of intensive arable agriculture (NCC,1982, Lloyd,1973b). This poses a potential threat to arable areas because such communities might act as reservoirs in hedgerows, providing for incursion of the Onion Couch variety which thrives under arable systems.

It is notable that despite its notoriety as a weed of considerable local importance, there has been remarkably few detailed agro-ecological studies. The reported (Ayres, 1985; Pierce, 1984) high variability in the results of control measures in arable infestations of Onion Couch and the spread of Onion Couch with change in pattern of cropping and other agricultural practices, clearly indicates the presence of gaps in knowledge of the biology of Onion Couch.

1.4 Aims of this work

The work was planned in such a way as to take account of the importance of knowing which attributes of the two varieties of Arrhenatherum were responsible for the existence of one of the varieties as a weed and the other as a successful dominant in grassland. In other words, studies were made to gain an appreciation of the diversification of adaptive strategies of the two varieties in response to selective forces imposed by their environments. It was planned to meet this objective: by studying the growth and development of the two varieties, by identifying physiological and morphological differences inherent in them, and by studying the strength of the sources and sinks of reproductive structures in response to their environments.

In a well managed field, the crop has been shown (Spitters and Van Den Bergh, 1982; Cussans, 1968) to be an aggressive competitor, suppressing all aspects of the growth and development of associated weeds. In spite of this, weeds are known to reduce crop yield (Cussans, 1970) because they compete with the crop for nutrients, water and light. In order to detect any harmful aspect of the two varieties on crop yield and also the reciprocal affect of the crop on the two varieties of Arrhenatherum, competition studies between the two varities of Arrhenatherum and a crop are given special emphasis. It was intended that the experiments would not only provide a greater understanding of the biology and agro-ecology of the species as a whole but also an insight into the competitive relationship between the two varieties of Arrhenatherum themselves and with a crop.

It has been emphasized (Sagar and Mortimer, 1976) that data on population biology is essential to understand the dynamic behaviour of a weed population. The recent trend in the objectives of weed-crop control has also shifted towards assessing weed control in relation to a quantity damage function (Mortimer, 1984). Attention towards this aspect of weed control interaction has been described (Mortimer, 1984 and 1985; Glauninger and Holzner, 1982) as more realistic, not only from the economic, but also from the ecological viewpoint, especially concerning intractable weeds. The ecological and economic basis of this approach lies in the fact that it would incorporate interactions between the intrinsic regulatory mechanism in the weed population and weed control measures; involving mechanical means or crop husbandary refined and integrated with the use of herbicides.

Onion Couch can be regarded as an intractable weed as it has always been claimed as a weed difficult to erradicate on certain soils (Underwood, 1912; Armstrong, 1948; Pierce, 1984; Ayres, 1985). It seems that the intractable nature of Onion Couch infestations stems from a lack of knowledge of its pattern of growth and spread in an arable system, or some other facet of the agro-ecology of Onion Couch.

Keeping the comments made in the previous paragraph in mind, it was thought essential to plan field observations to monitor the growth and development of Onion Couch in natural infestations during the crop growth cycle, in order to identify components of Onion Couch yield and their response to interference from the crop and management systems, and to assess the recurrence of damage to a future cropping cycle from the resulting vegetative propagules. In addition, the direct effect in terms of yield loss of the current crop would be asessed and compared with artificially planted plots to appreciate the quantity of damage in the two situations.

The present day agricultural industry uses modelling techniques for every aspect of studying how systems work and interact. It was hoped in this study to develop a structured model (e.g. Fawcett, 1983) based on the system analyses/simulation modelling approach (Norton, 1979, 1980). The proposed model would demonstrate and predict the potential of Onion Couch based on the reproductive capability of a limited population, encompassing its inherent physiological and morphological pattern in response to agricultural practices (crop husbundary and control measures).

The success of a perennial weed in arable land is considered (Barrett, 1982; Hakansson, 1983; and Leakey, 1984) to be determined by its ability to take advantage of agricultural operations, by strategies of spread and incursions into new territory and by the efficiency of regeneration of vegetative propagules. Consequently, an attempt would be made to compare such weedy attributes as they might exist in Onion Couch with a more common and notorious perennial grass weed, Elymus repens.

The thesis is written in seven chapters:

Chapter 2 includes a review of the existing knowledge based on the distribution, morphology and biology of the two varieties of Arrhenatherum. A survey dealing with the distribution of the two varieties of Arrhenatherum in farming areas, and a survey conducted to plan the experiments needed to fill the gaps in information about the agro-ecology of the species are reported.

Chapter 3 consists of the results of the experimental work carried out in controlled and semi-controlled conditions with the object of understanding ecologically important responses, identifying morphological attributes capable of surviving the arable system and also to study the interaction between the two varieties in order to understand the selective forces operating in their respective habitats.

Chapter 4 examines the performance of Onion Couch during the crop growth cycle in natural infestations and also assesses the concept of damage to crop yield by Onion Couch in these natural infestations.

Chapter 5 applies a structured modelling approach in a preliminary way to the control of Onion Couch under different management systems.

Chapter 6 is a general discussion and evaluation of the status of Onion Couch as a weed and its control in arable systems is reviewed in the light of this work.

The final Chapter is based on the summmary of this work.

CHAPTER 2

THE BIOLOGY AND ECOLOGY OF ARRHENATHERUM ELATIUS

2.1 Introduction

This chapter describes the biology and ecology of Arrhenatherum elatius and also identifies the range of attributes which confer the ability on the Onion Couch variety to succeed as a weed of arable land. This chapter describes, what is known of the biology, agro-ecology and distribution of Arrhenatherum by referring to the literature and by survey and observations to evaluate the pattern of distribution of the two varieties, their possible interactions and the status of Onion Couch (from the farmer's point of view) as a weed of economic importance. It was intended that such studies would help in planning the experiments needed to fill any gap in the knowledge of the biology of the species. Realizing the practical importance of distinguishing between the Onion Couch variety of Arrhenatherum elatius and the species Arrhenatherum elatius as a whole (Tall Oat-grass) for this work, the topic of the Onion Couch variety is dealt with separately.

2.2 Terminology

Arrhenatherum elatius (L.) J & C. Presl. is a moderately tall (50-150cm), loosely tufted, perennial coarse grass of bitter foliage. Its roots are deeply penetrating and of chrome-yellow colour. The basal nodes of culms are often thickened, or bulbous, and sometimes coloured like the roots (Armstrong, 1948). The main features of its vegetative morphology are shown in Fig.2.1. Onion Couch is identical in most morphological characteristics to Tall

Oat-grass except that at the base of its stems the adjacent nodes are swollen and form chains of bulbs.

The terminology adopted for naming the extreme varieties in this thesis is as follows:

1. The extremely bulbous form of arable situations is referred to as 'Onion Couch'.
2. The less bulbous form of grassland situations is referred to as 'Tall Oat-grass'
3. Arrhenatherum is used when both forms are encompassed.

The following terminology has been adopted for describing the perennating organs (shoot bases) of the two varieties of Arrhenatherum. The adjacent internodes on the shoot bases of both varieties of Arrhenatherum may number from two to five and each bud on the nodes is capable of acting as a regenerating organ on separation at the nodes. Natural abscission of these nodes at the shoot base is not possible without damage, therefore a single shoot base (Fig. 2.1) comprised of three internodes (the most frequently encountered number) is described here as a 'single ramet', and a connected group of single ramets is described as an 'aggregate'. In addition, since single ramets and aggregates of Onion Couch also act as vegetative propagules, the term 'vegetative propagule' is used when referring to single ramets or aggregates of Onion Couch.

2.3 Polymorphism in Arrhenatherum elatius

Pfitzenmeyer (1959) has described the growth and development of Arrhenatherum elatius in detail. According to Pfitzenmeyer (1959), tillering is a means of perennation rather than propagation and is

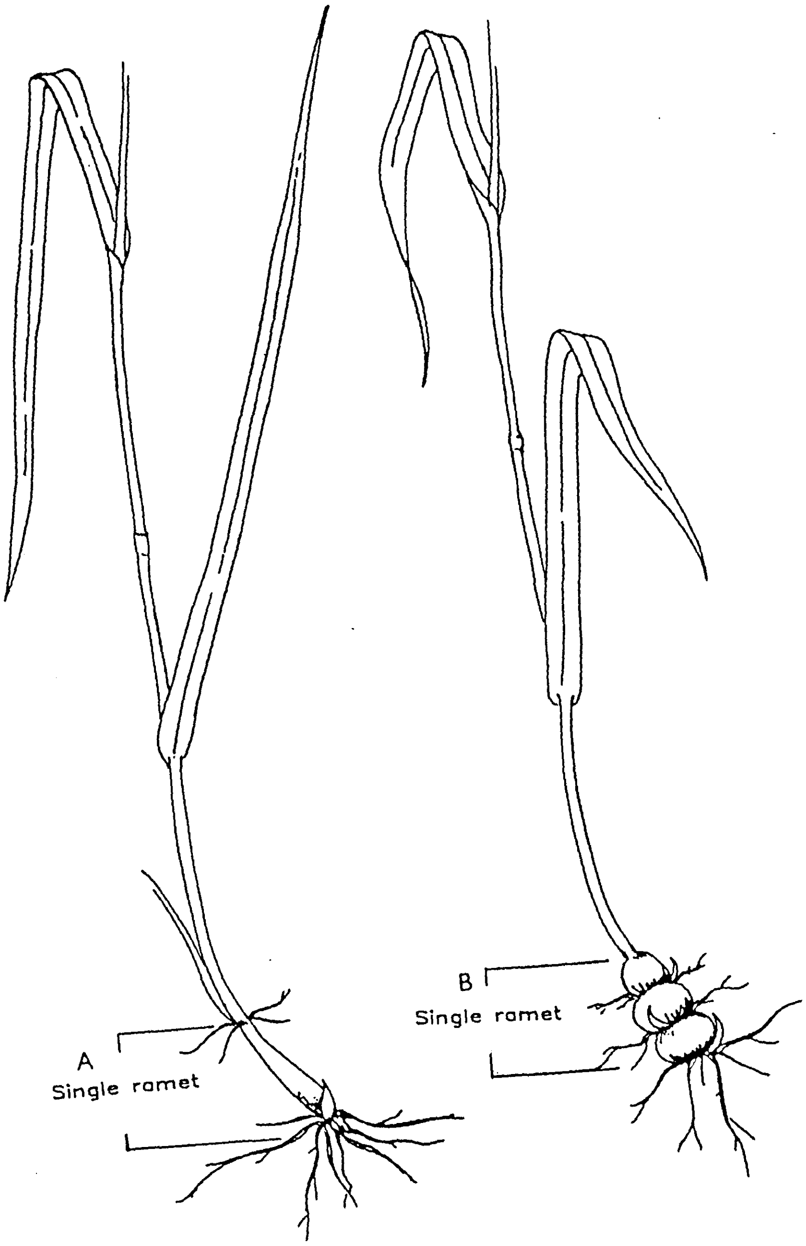


Fig. 2.1 Arrhenatherum elatius (L.) J. &. C. Presl.

Tall Oat-grass (A)

Onion Couch (B)

of much less importance than sexual reproduction for the spread of the species and seeds can germinate as soon as they ripen. He described most of the plants as caespitose, though very occasionally a rhizome could be produced 30cm or so away from the old tussock. Tillers are produced from axillary buds situated at the base of the old shoot, sometimes below ground level, and the capacity of the plant to produce tillers is dependent on the numbers of axillary buds developing into new shoots, in other words, on the number of bud bearing basal internodes (Pfitzenmeyer, 1959). The species is considered to be polymorphic and this variation depends to a considerable extent on the habitat as well as genetic constitution. Polymorphism in Arrhenatherum elatius takes the form of continuous variation in (a) tiller and leaf number and (b) bulbosity of the basal internodes. In the first (a) associated range of morphologies, the extremes are represented by erect and prostrate plants. Prostrate plants possess a greater number of basal iternodes compared to erect forms and thus have a better chance of regrowth after being cut or grazed (Pfitzenmeyer, 1959). It is suggested that these morphologies are genetic in origin and are retained under a variety of environmental conditions (Mahmoud, Grime and Furness; 1975). In the second (b) range of morphologies, the short basal internodes of the culms are bulbous or pear shaped in varying degrees. The bulbs may number from 2 to 5 in adjacent internodes. The bulbous extreme or Onion Couch has usually been regarded as forming a separate variety but this classification is no longer held to be valid, since it interbreeds freely with other forms and all intermediates between the two extremes can be found (Jenkin, 1931). Jenkin (1931) studied the genetic transmission of the bulbous character and came to the conclusion that the non-bulbous form only corresponds to one extreme in a large range of variation in bulbosity and appears in plants homozygous for all the loci involved (an instance of quantitative inheritance). Darmency and Gesquez (1977) made an attempt to divide the populations of Tall Oat-grass and Onion Couch on the basis of soluble proteins of the leaves and the tubers but failed to separate the two varieties on those bases.

2.4 Distribution, phytosociology, habitats and competitive ability of Tall Oat-grass in grassland.

Phytosociology

Arrhenatherum elatius (L.) beauv. J. and C. Presl is distributed throughout Europe and W. Asia and has been introduced into N. America, Australia and New Zealand (Hubbard,1984). It is common in all parts of Britain and has been reported in every county (Clapham, Tutin and Warburg, 1957). The distribution of Arrhenatherum elatius in the British Isles is shown in Fig. 2.2. According to Pfitzenmeyer (1959) the limits to the distribution of the species are governed more by climatic than by pedological or edaphic factors and are mainly under the influence of latitude and altitude.

The Nature Conservancy Council's (NCC, 1982) report on the National Vegetation Classification of mesotrophic grasslands) has recognised two communities as Arrhenatherum elatius grassland. The two communities are very clearly marked off by the constant presence and frequent dominance of Arrhenatherum elatius, the prominence of coarse Molinio-Arrhenathereta grasses such as Holcus lanatus, Dactylis glomerata and strongly preferential occurrence of tall herbs. The report states that these two communities are British

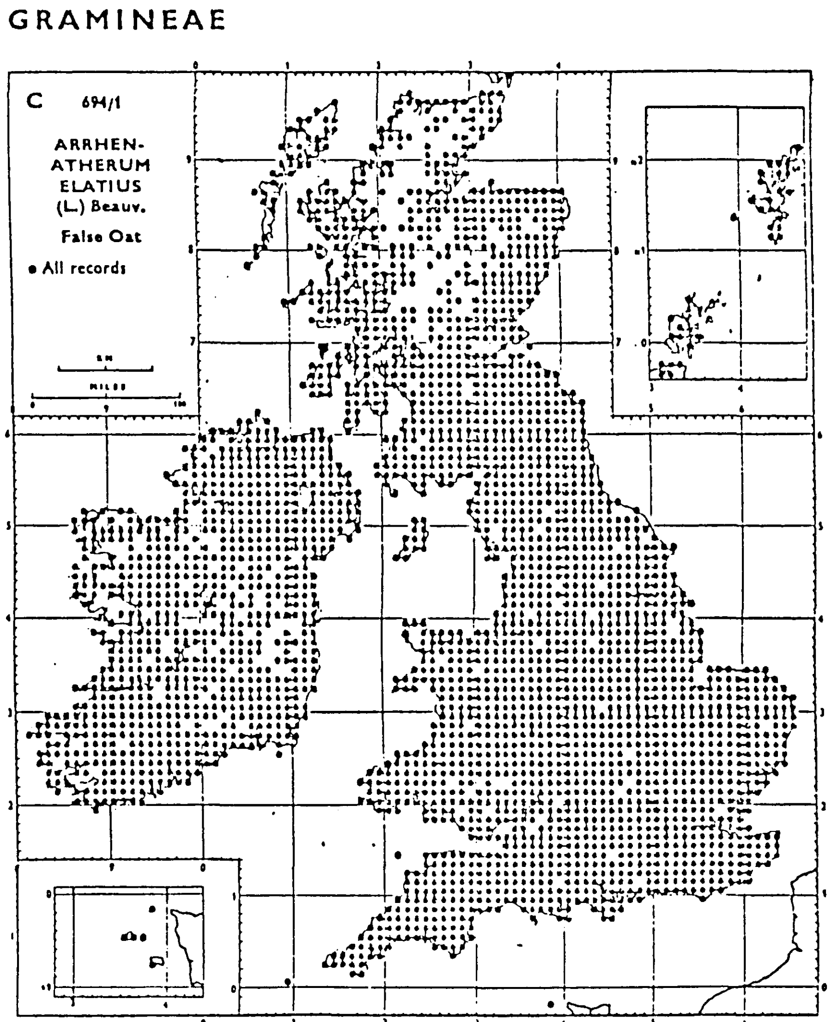


Fig. 2.2 The distribution of Arrhenatherum elatius in the British Isles. Each dot represents atleast one record in a 10 KM square of the National Grid. (after Perring and Walters, 1982).

representatives of Arrhenatheretum elatoris, an alliance of coarse tussocky swards dominated by Arrhenatherum elatius on freely draining mesotrophic to eutrotrophic soils. The two communities recognised are as follows:

1. Arrhenatherum elatius coarse grassland: The bulk of the vegetation of this kind has been included here in a single large and rather variable community, which includes some richer types as well as including the very widespread, more species poor Arrhenatherum elatius vegetation common on road-side verges.

2. Filipendula ulmaria-Arrhenatherum elatius tall herb grassland: This community is confined to sheltered localities in northern England, almost exclusively on carboniferous limestone. Although clearly related to mainstream Arrhenatheretum, this community also shows some affinity with the field layers of woodland.

Habitat of Tall Oat-grass

Tall Oat-grass thrives best on ungrazed grassland and is characteristic of circumneutral soils throughout the British lowlands and occurs on road verges, railways embankments, church yards and in neglected agricultural and industrial habitats such as badly managed pastures and meadows, building sites, disused quarries and rubbish dumps. According to Pfitzenmeyer (1960), Tall Oat-grass grasslands are conspicuous in continental Europe and have been recognized to be characteristic of deep, often moist, near neutral soils which are regularly manured and cut for hay. Armstrong (1948) recommended Tall Oat-grass for leys of shorter duration than long duration leys, due to the duration and persistence of the species.

The N.C.C's report (1982) on Natural vegetation indicates that the key factor in the development of Arrhenatheretum on otherwise suitable sites is the absence or irregularity of grazing, amount of nutrients (N, P and K) and drainage. In the absence of mowing and grazing, stands of the community are rapidly invaded by shrubs and in such cases the Arrhenatheretum is a temporary stage in the succession to shrub and woodland. The Arrhenatheretum is sustained and maintained in the absence of grazing by regular but infrequent cutting (Roadside verges). The recent process of expansion of Tall Oat-grass has been also associated with the advent of myxamatosis and the gradual transition to intensive methods of stock production which has brought about a relaxation of grazing on many marginal grassland areas (Lloyd, 1973b). Fertilisation of improved meadows with subsequent lack of grazing may thus also account for some neutral stands of Arrhenatheretum. Verges and ditches in areas of intensive arable agriculture are frequently enriched with the mineral nutrients N,P and K in a somewhat raw fashion by runoff and ground water from fields and such communities are especially frequent in areas of intensive arable agriculture (NCC, 1982). These communities are of special interest, because Tall Oat-grass growing in hedgerows and field borders might provide a seed source for the bulbous form (Onion Couch) which is found in the arable land.

The Competitive ability of Tall Oat-grass in a grassland situation

Tall Oat-grass is an indicator of good to moderate water supply and of nutrient rich soils where it act as a strong competitor, as has been shown in competition experiments conducted by Shariffi (1978), Salinger and Borkamm (1982) and Strehlow et al, 1982. Investigation by Grime and Curtis (1976) also suggests that Tall Oat-grass is vulnerable to desiccation under conditions in which seedling growth and in particular root penetration is limited by deficiency of P and N. Tall Oat-grass is one of the few grasses which are capable of attaining co-dominant status with strongly competitive dicots and thus suppresses the yield of smaller and slow growing species, as demonstrated by Mahmoud and Grime (1976) and Grubb (1982). It has also been described as very susceptible to metal toxicity (Mahmoud and Grime, 1977). Grime (1973) suggested that if the growth of the larger species like Tall Oat-grass remained unchecked, a process of exclusion could occur and this may eventually result in the development of a monoculture or a near monoculture. He suggests that here the dominant species owe their dominance to relatively undisturbed conditions which allow them to: 1) attain a large standing crop during the period June to August, 2) move photosynthate in to large storage organs which provide the impetus for expansion of growth in the next growing season and 3) accumulate large quantities of persistant litter which prevent incursions of species with complimentary phenologies.

2.5 Distribution, severity of infestation and weedy attributes of Onion Couch

Distribution

Onion Couch is regarded in some parts of Portugal and France as an important grass weed of arable land (Ribeiro, 1978; Barralis, 1961), It has also been reported on light sandy soils in East Frisia (Germany) as an introduced weed (Richter and Brederlow, 1970) and as a naturalised weed in Australia (Lamp and Collet, 1983) and South

America (Little, 1967). It occurs spasmodically throughout Britain, and it is regarded as a weed of some importance in arable fields in the South West, particularly on chalk loam and clay loam with flint.

Incidence and severity of Onion Couch infestation.

A survey of arable grass weeds in central and southern England (Froud-Williams and Chancellor, 1982; Chancellor and Froud-Williams,1983) and north east of Scotland (Scragg and Kilgour, 1984), does not show any significant increasing trend in percentage of fields affected by Onion Couch. It is not one of the most serious weeds of the British isles but recent concern suggests that it is becoming more important with the advent of minimum tillage like other perennial grasses (G. Cussans, personal communication). According to P. Attwood (personal communication) Onion Couch first became apparent in the south east region about ten years ago and was soon found to be a problem on a field scale (whole field infestation) rather than just a patchy nuisance in the south west region. A recent article by Pierce (1984) shows an increasing concern about the species which is now being taken seriously by commercial companies and advisory services and researchers. Pierce (1984) further suggested that, in addition to minimum tillage, another factor that favours the growth and spread of Onion Couch is the shift from spring cereals to winter corn and the poor leys. According to E. Scragg (personal communication), the weed was extremely common in North East Scotland in the days of shallow ploughing by horse drawn implements but deeper ploughing made possible by the introduction of tractors and the vigour of present day barley crops compared with the much lower yielding oat crops formerly grown in that region has brought about a decline in the weed.

Weedy attributes of Onion Couch

Unlike the Tall Oat-grass of natural communities, very little literature is available on the biology and agro-ecology of Onion Couch. Few papers available have dealt with the performance of the vegetative propogules of Onion Couch in an arable system. It is described (Underwood, 1912; Armstrong, 1948) as a dangerous weed on the arable land, as the chains of bulbs formed at the shoot bases are capable of breaking off and giving rise to new plants. LeClerch (1977) described that a splitting of the chains of bulbs into individual bulbs enhances the vegetative reproduction and the vegetative propagules of Onion Couch when burried remain viable for two years. Richter and Brederlow (1970) described the vegetative propagule as exceedingly tenacious and could produce regrowth even after eight weeks of subjection under dry conditions to exposure and burial. They also reported that the vegetative propagules of Onion Couch possess the capability of regenerating even when ploughed to a depth of 30cm. Ayres (1977, 1981, 1985) working on the control of Onion Couch provides some factual evidence on the relative rate of growth under a range of cultivation regimes and herbicides. His experiment with seedlings showed that ingress of Onion Couch by seeds in arable land may not be a problem as cultural and chemical treatment can control the seedling population. His experiment with the germination also demonstrated the heterozygous nature of the seeds (resulting from interbreeding with the more widespread Tall Oat-grass variety). The evidence thus suggests that at least some of the 'weedy attributes' of Onion Couch are related to its capacity to produce bulbs.

2.6 Surveys of some farms with affected fields

Introduction and method

Because little information was available about the agro-ecology of Onion Couch through published work and the survey data on Onion Couch infestations were also very limited (Pierce, 1984) and with the increasing concern about its becoming more widespread, two small scale surveys were conducted with the intention that it might highlight the research that needs to be done. The first survey (1984) was conducted by post with the ADAS offices in England regarding the occurrences of Onion Couch as a weed in crop situations and Tall Oat-grass in the hedgerows. The second survey (1984-85) was based on a postal questionnaire (Table 2.1) and interviews with farmers who had some fields infested with Onion Couch, their addresses being provided by agricultural merchants, ADAS offices and by farmers. The questionnaire was aimed at identifying and understanding the problem of history of incidence, management system, soil texture and the effectiveness of the control methods adopted.

Results and Discussion

The results (Table. 2.2 and 2.3), although based on very small scale surveys conveyed the basic information needed about the distribution of Arrhenatherum. It is clear from the results that the cosmopolitan presence of Tall Oat-grass in hedgerows and field borders might not always provide a seed source for the Onion Couch, which unlike Tall Oat-grass was found to be very localised and infrequent in its distribution. Onion Couch seems to be reported on all soils ranging from chalk loams and other light soils where it

1. History of the affected field.

a) Number of farms affected in the field.

b) Duration of infestation (recent or always)

c) Pattern of its distribution (Patchy or whole field)

d) Weedy attributes of Onion couch in terms of: yield loss, poor tilth and harvesting difficulties.

e) Soil texture and other characteristics of the field.

2. Agricultural practices.

a) Type of tillage pratices (direct drilling, mouldboard, shallow or deep tyne, etc.)

b) Type and kind of crop.

c) Annual yield.

3. Methods of control.

a) Cultural practices.

b) Chemical control (timing of application and frequency)

c) Effectiveness of control measures (satisfactory or unsatisfactory).

Table 2.1 Showing the outline of the questionnaire

Areas	Presence of Tall Oat-grass in hedgerows	Presence of Onion Couch in arable land	Soil Type
Ncrthen regions			
Cumbria:			
Carlisle area	infrequent	nil	
Cockermouth	infrequent	nil	
Kendal area	frequent	infrequent	
Northumberland:			
N.Northumberland	infrequent	infrequent*	
S.Northumberland	frequent	infrequent	
Tyne and wear	frequent	infrequent	
Durham:			
N.Durham	infrequent	infrequent	heavy to
S.Durham	infrequent	infrequent	medium
Cleveland	frequent	infrequent*	textured
Barnard castle	nil	nil	soils
N.Yorkshire:			
Northallerton	infrequent	infrequent	
Harrogate	frequent	infrequent	
Skipton	infrequent	nil	
S.Yorkshire and Humberside:			
Mirfield area	infrequent	nil	
Pontefract area	infrequent	infrequent	
Beverley	infrequent	infrequent	
Midland region			
Wolverhampton	frequent	nil	
Lancaster	frequent	infrequent	
Derby	frequent	infrequent*	light soils
Oakham	frequent	infrequent	Boulder
Leicester	frequent	infrequent*	clays
South west England			
Devon	frequent	infrequent*	
Salisbury	frequent	infrequent*	chalk down
Winchester	frequent	infrequent*	or brashy
Central Southern England:			soils
Berkshire	frequent	infrequent*	heavy chalk
Wiltshire	frequent	infrequent*	soils and
N.Oxfordshire	frequent	infrequent*	clay loam
Buckinghamshire	frequent	infrequent	with flint

* areas where above average incidence of Onion Couch has been noted.

Table 2.2 Occurrence of Tall Oat-grass and Onion Couch in arable areas.

spreads more, to medium loams and boulder clays, but does not seem to be occurring on heavy clay soils. The surveys also suggested that Onion Couch infestation is a problem on fields where it always occurred and there is no incidence of its spread to the adjacent farms in spite of the fact that it is capable of propagating both by seed and vegetative bulbs. This pattern of infestation (patchy) in the field and inefficient dispersal to the adjacent field could be due to the fact that the main propagating units of dispersal are the vegetative propagule rather than the seeds (which are more mobile and can spread further afield in a shorter period of time). The inefficiency of the dispersal of the plant by seeds seems to be also due to, as Ayres (1977) suggested, the susceptibility of seedlings to agricultural practices.

The history of occurrence of Onion Couch in some farms seemed to be long, whereas in others it seems rather recent and one of the farmers strongly believed that Onion Couch in his farm started with the advent of winter cereals. Most of the field surveyed were cultivated. Some of the farmers seems to be very much satisfied by the performance of Roundup. Others were disappointed with the results, as according to them pre-harvest treatment is not very effective as the plants have insufficient green leaf at that time (by normal application dates) and post harvest treatment was also ineffectve because slow and limited regrowth make the foliar active herbicide inefficient. Fallow is regarded by most of the farmers as costly and can finish up with a bad control and in a wet summer one can finish with more than one started with.

Farm location	No. of fields infested in the farm	Pattern of distribution in the field	Duration of infestation	soil type	Cultivation practice	Kind of crop	Herbicides timing frequency	Effectiveness of control measures
Shalbourne (Wilts)	1	whole field	always	chalk loam	continuous plough	continuous cereals (winter corn and oat)	round up post harvest alternate years	not satisfactory
Ham (Wilts)	whole farm	patchy	with the advent of winter corn	chalk loam	continuous plough	continuous cereals (winter wheat)	round up post harvest annually	not satisfactory
Liechfield (Wilts)	2	patchy	5 years	chalk loam	continuous plough shallow tyne	continuous cereals (winter wheat)	round up pre and post harvest anually	not satisfactory
Woodhay (Wilts)	3	patchy	always	boulder clay	direct drill	continuous cereals(winter and barley)	round up pre and post harvest annually	satisfactory
Radley (Berks)	1	patchy	always	clay with flint	continuous plough shallow tyne	continuous cereals (winter wheat)	round up pre and post harvest annually	satisfactory
Hungerford (Berks)	5	patchy	always	clay with flint	continuous plough shallow tyne	continuous cereals (w.wheat)	round up post harvest annually	not satisfactory
Chilton (Berks)	2	whole field	always	chalk loam	continuous plough	continuous cereals (corn,w.wheat)	round up post harvest alternate years	not satisfactory
Oldham (leicester)	2	patchy	10 years	boulder clay	direct drill	continuous (w.wheat)	round up pre and post harvest alternate years	not satisfactory
N.E.Scotland	1	patchy	always	medium loam	continuous plough (mouldboard)	continuous cereals (w.barley)	round up pre and post harvest annually	satisfactory
N.E.Scotland	1	patchy	always	medium loam	continuous plough (mouldboard)	continuous cereals (w.barley)	round up pre and post harvest annually	satisfactory

Table 2.3 Summary based on the results of a questionnaire

2.7 Conclusion

The published work and survey results clearly show that Arrhenatherum can become a weed of considerable importance, especially, on chalk loam where whole field infestation was observed. It is also evident that a farmer with Onion Couch on his land is faced with a number of decision problems: 1) what levels of infestation actually represent a threat ? 2) What is the significance of controlling propagation by seeds and the risk from seed produced by the two varieties ?. 3) What is an effective method of control and what is the potential of vegetative propagules to reproduce and survive under various agricultural practices ?. It is clear from the results that the two varieties of Arrhenatherum, i.e Tall Oat-grass and Onion Couch follow two strategies for the invasion of new territory, i.e by seeds and basal bulbs (vegetative propagules) respectively. There is, however, need for more detailed studies of the strategies and adaptations found in the two varieties colonizing different ecological niches and several aspects of the dynamics of the species needs investigation in order to fully appreciate or assess the possible economic threat of the species. In addition, there is little information on what effect Onion Couch really has on the crop. The variable and unsatisfactory results of control measures in natural infestations also suggests that field observations based on the behaviour of vegetative propagules and their growth and development under different management systems is needed to fill in the wide gaps in the information regarding the agro-ecology of Onion Couch.

CHAPTER 3

EXPERIMENTS TO STUDY THE COMPARATIVE BIOLOGY AND AGRO-ECOLOGY OF THE TWO VARIETIES OF ARRHENATHERUM.

3.1 Introduction

The objective of these studies was to investigate several aspects of the biology and agro-ecology of the two varieties of *Arrhentherum* by means of pot and field experiments. The comparative studies planned were of interest not only from a purely ecological point of view but also from an agronomic view, because of the added interest of one of the varieties being an agricultural weed. It was hoped that such a comparative account would also indicate the lines along which evolutionary changes might have taken place between the two varieties in adapting them to two different habitats. Because the two varieties freely crossbreed, and in order to avoid the resulting wider range of variation in bulbosity, perennating organs (shoot bases) collected from natural habitats were used in these experiments rather than seeds. Perennating organs of Tall Oat-grass were collected from a grassland situation located in Windsor Great Park and described (Tingley, 1983) as an *Arrhenatheretum*. Perennating organs of Onion Couch (which also act as vegetative propagules) were brought from populations maintained in plots at the Weed Research Organisation (WRO) near Kidlington, Oxfordshire, where they were originally transplanted from an arable farm in Wiltshire in 1976. A 4x4 metre plot of Onion Couch transplanted from WRO was maintained at Silwood park as stock for future experimentation. A single ramet in the following experiments is comprised of the base of a single shoot of either of the two varieties of Arrhenatherum.

The experiments described in the following sections (3.2-3.8) were performed to investigate the adaptive significance of morphological and physiological differences between the two varieties.

3.2 Dry matter production and its allocation during the early stages of growth of the two varieties of Arrhenatherum.

3.2.1 Introduction.

As the two varieties under study were dissimilar in growth form it was important to understand the inherent potential of the two varieties by following the trends in the dry matter production and its allocation into further photosynthetic and structural units. A sand culture experiment was planned in pots under a cold frame. As the two varieties can cross breed (Chap.2) perennating organs were used for both varieties, but seeds were also used for comparison between the performance of the varieties when grown from different starting material. It was felt that in this way it might answer the agricultural question about the comparative amount of growth from seeds and ramets during the establishment phase in an arable field.

3.2.2 Methods

The single ramets were obtained from the populations described in Chap. 3.1, and the seeds of the commercial prostrate variety (B-207) were obtained from the Welsh Plant Breeding Station at Plas Gogerddan near Aberstwyth.

The criterion used for the selection of the ramets of both varieties was that they should have one shoot base comprising of approximately three bulbs or internodes, whereas the seedlings were planted at the one leaf stage. One seedling or single ramet was planted per pot, and four replicates were used per harvest. Twelve harvests were taken at weekly intervals over the first ten weeks of growth, the first harvest being taken two weeks after planting to avoid the early growth variability.

Plastic pots of 9cm diameter and 11cm depth, filled with sterilised sand were used. The nutients were supplied in the form of Hoagland's solution. After planting, the surface of the soil was covered with a layer of Alkathene granules to avoid any algal growth. The watering regime involved the addition to each pot of 20ml of nutrient solution and distilled water on alternate dates. The drainage holes of the pots were covered with muslin cloth to hold the sand, and the pots were kept in trays under a cold frame. The experiment was initiated on the 29.7.84.and final harvest was made on the 12.10.84. The following measurements were made at each harvest:

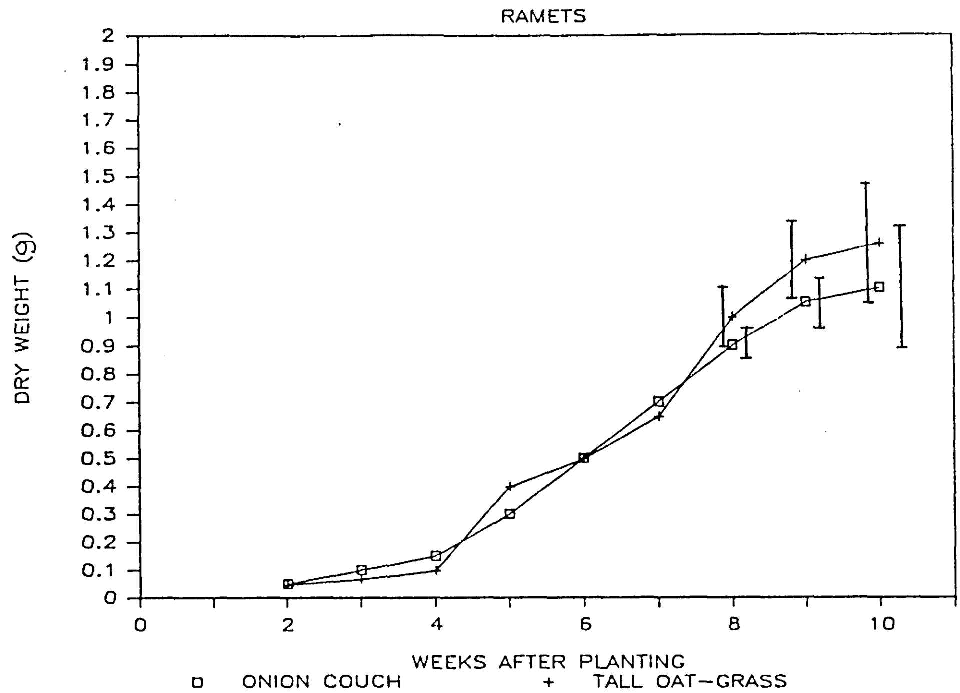
1. Dry weights of roots, shoots and basal internodes (plants were washed then dried at 100°C).
2. Height of tillers .
3. Number of tillers.
4. Number of leaves .
5. Number of new bulbs.

3.2.3 Results.

The seedlings grown from the commercial variety followed the same general pattern of growth as the other two varieties, except that the growth was significantly slower campared to the varieties grown from ramets. Generally, it behaved more like Tall Oat-grass in not developing the characteristic swollen internodes of Onion Couch, but possessed less tillering potential and also produced wider confidence interval compared to the Tall Oat-grass.

The description that follows is confined to the two varieties developing from ramets in order to identify the inherent differences in their earlier growth forms. The results show that the dry weight increases over the first 10 week period though the increase seems to be slower in the later harvests, probably reflecting the greatly fluctuating autumn temperatures under the cold frame.

There seems to be no significant difference between the dry weight production of the roots of the two varieties though there seems to be slight trend towards greater dry weight of roots in Tall Oat-grass than Onion Couch towards later harvests (Fig. 3.2.1). Fig. 3.2.2 shows significantly greater increase in the dry matter production of the shoots of the Onion couch compared to Tall Oat-grass (especially from the fifth harvest onward). This difference in dry weight production of shoots of Onion Couch corresponds morphologically to bulb initiation at the shoot bases, and this phenomenon is also reflected in the root:shoot ratio (Fig. 3.2.3) where significant lowering of the ratio was observed after the fifth week, demonstrating that Onion Couch at this stage allocates more production to realise the inherent trend of storing reserves in the basal internodes of the shoots.



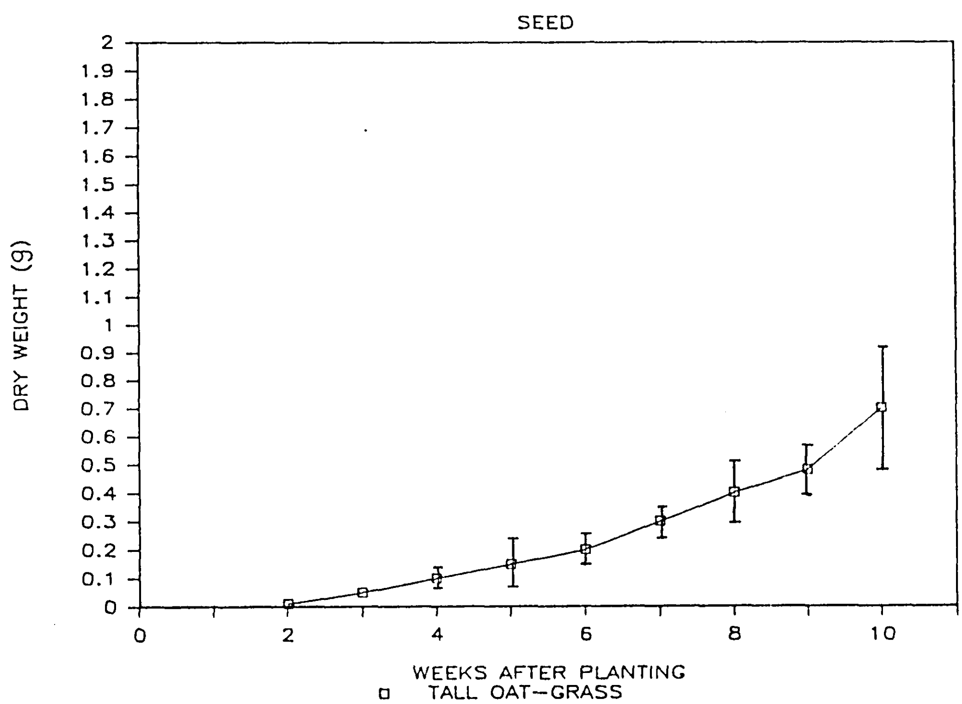
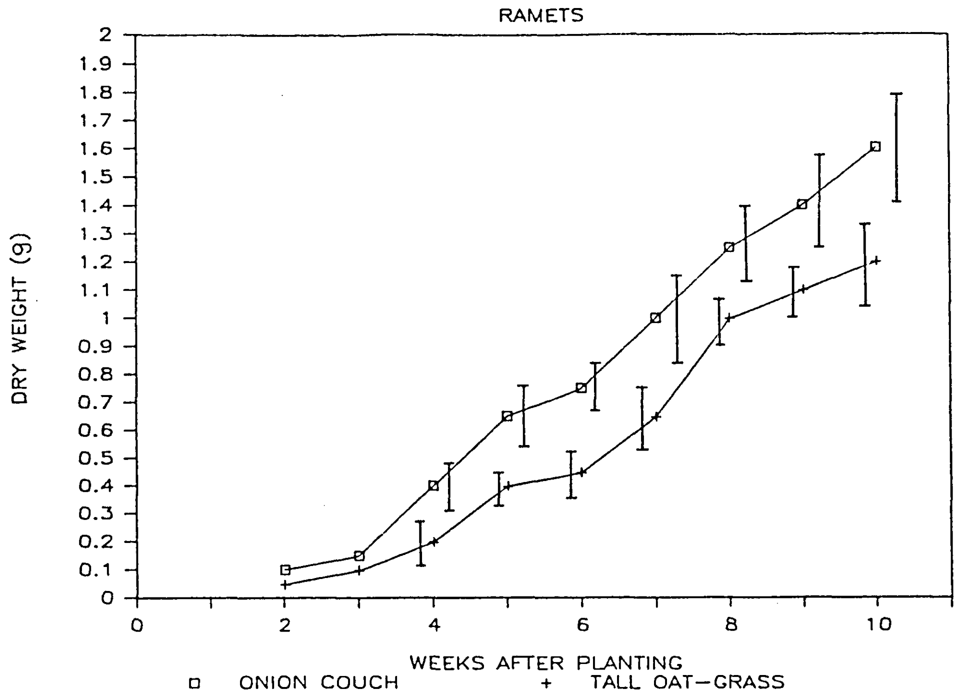


Fig. 3.2.1 Mean dry weight of roots produced from ramets of the two <u>Arrhenatherum</u> varieties, and seeds of a commercial variety of Tall Oat-grass, during the first ten weeks of growth. With 95% confidence limits.



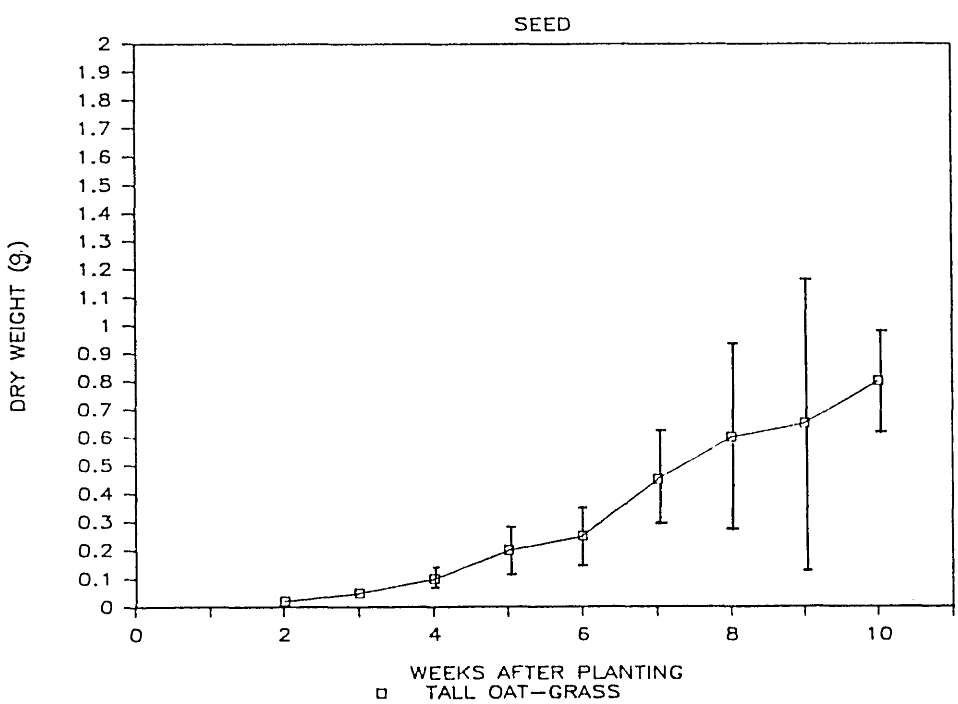
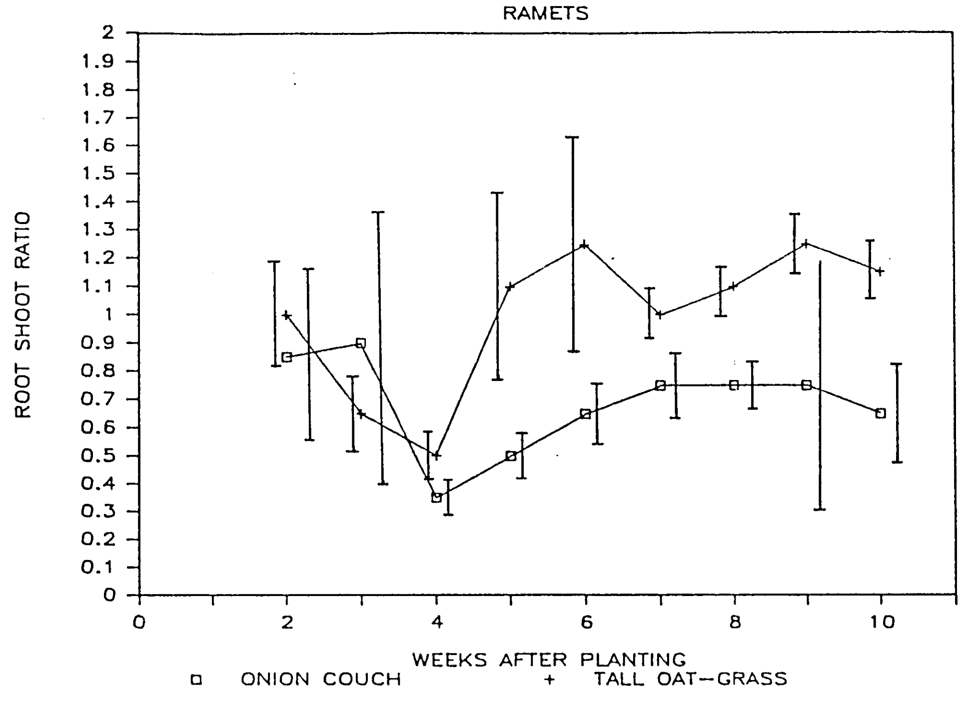


Fig. 3.2.2 Mean dry weight of shoot produced from ramets of the two <u>Arrhenatherum</u> varieties, and seeds of a commercial variety of Tall Oat-grass, during the first ten weeks of growth. With 95% confidence limits.



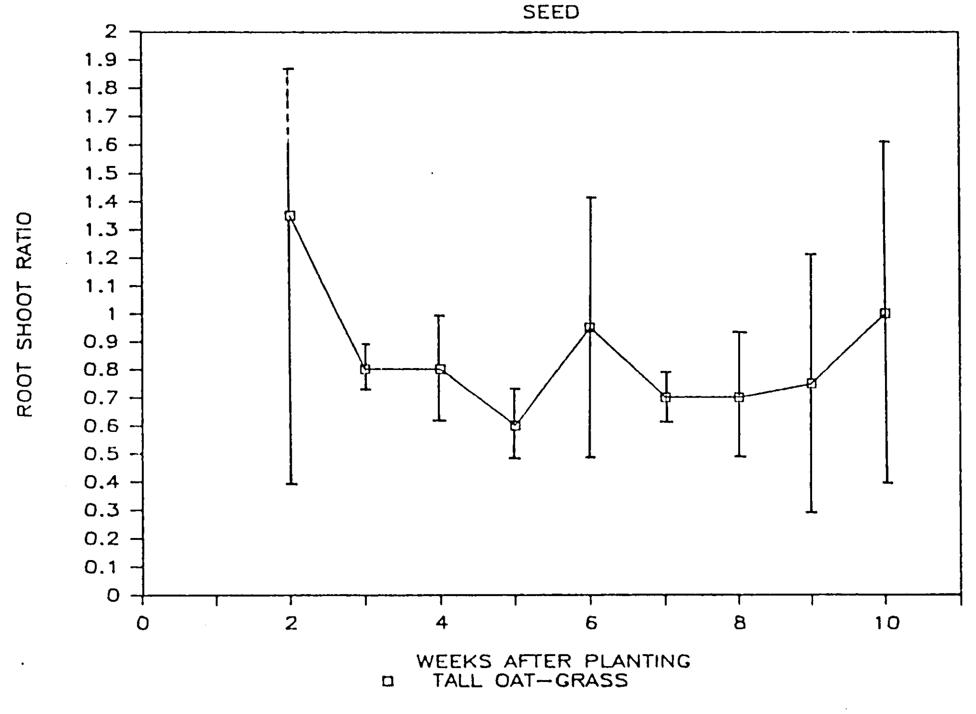


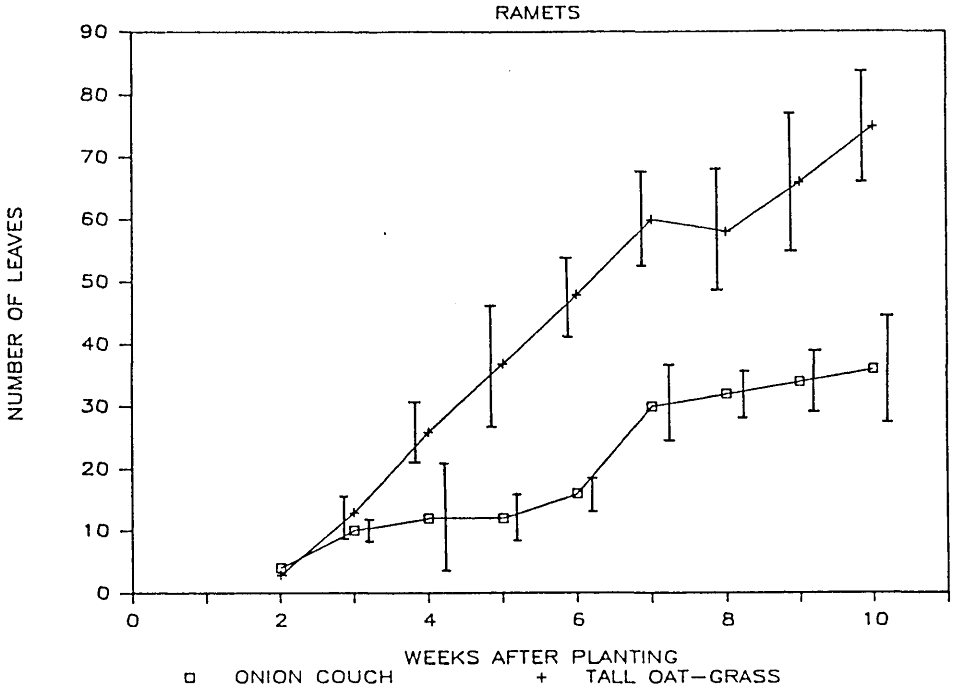
Fig. 3.2.3 Mean Root/shoot ratio (dry weight) produced from ramets of the two Arrhenatherum varieties, and seeds of a commercial variety of Tall Oat-grass, during the first ten weeks of growth. With 95% confidence limits.

It is also evident from the Figs. 3.2.4 and 3.2.5, that an obvious correlation exists between tiller number and leaf number, expressed as the number of leaves and tillers per ramet. It is clear from Figs. 3.2.4 and 3.2.5, that the number of tillers and leaves is significantly higher in Tall Oat-grass compared to Onion Couch. Although Tall Oat-grass possessed greater tillering potential, the height of tillers per ramet (Fig. 3.2.6) was less (a trend exists which is not significant at all harvests) compared to Onion Couch. In addition, it was observed that tillers of Tall Oat-grass exhibit a more prostrate habit compared to the tillers of Onion Couch which were always erect.

3.2.4 Discussion.

The results clearly demonstrate that the marked differences in the sizes of the starting material (seeds and ramets) resulted in significant differences in the resulting regrowth. This gives a clue to the easier establishment of the regrowth from ramets compared to seeds in an arable field. There is also evidence from Ayres (1977) suggesting that ingress of Onion Couch by seeds in arable land cannot become a problem because cultural and chemical treatments would be enough to control the seedling population. The wider confidence interval resulting from the seedlings developing from the commercial variety probably shows the heterozygous nature of the seeds.

The performance of the two varieties during the establishment phase is clearly reflected in the dry weight and the morphological charateristics recorded. The differences in tiller production between the two varieties during this early growth was found to be



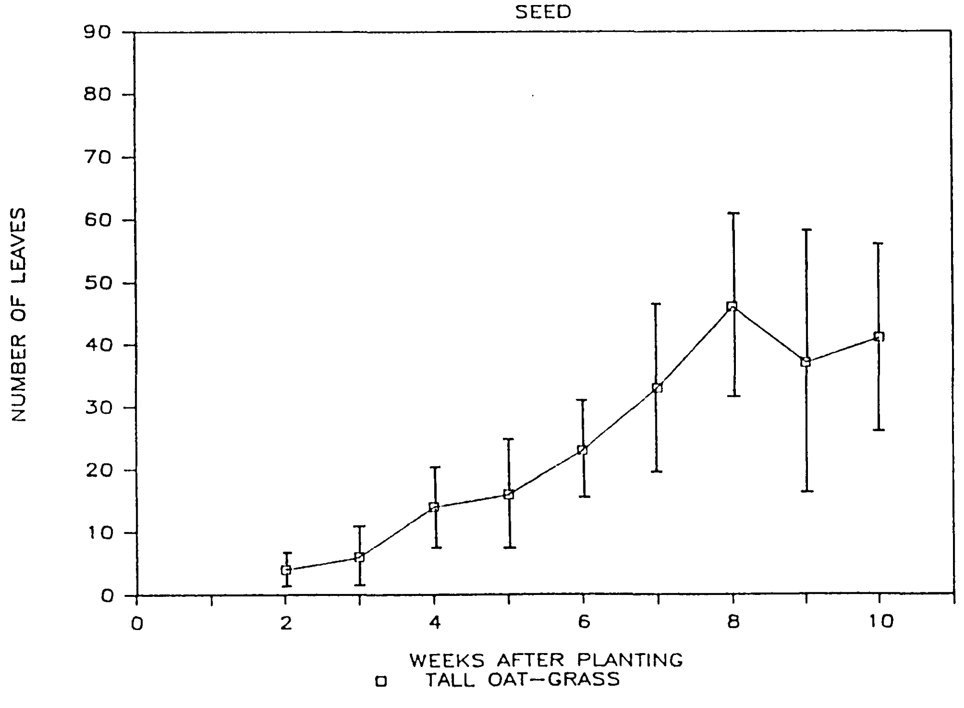


Fig. 3.2.4 Mean number of leaves produced from ramets of the two <u>Arrhenatherum</u> varieties, and seeds of a commercial variety of Tall Oat-grass, during the first ten weeks of growth. With 95% confidence limits.

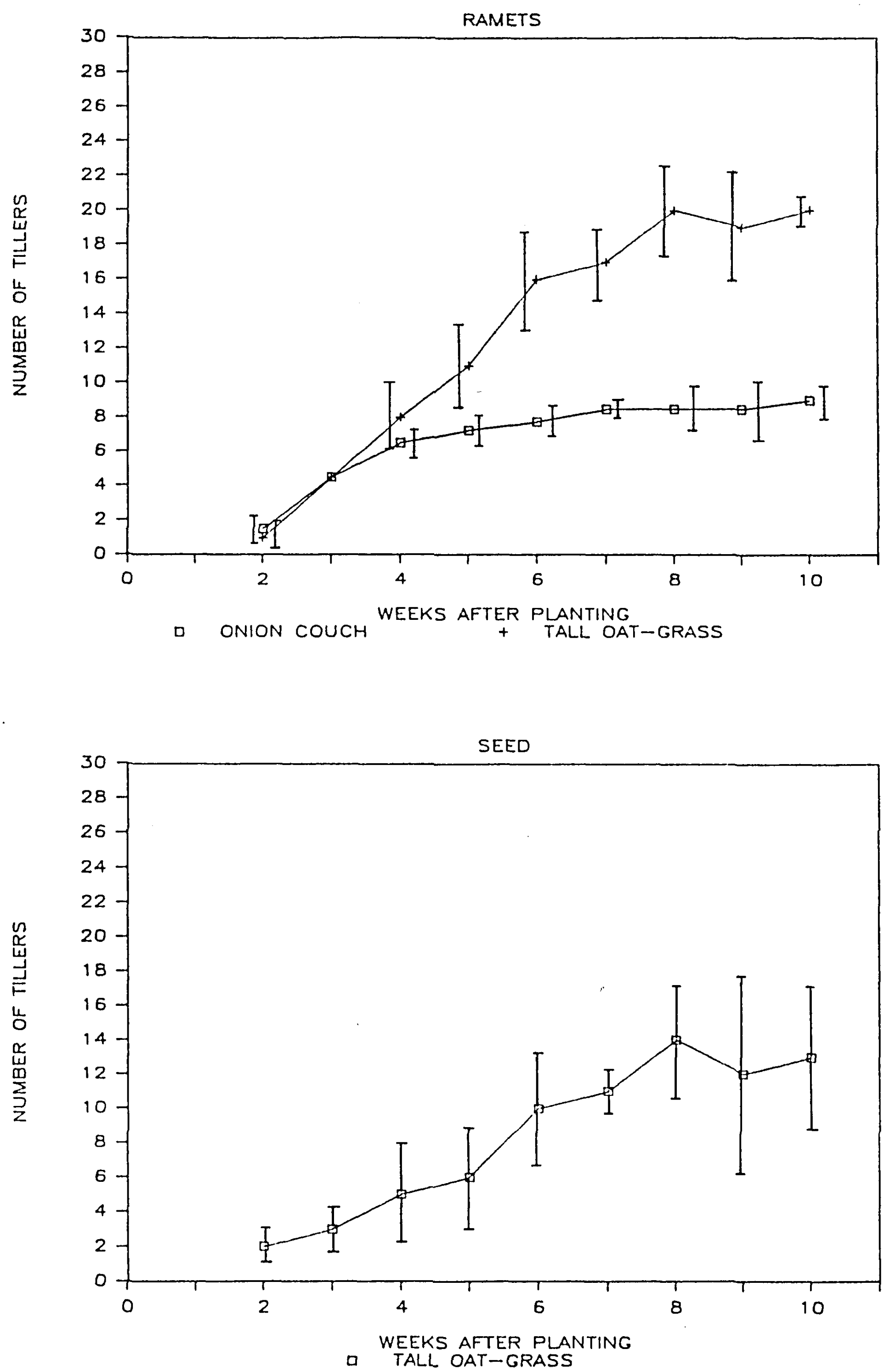
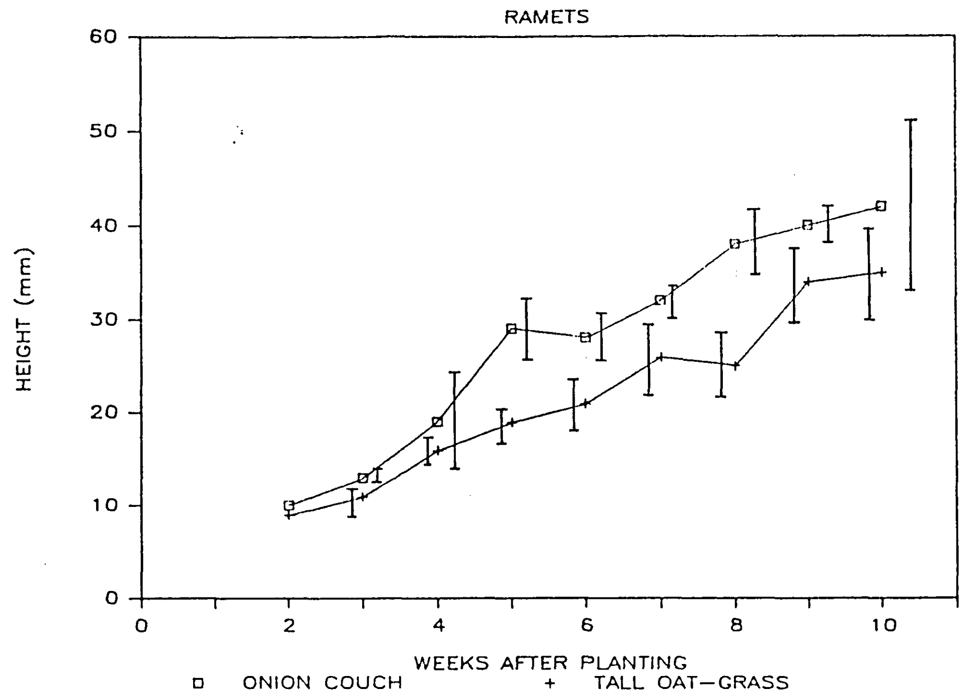


Fig. 3.2.5 Mean number of tillers produced from ramets of the two <u>Arrhenatherum</u> varieties, and seeds of a commercial variety of Tall Oat-grass, during the first ten weeks of growth. With 95% confidence limits.



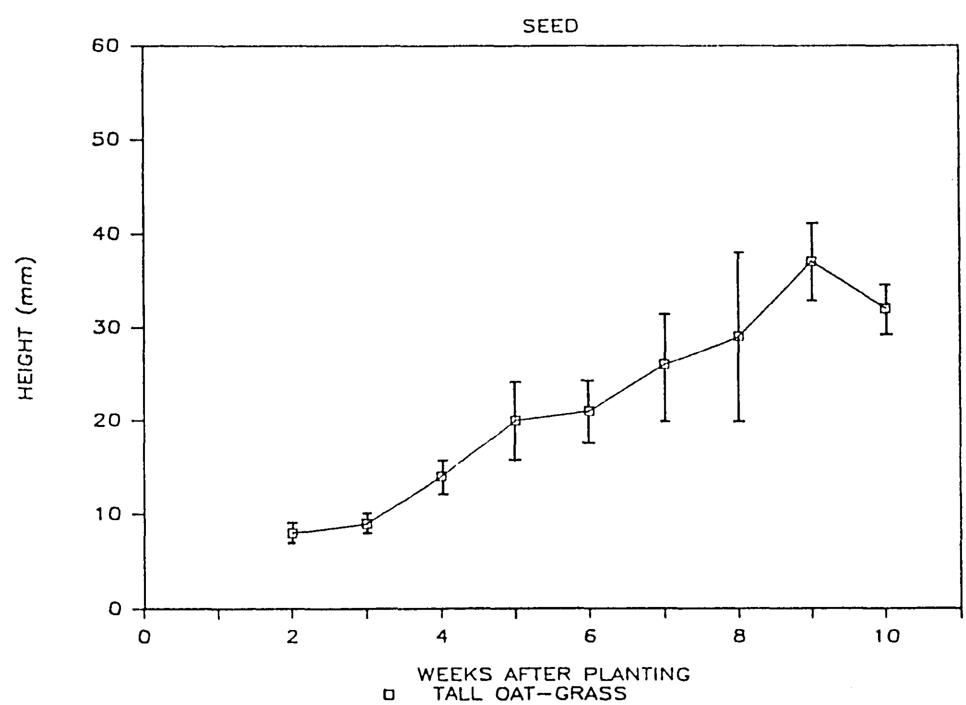


Fig. 3.2.6 Average height of tillers produced by Onion Couch and Tall Oat-grass from ramets, and seeds of a commercial variety of Tall Oat-grass, during the first ten weeks of growth. With 95% confidence limits.

very significant. The rapid tillering during the seedling establishment of Tall Oat-grass was also observed by Pfitzenmeyer (1957), who regards production of new leaves and new tillers as interdependent and as an indicator of seedling development. It is also reported (Cooper, 1949; Langer, 1979) that in most grasses the rate of tillering in the seedling stage is exponential and as a result of this tendency they develop a stock of axillary buds. It seems that Tall Oat-grass follows a general trend of tillering common in most grasses.

The findings are also consistent with the ecological niches of the two varieties and an explanation can be attempted by considering the forms of natural selection which operate in the respective habitat of the two varieties. Thus, it means Tall Oat-grass like many other grasses possesses a greater tillering capacity during the establishment phase and, although the tillers formed are less vigorous, it is probably this greater tillering potential (and as a result, development of a stock of axillary buds) which helps it to coexist in a grassland situation where it competes with species of similar growth forms. Unlike other grasses, Onion Couch, on the other hand, behaves more like cereals during its early phase of establishment it produces fewer, vertical and more vigorous tillers compared to Tall Oat-grass. The vigorous tillers of Onion Couch, at the same time differentiate storage tissues in the form of swollen internodes to ensure its continuance and coexistence in the arable system.

3.3 The potential of the two varieties of Arrhenatherum for producing the Onion Couch variety by means of seed.

3.3.1 Introduction.

As Onion Couch is a well known troublesome weed of arable fields and Tall Oat-grass is frequently a dominant grass in hedgerows and field margins, contribution by their seeds towards future ingress in arable fields by dispersal seems to be a question of some agricultural importance. A small pot experiment was set up with the object of quantifying the contribution of seed from the two varieties, collected from different locations, in producing the characteristic bulbous plants of Onion Couch.

3.3.2 Methods.

Seeds from different locations (Table 3.1) were collected in the summer of 1984. They were germinated in the trays on 1.3.1985, and about 80% germination was observed. One week after germination they were selected at random and were planted in polythene bags filled with John Innes compost No.3. Twelve seedlings were planted per pot and three replicates per location. The pots were kept in the green house with sixteen hours of Metal-halide lights at 245 $\mu E\ s^{-1}\ m^{-2}$ intensity. The temperature ranged from average of 12°C in March to 22°C in April and May. In the begining, attempts were made to classify the plants on the basis of number of bulbs per tiller and number of tillers per seed as used by Ayres (1977), but this was found time consuming and sometimes ambiguous, so a more straight forward method of practical significance was adopted; plants with characteristic superimposed bulbs at the shoot bases were regarded Onion Couch, and all other types as Tall Oat-grass (Plate 1 and 2).

3.3.3 Results.

Table 3.1 Shows the locations and habitats from where the seeds of the two varieties of Arrhenatherum were collected. Seeds collected from Tall Oat-grass plants always produced Tall Oat-grass, whereas seeds collected from Onion Couch, did not always produce plants resembling Onion Couch. It seems that the percentage of seed developing into Onion Couch varies with the locality from which it was collected. Seeds collected from large populations of Onion Couch (assumed to be self pollinated) produced plants of which approximately 75% were Onion Couch and 25% Tall Oat-grass (plate 1). Seeds collected from Onion Couch growing in the proximity of Tall Oat-grass (assumed to be cross pollinated) did not produce a single plant with characteristic swelling of Onion Couch (plate 2). These plants were classified as Tall Oat-grass, as no attempt was made to classify intermediate forms.

3.3.4 Discussion.

The practical significance of these results is that the Tall Oat-grass which commonly is a dominant grass in hedgerows and headlands (Chap. 2) and does not produce superimposed bulbs like Onion Couch will produce seeds that will develop into plants resembling Tall Oat-grass. This eliminates the chance of Tall Oat-grass acting as a seedbank for the spread of Onion Couch in the Field, which is consistent with the findings of the surveys in Chap.2. This conclusion may appear overbearing and open to argument, especially, if the size of the sample is examined in the context of the natural phenomenon; where even if a bulbous form is produced at a rate of 1/1000, it could represent an important source, but observations (Chap. 2) suggests that this event must be a rare one.

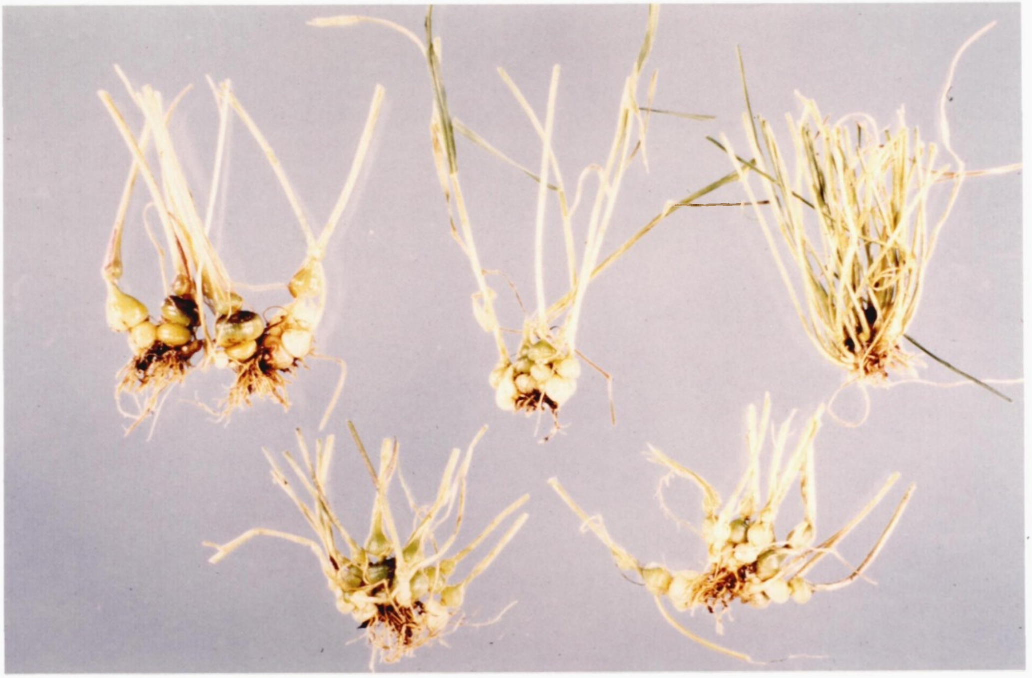


Plate 1 Seedlings of Arrhenatherum elatius developing from seeds of Onion Couch variety growing in pure stands, selected to illustrate the ratio of Onion Couch : Tall Oat-grass.

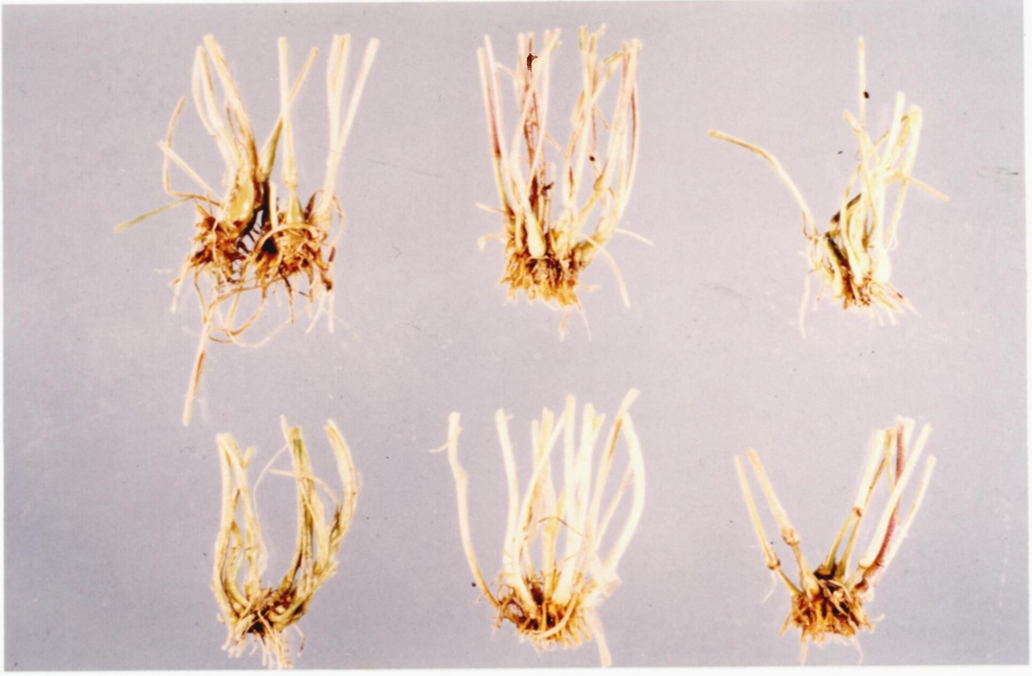


Plate 2 Seedlings of Arrhenatherum elatius developing from seeds of Onion Couch growing with Tall Oat-grass, selected to illustrate variation in bulbosity.

LOACTIONS	HABITATS	VARIETY	% OF PLANTS FORMING PROMINENT BULB CHAINS	% OF PLANTS NOT FORMING PROMINENT BULB CHAINS
HUNGERFORD, BERKS.	ARABLE LAND (SMALL PATCH CENTRALLY LOCATED)	ONION COUCH	60	40
WEED RESEARCH ORGANISATION (WRO) OXFORD.	MONOCULTURES	"	82	18
SHALBOURNE, WILTS.	ARABLE LAND (BIG PATCH CENTRALLY LOCATED)	"	74	26
HIGHWYCOMBE, BUCKS.	ARABLE LAND (SMALL PATCH TOWARDS THE MARGIN).	"	0	100
WRO(BULBOUS) & WINDSOR GREAT PARK (NON BULBOUS)	ARABLE LAND & GRASS LAND (GRWON TO-GETHER)	"	0	100
WINDSOR GREAT PARK, BERKS.	GRASS LAND	TALL OAT-GRASS	0	100
SILWOOD PARK,	ROAD VERGES	"	0	100
HUNGERFORD, BERKS.	HEDGEROWS (FIELD MARGINS)	"	0	100

TABLE 3.1 Potential of the seeds of the two Arrhenatherum varieties to produce Onion Couch (Bulbous variety).

In addition, the finding that even the Onion Couch growing in the centre of the field in large patches would produce seeds all of which will not grow into Onion Couch (in fact some of them will be very typical Tall Oat-grass) further diminished the importance of dispersal by seed even by Onion Couch. The results are also in agreement with Ayres (1977) who found only 50% seeds from Onion Couch, produced plants suffiently bulbous to be potential weeds of arable land. Furthermore, if there is cross-pollination between the two varieties growing in the vicinity of each other it would seem that there is little or no chance that the resulting seed would produce Onion Couch. The result agrees with Jenkin (1931) who found that plants from cross pollinated seeds were decidedly less bulbous than the ones developed from the orignal bulbous variety.

Jenkin's (1931) argument that to produce full bulb development of Onion Couch more than two genetic factors would be necessary means that in the absence of any one of these factors the resulting seed would develop into the rest of the type in the series the so called 'Tall Oat-grass'. In that respect Onion Couch could be regarded as a recessive variety (in terms of sexual reproduction) in the sense that the chance of getting all the factors together even in the seeds collected from Onion Couch selected from monocultures is not 100%. These arguments are in favour of the view adopted earlier (Chap. 2) that sexual reproduction does not appear to be an effective means of propagation even from seeds of the Onion couch variety.

3.4 Response of the two varieties of *Arrhenatherum* to clipping.

3.4.1 Introduction

The aim of this investigation was to examine the effect that occasional cutting could have on the two varieties, in the hope that the result would help in explaining the complete absence of Onion Couch from habitats where Tall Oat-grass dominates. There are examples in the literature (e.g. Mahmoud 1973) suggesting that Tall Oat-grass is susceptible to cutting management, so a light cutting regime, resembling the one practiced in some grasslands and roadside verges was used in this experiment. It was also hoped that the result would reveal the relevance of the old cultural control, 'laying land down to grass' practiced in heavily infested fields and believed to decrease the vigour and diminish the bulb size of Onion Couch (Chap. 2.6).

3.4.2 Methods

In order to examine the way the two varieties reacted to this cutting regime the two varieties were grown in monocultures and were replicated eight times in $1m^2$ plots. Single ramets comprising of one shoot base were used and 33 ramets per plot were planted on 20.8.84. The plots were subjected to the following treatments:

1. Uncut control (three replicates for each variety).
2. Cut after three to four week intervals at 3 to 4cm from the soil surface (plots replicated five times for each variety.).

The first clipping was done on 20.4.85. followed by five successive cuts until the final harvest (10.9.85). On the final harvest three replicates for each variety were dug up to see the effect of tillering on the basal internodes. The unclipped monocultures of the two varieties were harvested on 20.7.85. The plots were dug to retrieve the basal internodes which were washed, oven dried and weighed.

3.4.3 Results

Fig. 3.4.1 shows the reaction to cutting of the two varieties of Arrhentherum. The first cutting did not reduce the amount produced, in fact it showed a significant increase in the dry weight of the second cut. Onion Couch significantly produced more after the first cut but sufferred a sharp decline after the second cut and no new regrowth was observed after the third cut until the plants were dug up at the final harvest. On the other hand, Tall Oat-grass did not suffer such sharp fall until the fifth harvest, when the tillers did not grow to the height of cut. The dry weight at final harvest was significantly higher in Tall Oat-grass compared to the Onion Couch (Fig. 3.4.1).

Differences between the tolerance of cutting treatment also become obvious (Fig. 3.4.1) when the mean dry weight of the cuttings collected from successive cuts were compared. The total amount of cut material produced by Tall Oat-grass was higher than that of Onion Couch (Fig. 3.4.2). The comparison of total dry weight of successive cuts with the dry weight of the uncut plot has also shown (Fig. 3.4.2) that Onion Couch has comparatively suffered more under this cutting treatment. The effect of tiller removal was also reflected in the reduced weight of the basal internodes when compared with the shoot bases of the unclipped control plots (Fig. 3.4.2).

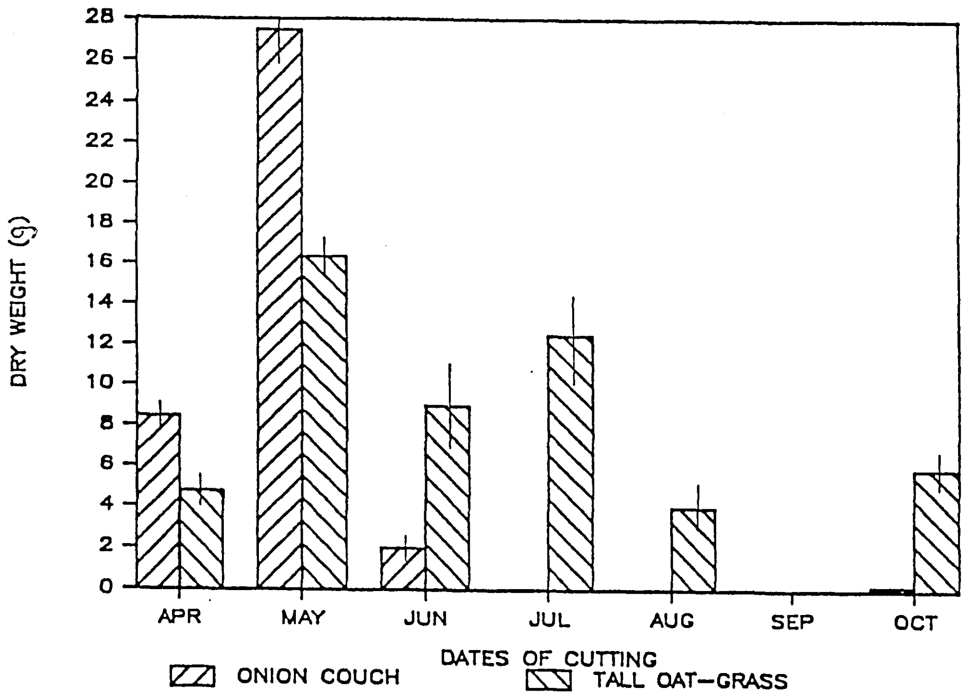


Fig. 3.4.1 Histogram showing dry weight of cuttings produced by the two <u>Arrhenatherum</u> varieties on different dates. With 95% confidence limits.

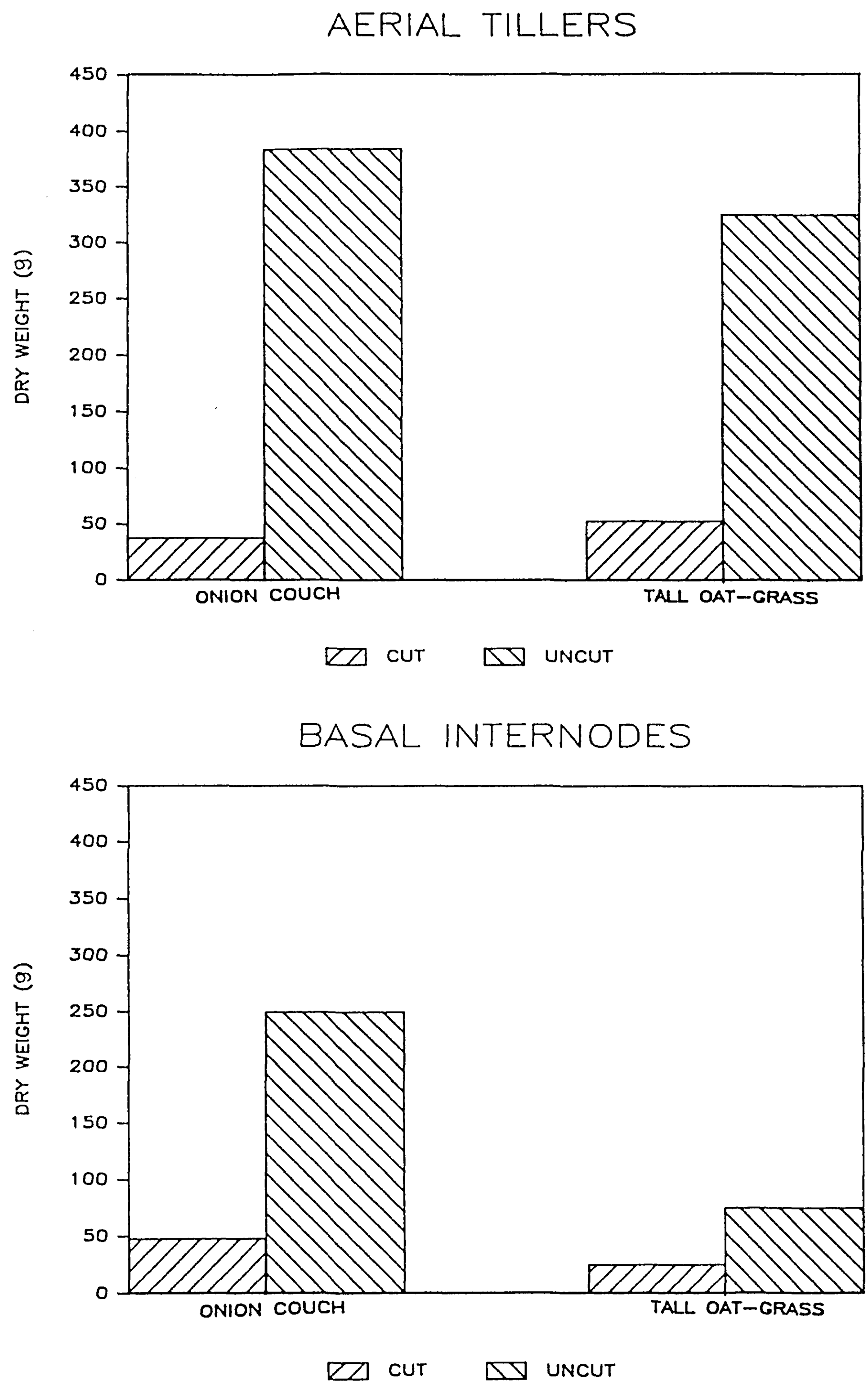


Fig. 3.4.2 Histogram showing the accumulative yield (dry weight) of aerial tillers, and dry weight of basal bulbs at the final harvest, of cut and uncut plots of the two Arrhenatherum varieties.

On examining the plants at the final harvest it was observed that many tillers had been killed under this treatment, the number of tillers killed seems much higher in Tall Oat-grass, as a lot of dry matter had accumulated around its tussoks. Furthermore, as no hand weeding was done after the fifth harvest the appearance of the plots at the final harvest changed considerably, especially in the plots with Onion Couch. Holcus lanatus and Elymus repens formed a complete cover and Onion Couch regrowth became evident only after digging the partially buried ramets, whereas in plots with Tall Oat-grass invasion by these grasses was observed only in the spaces between the tussocks.

3.4.4 Discussion

Tall Oat-grass proved to be more able to survive under occassional cutting management compared to Onion Couch which seemed to be more prone to destruction and probably elimination under even a mild cutting regime. The results of this experiment provide further proof of the conclusion reached in Chap 3.2, regarding the adaptation of the two varieties to the selection pressure operating in their respective habitat.

Onion Couch on the basis of producing fewer, erect and vigorous tillers, lost most of its regrowth in the initial and subsequent cuts and suffered a sharp decline in its photosynthetic output after the second cut. After the third cut the tiller bases looked dry and withered leaving a tiny bulb partially buried in the ground. No regrowth was observed from these bulbs until the final harvest. It seems that the newly formed ramets entered into a period of aestivation which seems to be coinciding with the summer months.

Tall Oat-grass, on account of its potential to tiller profusely during the establishment phase developed a stock (Chap. 3.2.) of axillary buds which easily replaced the tillers killed by cutting and thus survived under this cutting regime. Moreover it seems that dormancy and partial burial of the ramets of Onion Couch and complete absence of ground cover made it more susceptible to invasion by other species even in less frequently cut habitats compared to Tall Oat-grass whose tussocky growth habit and cover discourage easy establishment of the invaders.

It is obvious from the results that although possibly uneconomical, 'laying back to grass' could result in effective control of Onion Couch. The findings of this experiment which are based on a mild cutting regime (where the grass was cut 3-4cm above the soil surface) has shown considerable decrease in the size of new ramets of Onion Couch. It is possible that two or three clippings (or tillage operations) early in the growing season at some suitable interval might eleminate Onion Couch from the field.

3.5. Pattern of growth, space occupation and density dependent response of the two Arrhenatherum varieties and Wheat, in monocultures.

3.5.1 Introduction

The experiment reported in this section was mainly designed to calculate parameter β (de Wit,1960) for both Arrhenatherum varieties and Wheat. This parameter, which is derived from a spacing experiment with species grown in monoculture and harvested at intervals, is believed to give a good understanding of competitive relations in a mixture through defined growth stages (Spitters and van den Bergh, 1982). It was hoped that values of β which describe space occupation by whole plants would provide a basis for the construction of the proposed structured model for control and spread of Onion Couch under different cultivation regimes.

The design of the experiment was such that it was expected to provide data on the following aspects of the population dynamics of the two Arrhenatherum varieties (as there has been no published work dealing with the effect of density on life history parameters of these two varieties):

1. Dry weight production and its allocation to aerial tillers and basal internodes during the growth cycle.
2. Responses to density dependent stresses in the two Arrhenatherum varieties.

As these experiments involved destructive sampling, morphological stages rather than regular chronological samples were recorded.

3.5.2 Methods

The main experiment was conducted in the 1984-85 season but was repeated in the 1985-86 season with the two Arrhenatherum varieties to obtain complementary data at higher densities, firstly because density stress was not evident in plots with Onion Couch from the data obtained in the 1984-85 harvests. Secondly, edge effects were not considered in the the 1984-85 season experiment.

The single ramets of the two Arrhenatherum varieties (from the population described in Chap.3.1) and seeds of Winter Wheat (cv.Avalon) were planted in $1m^2$ plots laid out on land used for agricultural purposes at Silwood park. The soil is classified as a sand and it had been regularly limed.

Planting densities for the 1984-85 season were: Tall Oat-grass and Onion Couch at 9 single ramets m^{-2}, 33 single ramets m^{-2}, and 66 single ramets m^{-2}. Wheat was planted at 25 seeds m^{-2}, 150 seeds m^{-2} and 350 seeds m^{-2}. Planting densities for the 1985-86 season: Tall Oat-grass and Onion Couch at 7 single ramets m^{-2} and 134 single ramets m^{-2} .

Planting procedure: Top soil was raked from the surface of each $1m^2$ plot to a depth of 2.5cm. Freshly cut and washed single ramets of the two Arrhenatherum varieties and seeds of Wheat were then spread evenly over the entire metre square, after which the soil was carefully replaced.

Planting for the 1984-85 season took place on 20 and 21.10.84 for the two Arrhenatherum varieties, and 22.10.84. for the Wheat. Planting for the 1985-86 season took place on 29 to 31.10.85.

The plots were arranged in three adjacent blocks, one for each variety and the crop. Each block was composed of 45 plots to provide for five harvests on each of which three replicates of three planting densities were harvested. The plots were separated by paths of 0.25m. The plots were arranged randomly within each block with respect to planting density, intended date of harvest and replications. A similar arrangement was used for the 1985-86 season but only two densities were used for both the varieties.

Fertilizer treatments: All plots were treated with 31.25g m^{-2} of PK fertilizers (ICI No.10) in autumn, and the same amount of N fertilizers (ICI No.10) in spring for both years.

Harvest dates for the the 1984-85 season were: 20 March, 21 April, 19 May, 20 June, 19 July. Harvest dates for the the 1985-86 season were: 26 April, 25 May, 25 June, 24 July, 15 August, and on each date two separate harvests per plot (planted at higher density) were made: the central $0.25m^2$ and the outer edges (to estimate the edge effect).

The following observations were recorded per plot at each harvest.

For Wheat:

1. Number of tillers .
2. Shoot dry weight(clipped at the soil surface and oven dried at 100°C for 48 hours).

For Tall Oat-grass and Onion Couch:

1. Number of tillers, their average height and number of tillers with inflorescence.
2. Dry weight of aerial tillers (clipped at the soil surface and oven dried).
3. Dry weight of basal internodes (washed and oven dried).
4. Number of bulbs and proportion of two and three bulb ramets (in Onion Couch only).

In addition, the above mentioned observations were made on 7 single ramets of Onion Couch planted in a 1 m^2 plots for comparison with the regrowth of similar sized ramets from a natural infestation (Chap.4.2).

Calculation of values for parameter β: The dry weights of the whole shoots (including the basal internodes) of the two Arrhenatherum varieties and the crop from all harvests were plotted and a free hand curve was drawn through the observations for each density. The smoothed yield so obtained at the corresponding harvest dates was then plotted in a graph, with space per plant in cm along the horizontal axis and inverse of yield on the vertical axis. The assumption made for calculating β values is that the relationship between yield and planting density on successive dates may be described by the hyperbolic function (de Wit, 1960):

$$O_t = \Omega \beta_t Z (\beta_t Z + 1)^{-1}$$

where O is the observed yield, Z is the planting density, Ω is the hypothetical yield of an infinitely dense sward, t is time, and β measures the degree of curvature of the hyperbola. The equation can be converted to linear form thus (Spitters and van den Bergh, 1982):

$$O_t^{-1} = (\beta_t \Omega_t)^{-1} Z^{-1} + \Omega_t^{-1}$$

When O^{-1} is plotted against Z^{-1} the intersect on the Z^{-1} axis gives the value of β.

3.5.3 Results

In spite of the expectation no consistent marked edge effects were observed in any of the plots harvested in the 1985-86 season, probably due to the very narrow paths separating the plots from each other, therefore the results that follow are based on entire plots ($1m^2$).

Trends in values of β over the period of growth.

The relation betwen the dates of harvest and values of β are represented in Figs. 3.5.1 and 3.5.2 for the two seasons. The data used to calculate β for wheat and the two Arrhenatherum varieties on each harvest for both seasons are shown in Table 3.2.

Calculated β values were used to interpret the competitive relation between Tall Oat-grass, Onion Couch and Wheat in the manner of de Wit (1960) and Spitters and van den Berg (1982). Accordingly parameter β, which measures the curvature of the density curves, reflects the space occupied by a free growing plant.

The curves demonstrate that Onion Couch had the highest initial value followed by Wheat, whereas Tall Oat-grass show a very low (negative) value at this stage. In the second harvest the value of Wheat surpassed the value of Onion Couch and in the third harvest the β values for Tall Oat-grass also increased above that of Onion Couch. At the third and fourth harvests the curvature of the curve for Wheat is much higher compared to the two Arrhenatherum varieties. After the fourth harvest the curve flattens off more sharply for Wheat compared to Onion Couch. Tall Oat-grass shows a similar tendency though at a much lower value. Onion Couch on the

		WHEAT			ONION COUCH					TALL OAT-GRASS				
		1984-85 season			1984-85 season			1985-86 season		1984-85 season			1985-86 season	
PLANTING DENSITY		20 SEEDS	150 SEEDS	350 SEEDS	9 RAMETS	33 RAMETS	66 RAMETS	7 RAMETS	134 RAMETS	9 RAMETS	33 RAMETS	66 RAMETS	7 RAMETS	134 RAMETS
HARVEST DATES														
MARCH	X	2.43	8.16	22.02	2.11	6.37	11.17	-	-	0.91	5.12	12.07	-	-
	CL	0.98	0.77	4.12	0.55	1.37	4.38	-	-	0.55	1.80	4.55	-	-
APRIL	X	21.67	58.17	123.7	12.02	54.03	70.87	4.68	90.72	4.64	27.58	71.97	0.95	22.39
	CL	10.96	5.07	37.96	1.03	21.50	19.60	0.56	28.38	1.33	8.98	13.11	0.47	18.40
MAY	X	128.6	377.3	710.0	64.17	204.6	322.2	43.5	370.6	60.97	218.3	421.0	25.68	166.0
	CL	42.2	141.1	33.4	21.3	56.0	72.1	6.3	56.2	5.93	36.20	148.95	10.14	66.82
JUNE	X	451.3	770.9	1044.3	115.4	471.7	875.1	92.2	894.3	124.0	332.6	572.4	45.78	591.0
	CL	79.3	40.2	109.4	21.24	45.23	95.5	28.76	100.5	49.9	100.36	134.2	16.95	84.71
JULY	X	431.0	879.0	1202.0	180.6	600.5	1004.3	151.6	1030.1	131.3	427.0	616.6	85.6	619.3
	CL	88.5	109.4	47.4	37.9	80.9	68.7	8.9	86.5	16.1	103.5	111.9	13.5	66.43
AUGUST	X	-	-	-	-	-	-	129.8	1044.0	-	-	-	69.18	582.33
	CL	-	-	-	-	-	-	13.8	142.9	-	-	-	22.70	68.62

Table 3.2 Whole shoot dry weight g m^{-2} at harvest. Mean values of 3 replicates (X), and 95% confidence interval (CL).

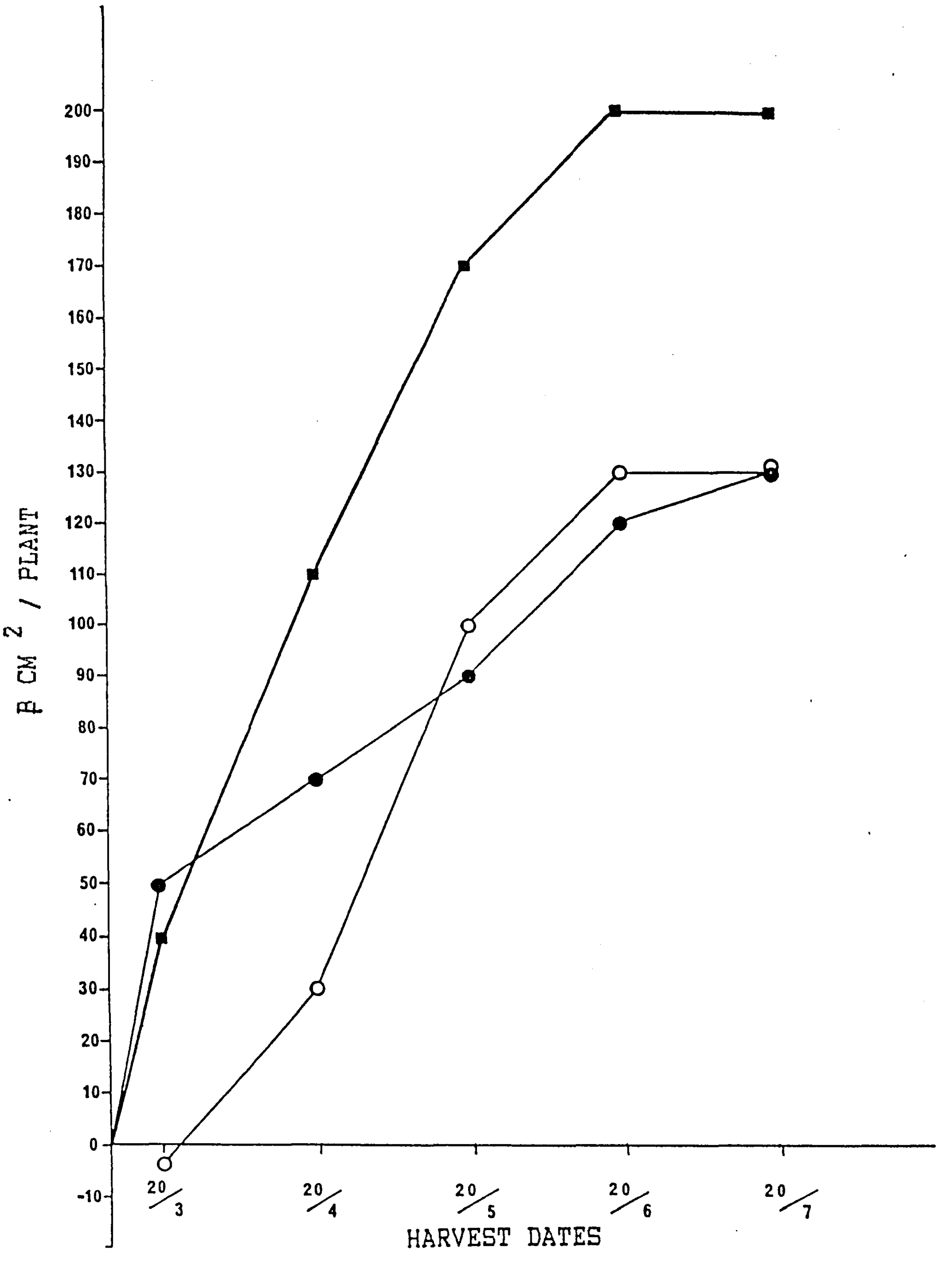


Fig. 3.5.1 Trends in the values of parameter β for wheat (■), Onion Couch (●) and Tall Oat-grass (○) for the 1984-85 season.

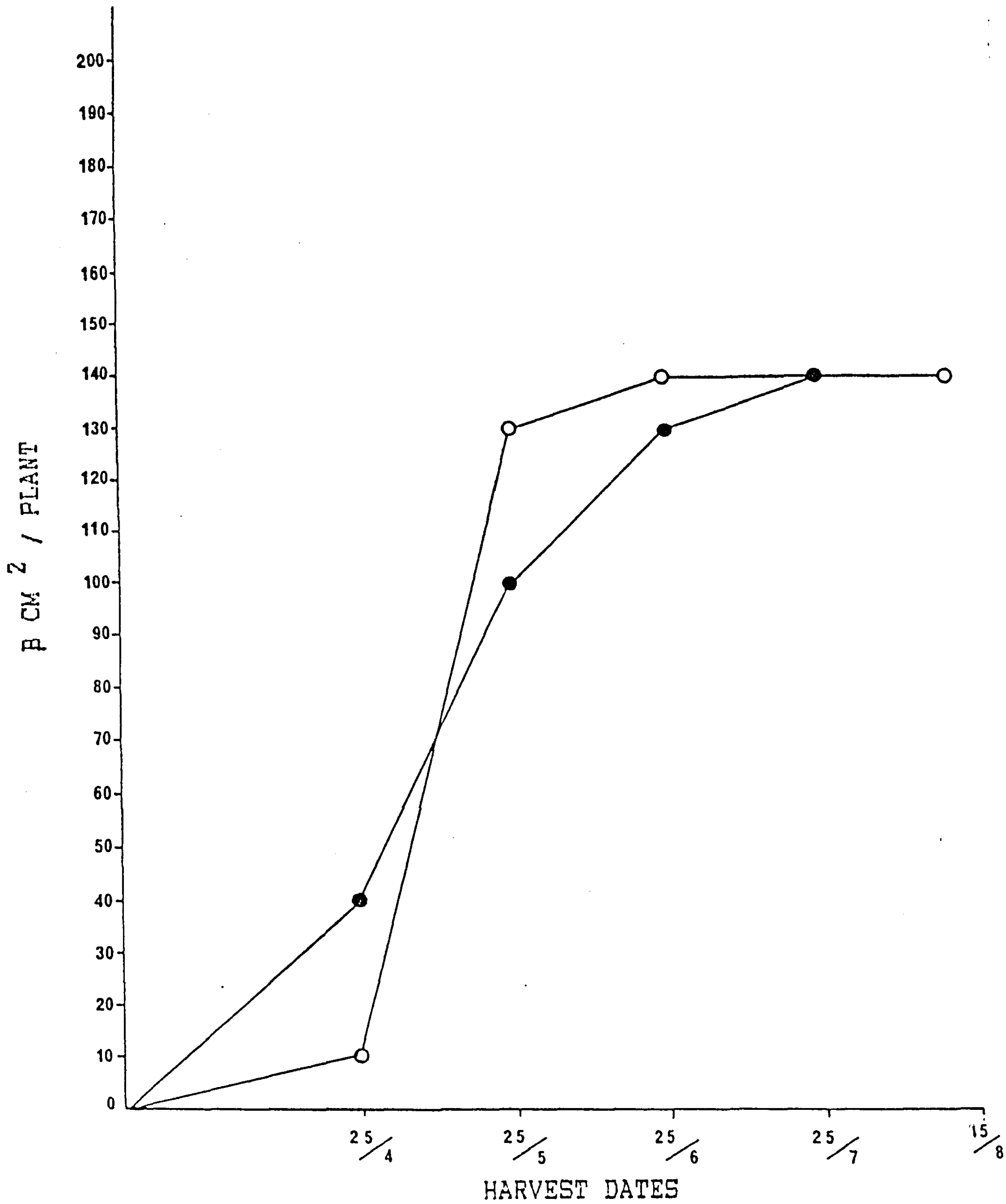


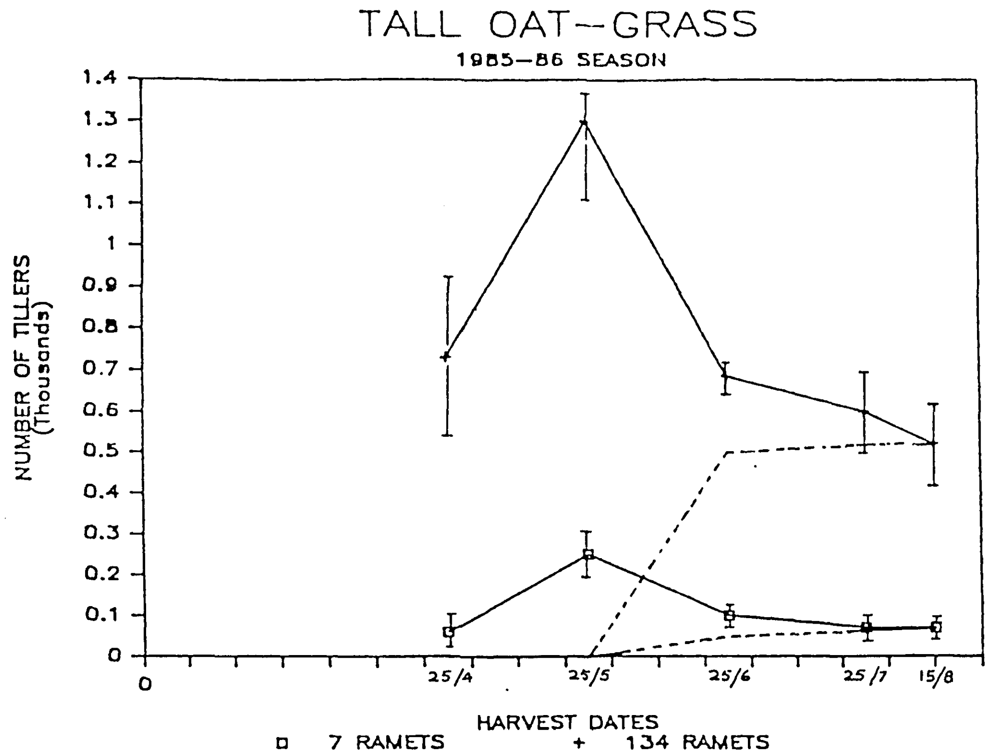
Fig. 3.5.2 Trends in the values of parameter β for Onion Couch (●) Tall Oat-grass (○) for the 1985-86 season.

other hand, in spite of higher initial β values, shows a much more gradual increase in the following two harvests until the fourth harvest when it shows an increase in the β value and also shows a slight increase in the β values even at the fifth harvest.

Similar trends of values for parameter β were observed (Fig. 3.5.2) in periodic harvests of the two Arrhenatherum varieties in the 1985-86 season. The initial values here were very low due to a delayed spring (6 weeks) followed by a sharp rise of values for β, corresponding to abrupt flowering which is stimulated by longer days and higher temperature.

Pattern of tillering

In both Arrhenatherum varieties and Wheat tillers appeared at the begining of November 1984. In the second experiment tillers of both Arrhenatherum varieties appeared by the begining of December 1985 (due to delayed planting and ground frost in November). There was very little increase in tiller number during the winter months (December to March). Rapid tillering was observed in April, when peaks were reached in the tiller numbers in Tall Oat-grass, Onion Couch and wheat. The tillering period was followed by a stem elongation period when the number of tillers fell rapidly (especially, at higer planting densities). The rate of thinning was faster in Tall Oat-grass and Wheat compared to Onion Couch. It is evident from Fig. 3.5.3 that the plots planted with few ramets m^{-2} did not suffer any significant thinning but in densely planted plots (33, 66 and 134 ramets) the final number of tillers tended to converge by the time of harvest to similar tiller densities irrespective of the differences in initial densities. The thinning



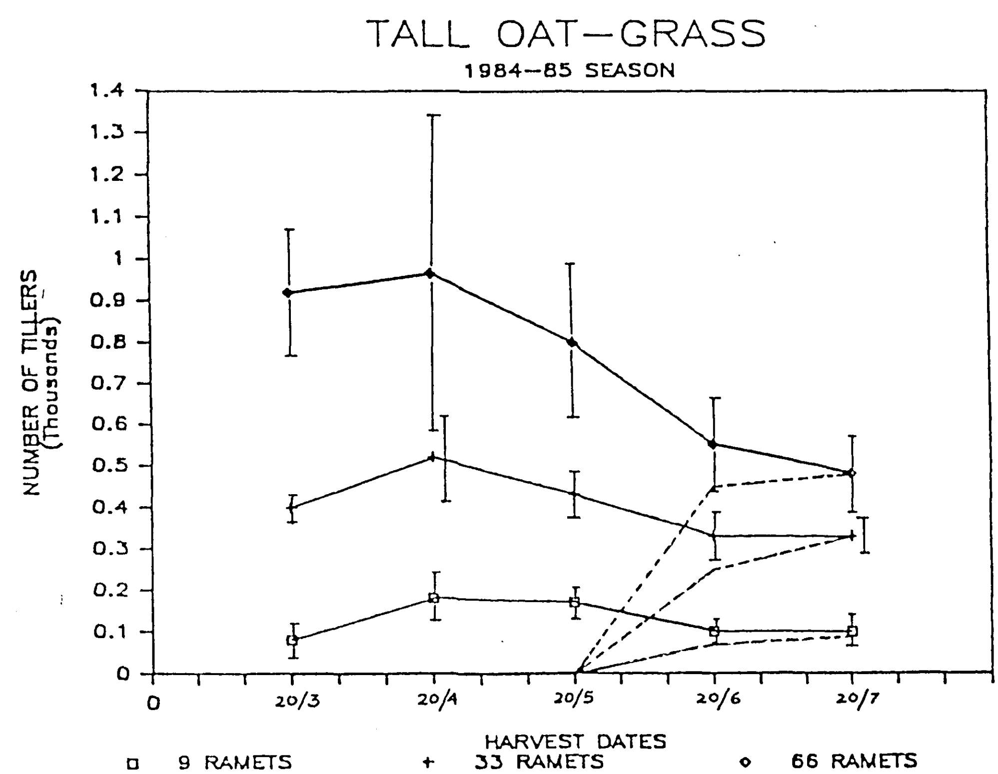
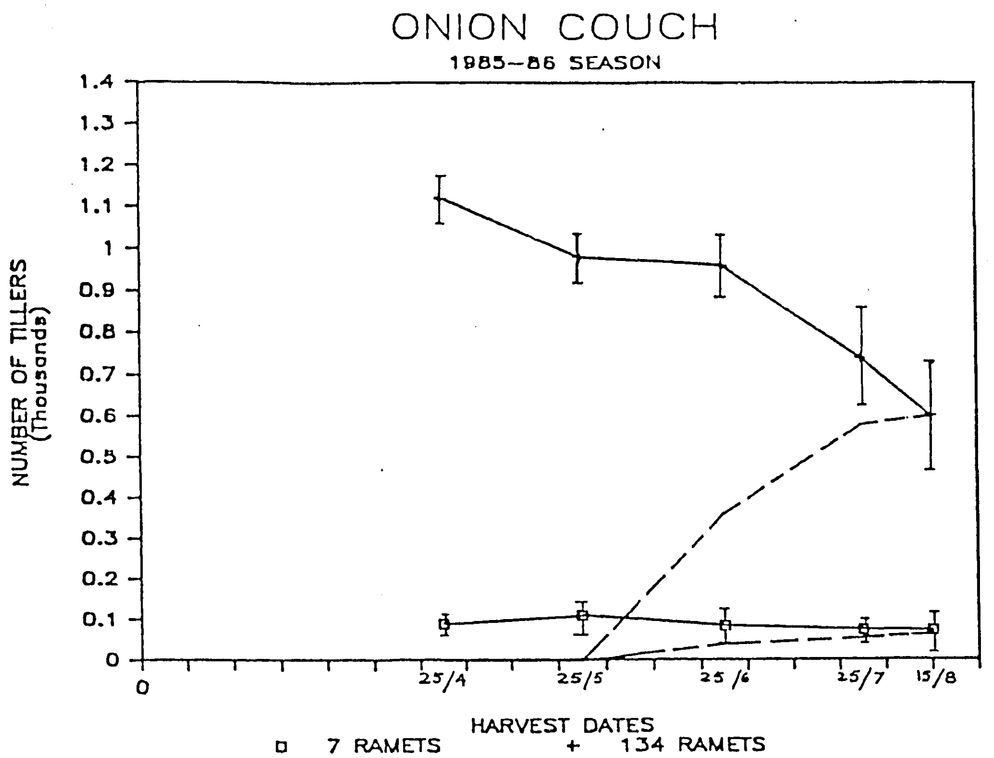


Fig. 3.5.3 Trends in mean number of tillers and density of inflorescence production by Tall oat-grass (m^{-2}) at different planting densities on five harvest dates, during two growing seasons. Tillers shown in solid lines and inflorescence in broken lines. With 95% confidence limits.



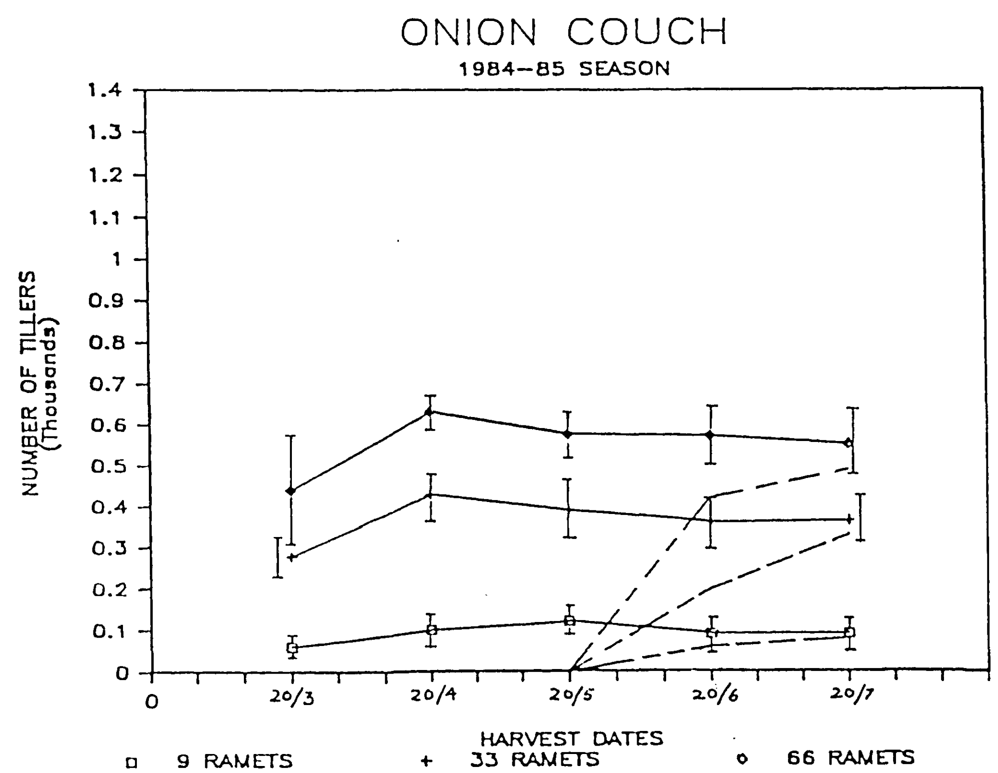
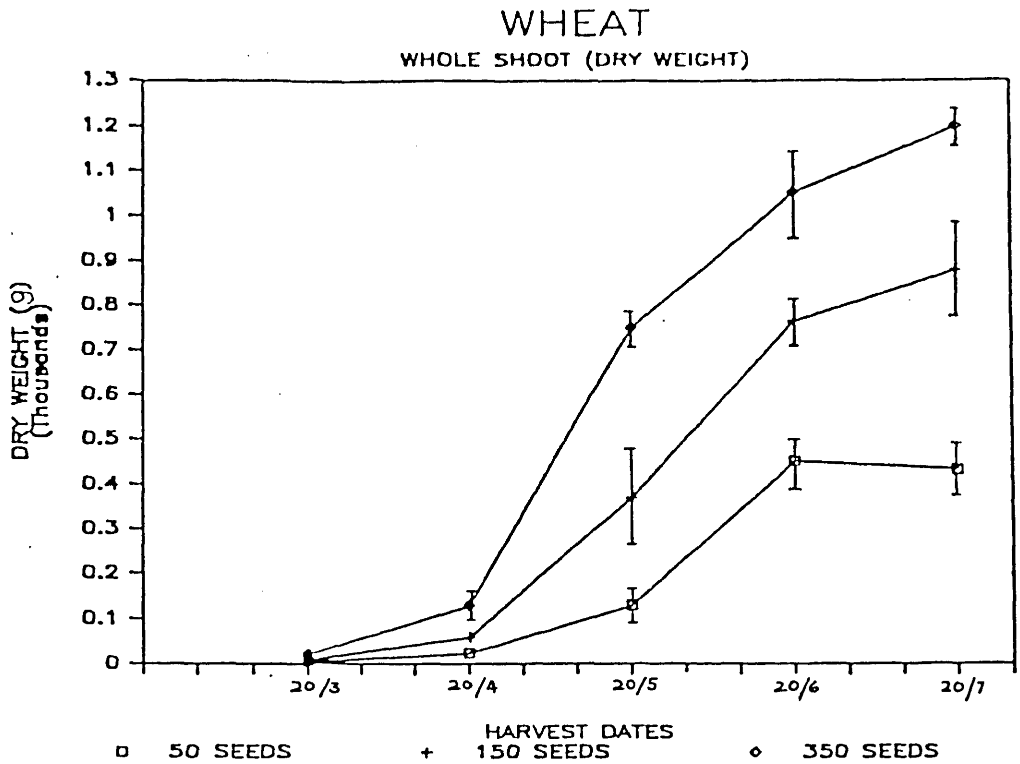


Fig. 3.5.4 Trends in mean number of tillers and density of inflorescence production by Onion Couch (m^{-2}) at different planting densities on five harvest dates, during two growing seasons. Tillers shown in solid lines and inflorescence in broken lines. With 95% confidence limits.



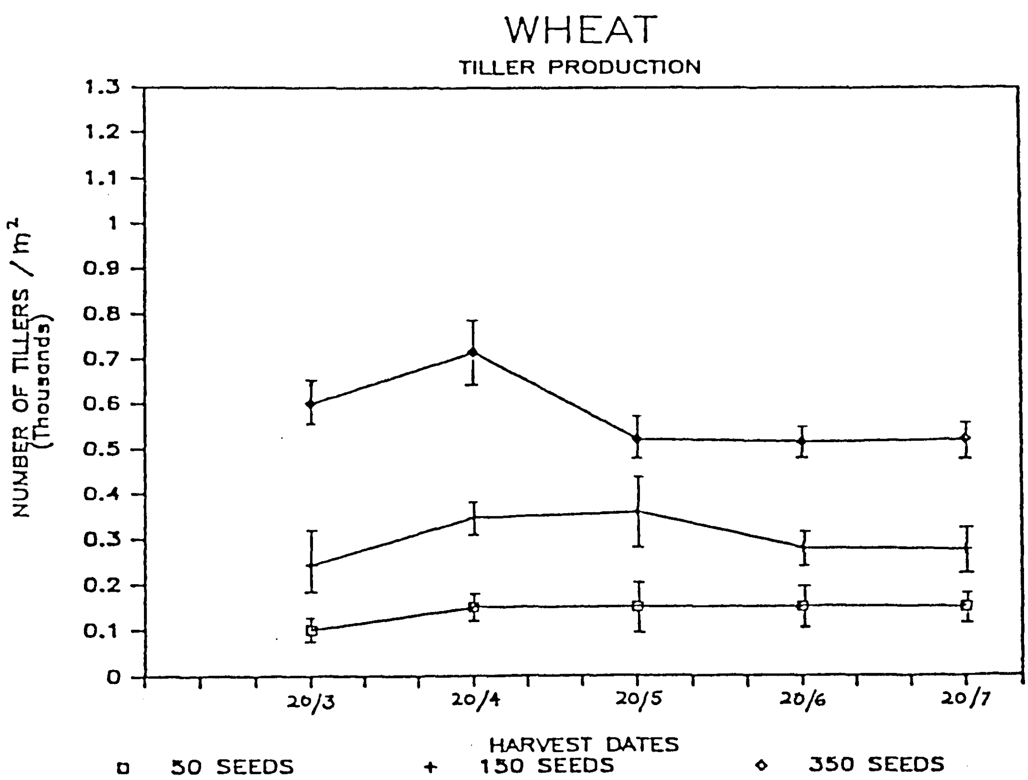


Fig. 3.5.5 Trends in dry weight and tiller production by wheat at different sowing densities on five harvest dates. With 95% confidence limits.

was more abrupt and significant at lower planting densities (33 and 66 ramets) in Tall Oat-grass (Fig.3.5.3) compared to Onion Couch (Fig.3.5.4), where no significant thinning was observed at corresponding densities. An obvious decline in tiller numbers was only observed in plots planted with 134 ramets, and even here the process was gradual rather than abrupt, as observed at the same density in Tall Oat-grass. Thinning in Wheat (Fig.3.5.5) took place in a manner similar to that observed in Tall Oat-grass. No new tillers were observed after the thinning phase in any plots throughout the period of the experiment. The tiller populations appeared to have stabilized after thinning (July harvest) and before entering the senescent phase, at approximately $550m^{-2}$ in Tall Oat-grass and Wheat and $700m^{-2}$ in Onion Couch.

Pattern of shoot elongation and heading

In Tall Oat-grass stems elongation started in April and accelerated in early May when stem produced flag leaves (Fig.3.5.3). Stems continued to increase in height until ear emergence which took place by the end of May (Fig.3.5.6). Onion Couch on the other hand remained vegetative during April and commenced elongation by the end of May and continued producing flower heads till the end of July. Differences in tiller height between the two varieties (Plate 3) during early months of growth nearly disappeared by the time of final harvest, when Onion Couch approached almost the same height as Tall oat grass (Fig. 3.5.6). In the 1985-86 season (apart from late tillering due to a delayed spring) stem elongation and heading in the two varieties followed a pattern similar to the 1984-85 season as is evident from Fig.3.5.3 and 3.5.4.

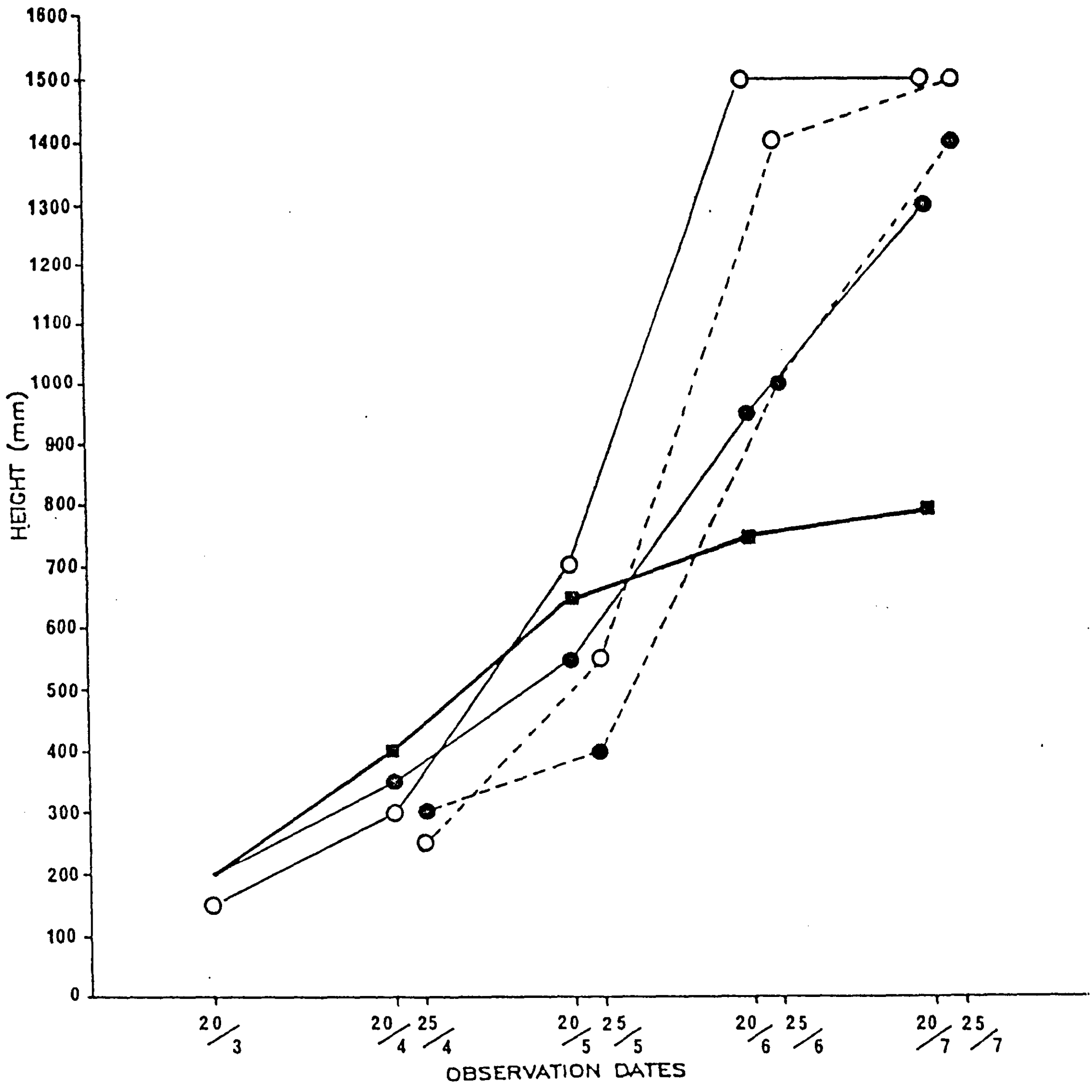
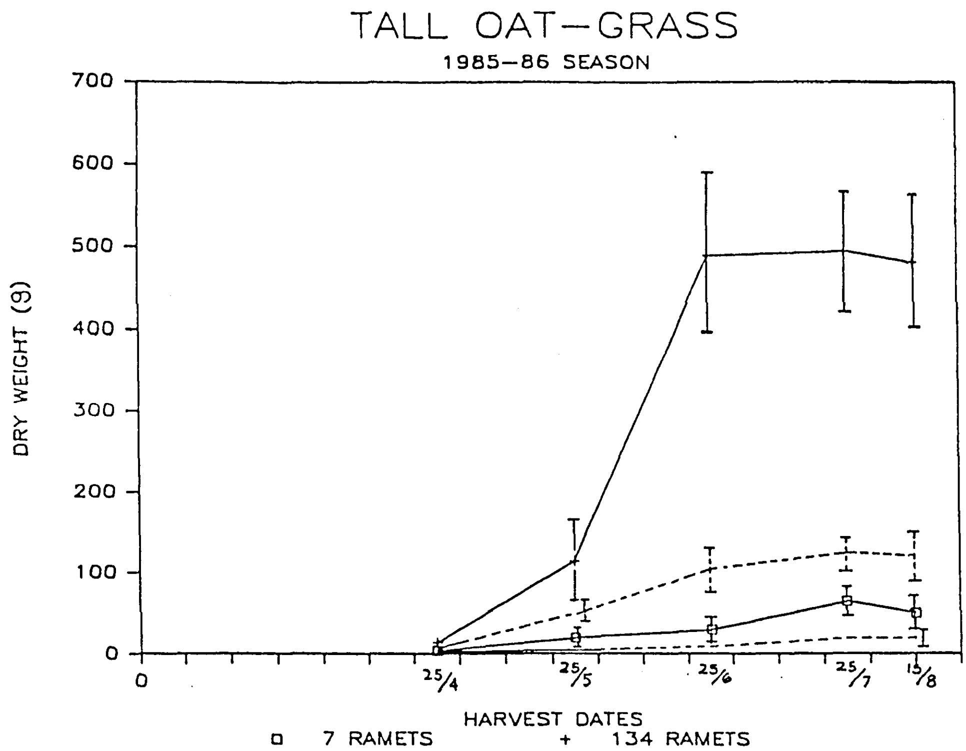


Fig. 3.5.6 Average shoot height of wheat (■), Onion Couch (●) and Tall Oat-grass (○) on five harvest occasions, during the two growing seasons:1984-85 seasons (solid lines) and 1985-86 season (broken lines).

Plate 3 Shoots of Tall Oat-grass (left) and Onion Couch (right) selected from the June harvest (25.6.86) to illustrate shoot elongation and flowering trends in the two varieties of Arrhenatherum.

Pattern of dry weight allocation to aerial tillers and basal internodes.

Dry weight production per plot increased rapidly for the first twelve weeks in both the varieties. In the third and fourth (May and June) harvests there was significantly greater increase in the dry weight of the whole shoot of Onion Couch compared to Tall Oat-grass (Figs. 3.5.9 and 3.5.10). Although no significant differences were found in the dry weight of the aerial tillers between the two varieties at the third and fourth harvests (in spite of the fact that the number of tillers was significantly less in Tall Oat-grass than Onion Couch), the dry weight of basal internodes was significantly higher in Onion Couch compared to Tall Oat-grass (Figs. 3.5.7 and 3.5.8). In Tall Oat-grass no significant change in the dry weight took place in the last two harvests (June and July) of the 1984-85 season (Fig.3.5.7), whereas in the last harvest (August) of the 1985-86 season the whole shoot lost dry weight presumably due to seed shedding and senescence during the ripening phase (Fig.3.5.9). In Onion Couch there was more marked change in dry matter production (especially, basal internode dry weight) between the last two harvests in the 1984-85 season (Fig.3.5.8) as most shoot were still gaining height and weight during this period of flowering (Fig.3.5.10). In the following season the aerial tillers of Onion Couch showed loss in weight in the final harvest (August) presumably due to seed shedding and senescence during this ripening phase, while basal internodes have shown slight increase in dry weight, presumably due to translocation of some metabolites during this ripening phase (Fig.3.5.8). Differences between final dry weight tend to be more convergent and less significant at lower planting densities (33, 66 ramets m^{-2}) in Tall Oat-grass compared to



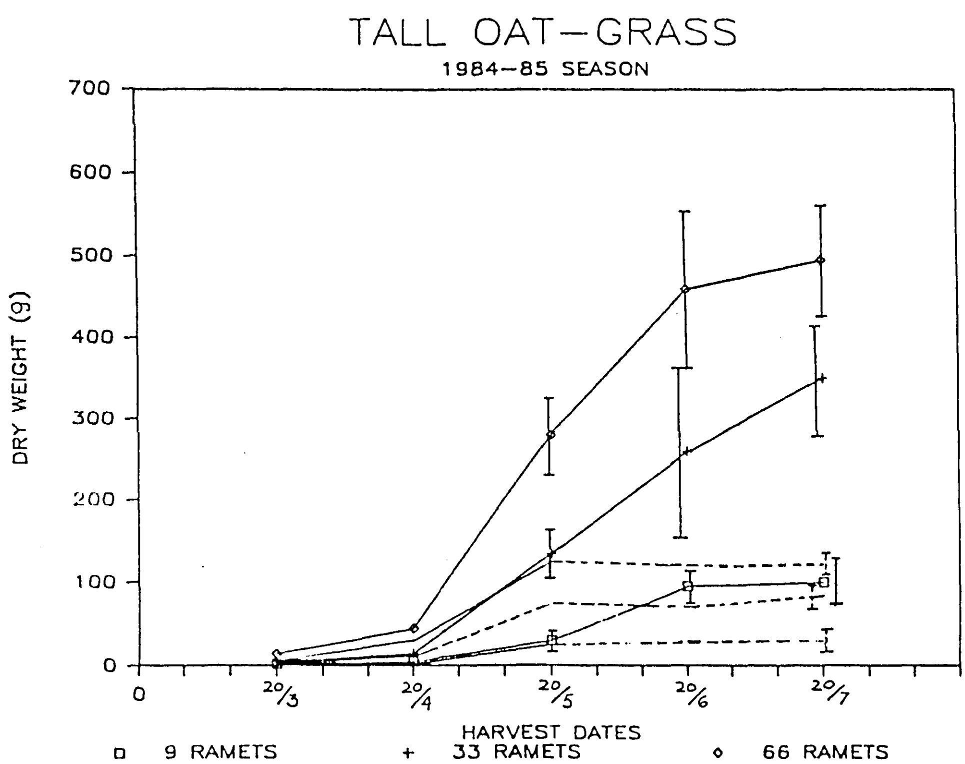


Fig. 3.5.7 The relationship between dry weight of aerial tillers (solid lines), basal internodes (broken lines) and planting density of Tall Oat-grass on five harvest dates during the two growing seasons. With 95% confidence limit.

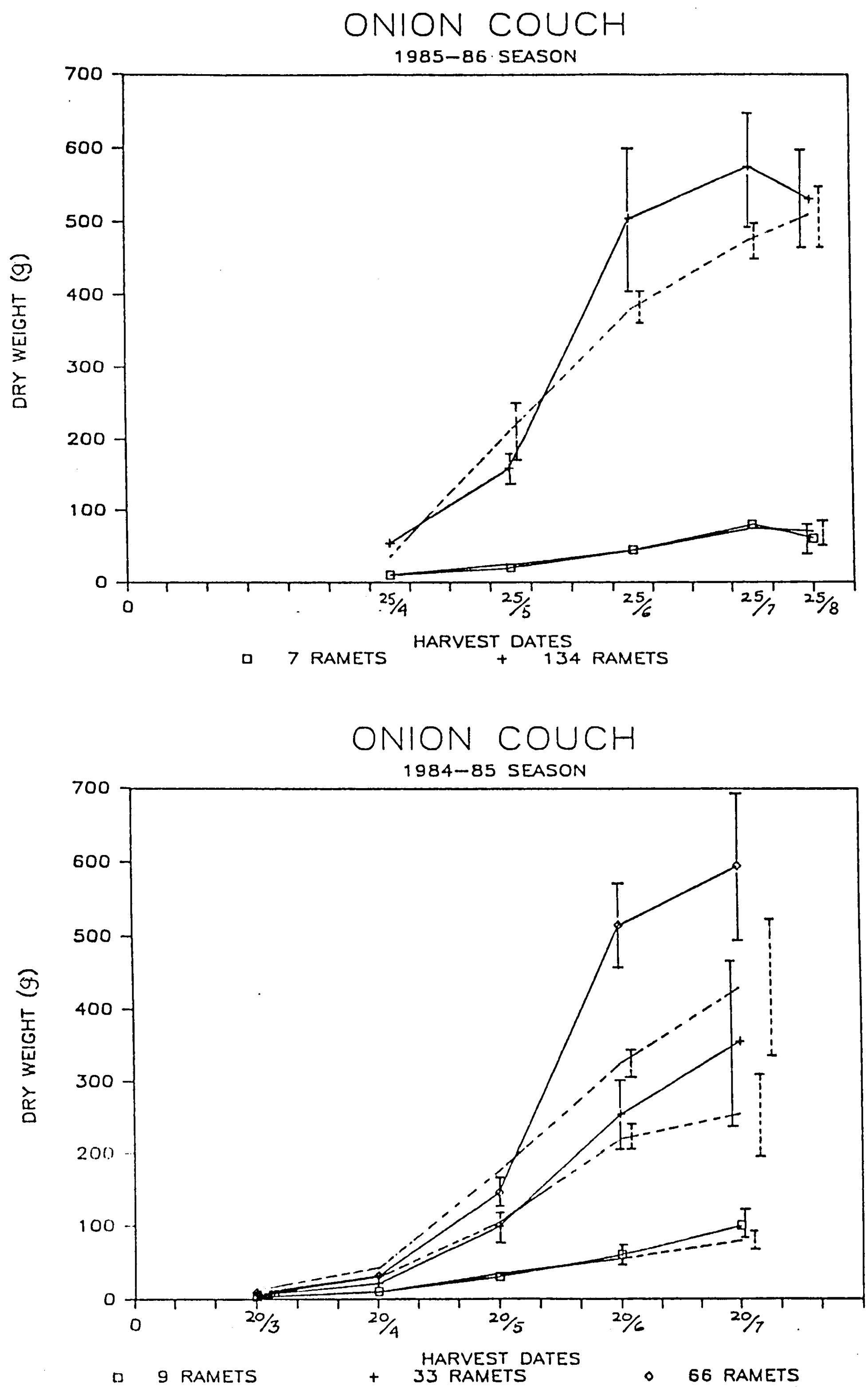
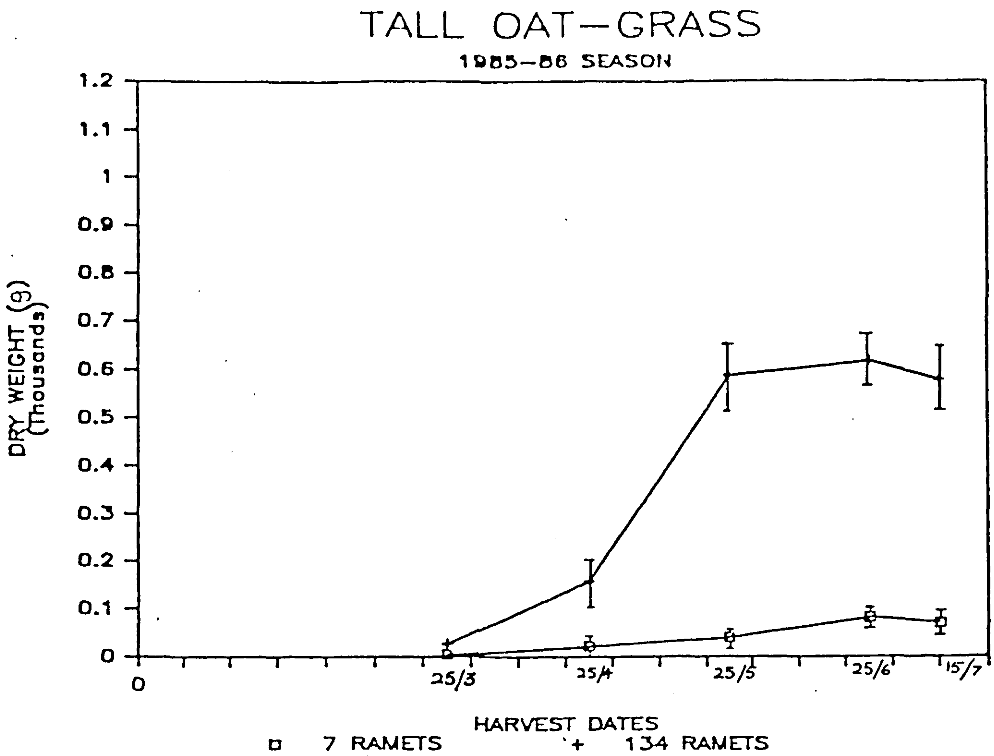


Fig. 3.5.8 The relationship between dry weight of aerial tillers (solid lines), basal internodes (broken lines) and planting density of Onion Couch on five harvest dates during the two growing seasons. With 95% confidence limit.



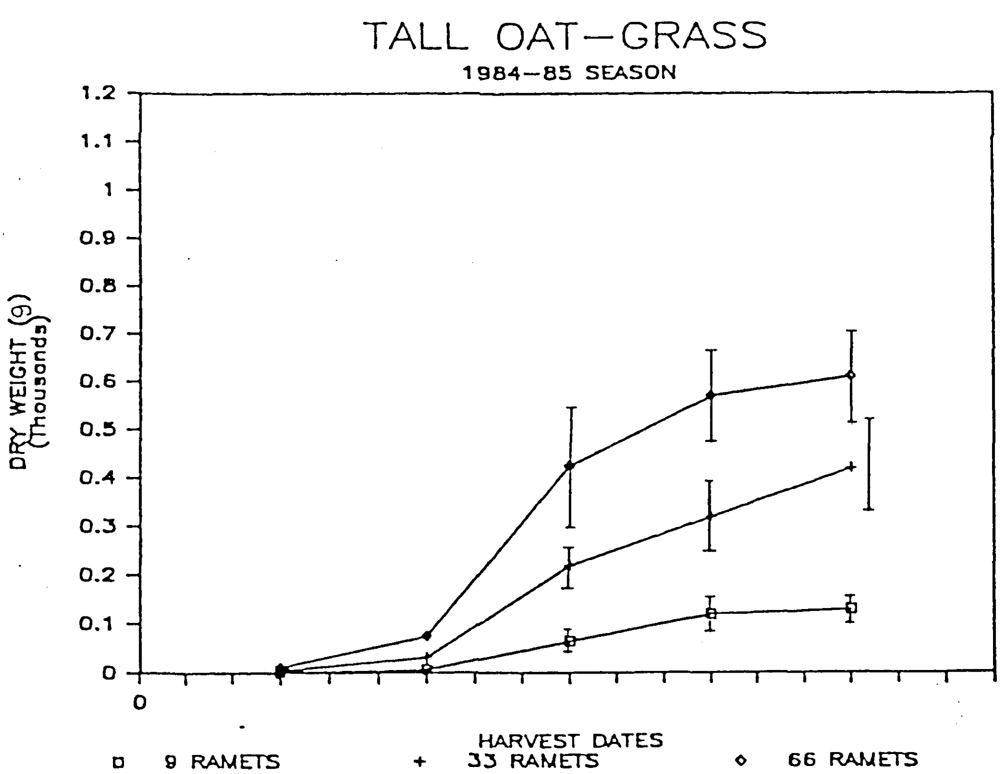
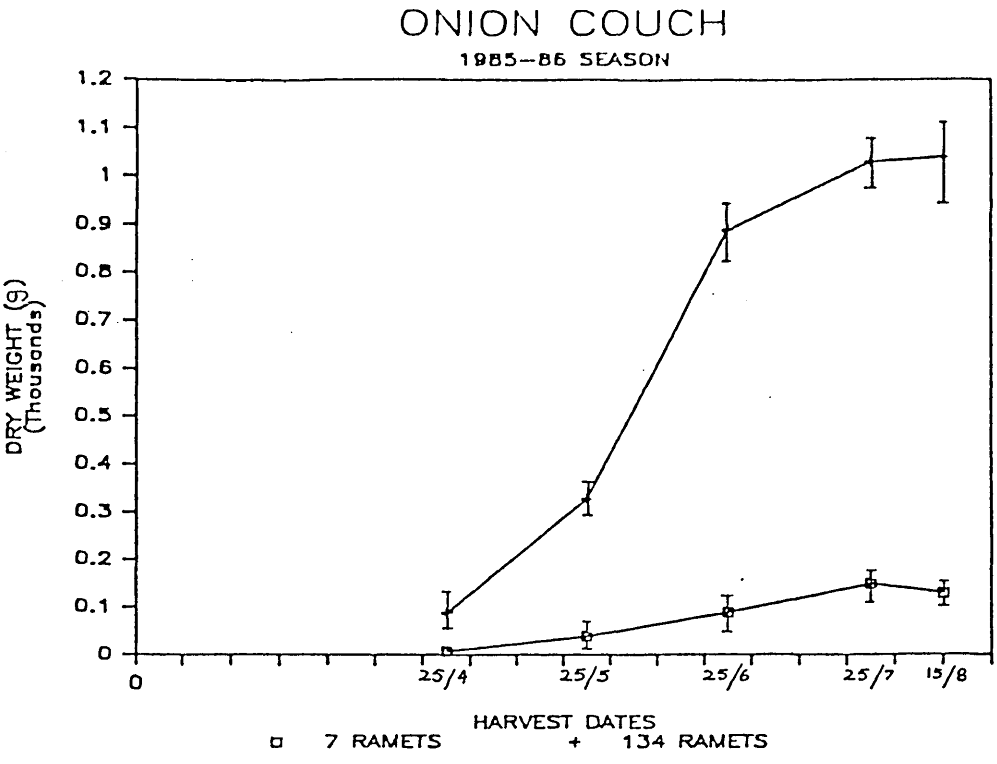


Fig. 3.5.9 The relationship between whole shoot weight and planting density of Tall Oat-grass on five harvest dates during the two growing seasons. With 95% confidence limit.



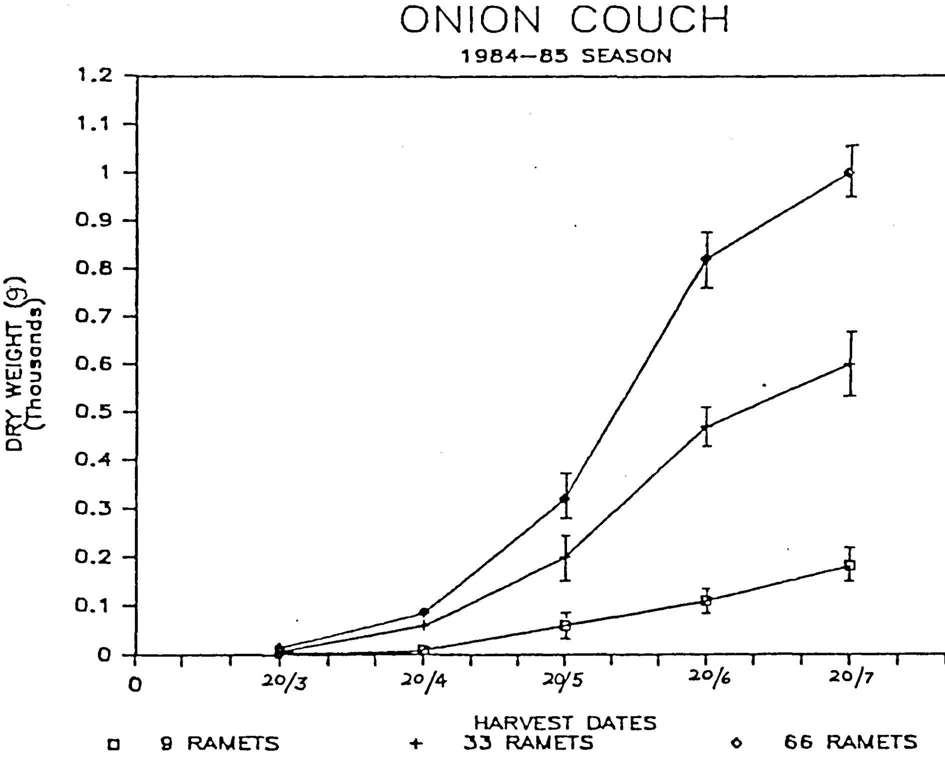


Fig. 3.5.10 The relationship between whole shoot weight and planting density of Onion Couch on five harvest dates during the two growing seasons. With 95% confidence limit.

Onion Couch at similar densities (Figs. 3.5.9 and 3.5.10).

Pattern of basal internodes dry weight as a proportion of whole shoot (aerial tillers plus basal internodes)

In Tall Oat-grass this proportion was slightly below 0.5 in the early harvests but dropped considerably below 0.5 in the later harvests, and never exceeded 0.5 at any stage during its growth cycle (Fig.3.5.11). In Onion Couch this proportion exceeded 0.5 during the early stages of growth (corresponding to the period of bulb formation after the tillering phase) and then slightly drops below 0.5 (coinciding with tiller elongation) but it generally remained around 0.5 throughout its growth cycle (Fig.3.5.11). Similar proportions were observed for the 1985-86 season (Fig.3.5.12).

Pattern of bulb production in Onion Couch

It is evident from Fig. 3.5.13 that the period of intense tillering in Onion Couch is followed by a period of bulb initiation. This morphological phase of bulb formation as indicated earlier in Chap. 3.1 is also reflected physiologically in increase in basal internode dry weight as a proporton of the whole shoot. Significant increase in the number of bulbs was recorded in May and it appears that most of the bulbs were initiated during this phase which extends from the middle of April to the end of May. Any tillers of Onion Couch which survived up to this stage resulted in the production of viable ramets which remained intact, although a large proportion of the aerial tillers which produced them were lost during the following phase of shoot elongation. Evidence of this contribution to ramet production comes from the number of ramets excavated at the final

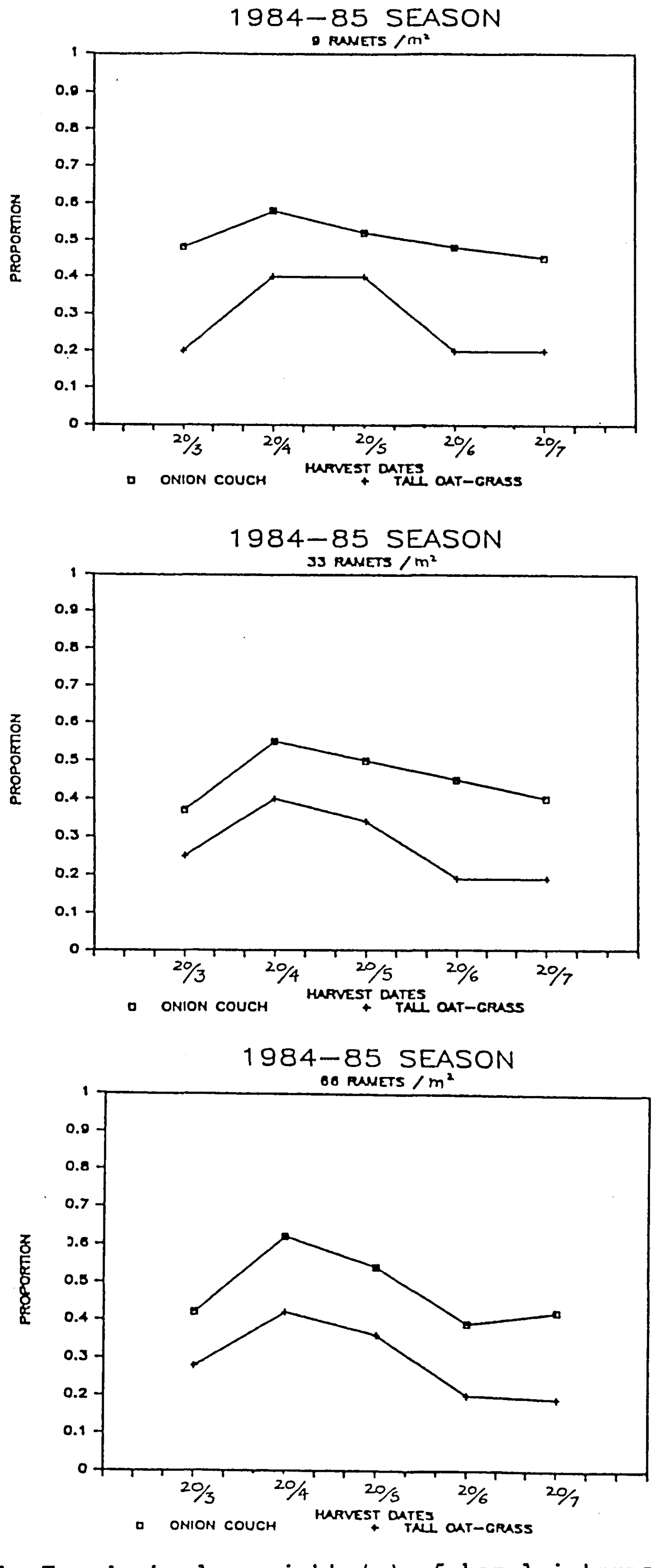
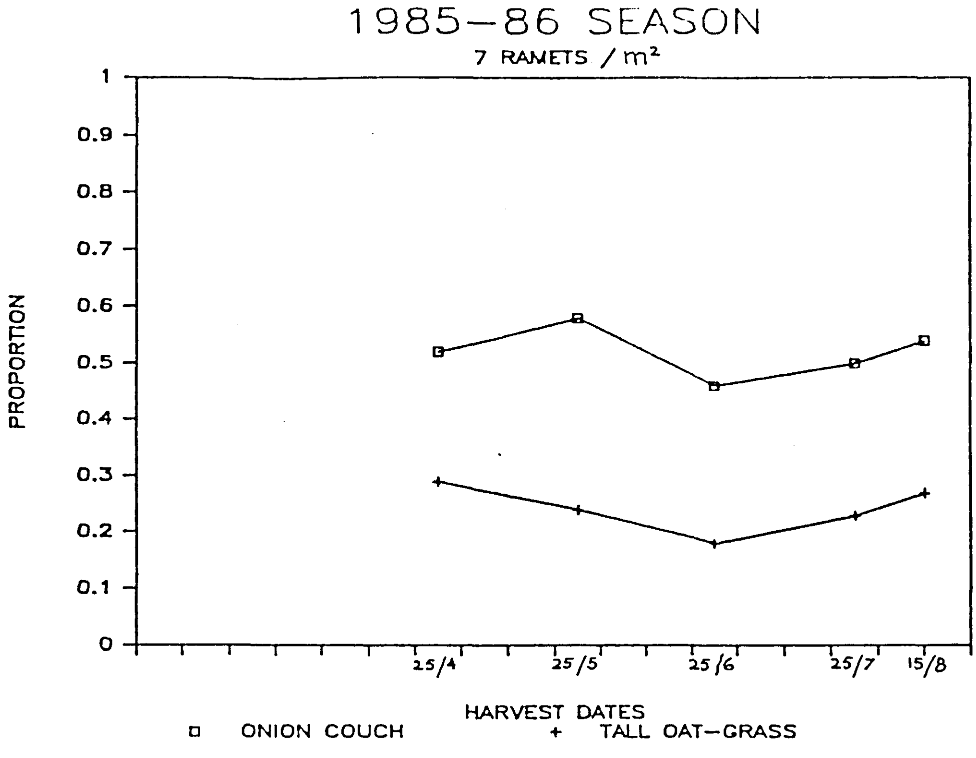


Fig. 3.5.11 Trends in dry weight (g) of basal internodes as a proportion of whole shoot in the two Arrhenatherum varieties planted at different densities on five harvest dates in 1984-85 season. With 95% confidence limit.



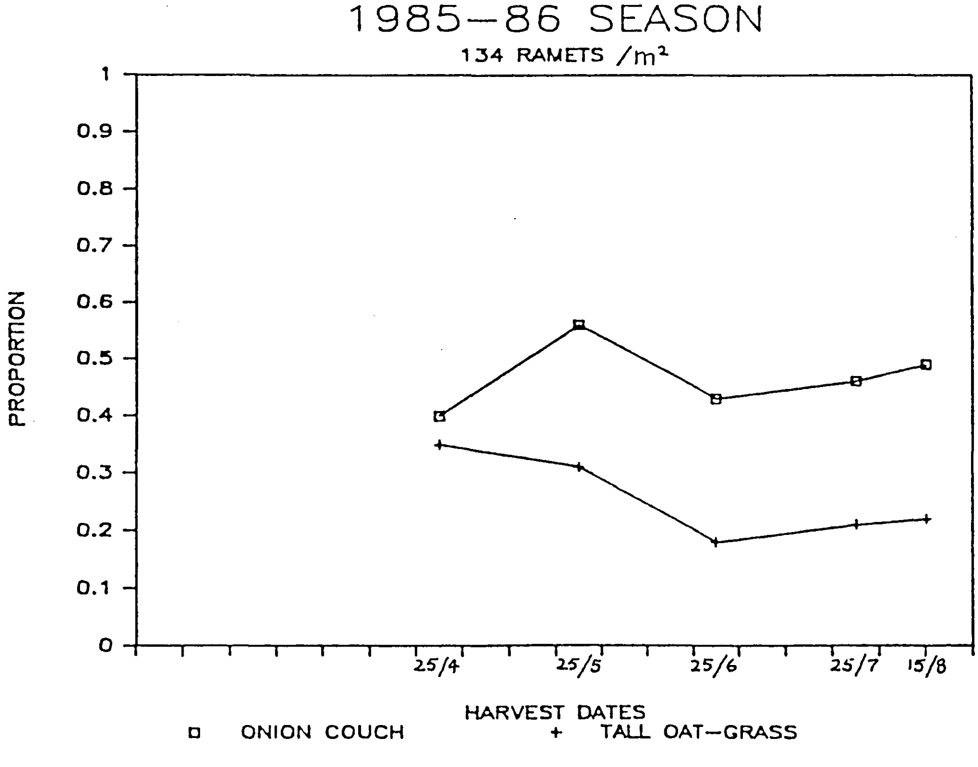


Fig. 3.5.12 Trends in dry weight (g) of basal internodes as a proportion of whole shoot weight in the two <u>Arrhenatherum</u> varieties planted at different densities on five harvest dates in 1985-86 seasons. With 95% confidence limit.

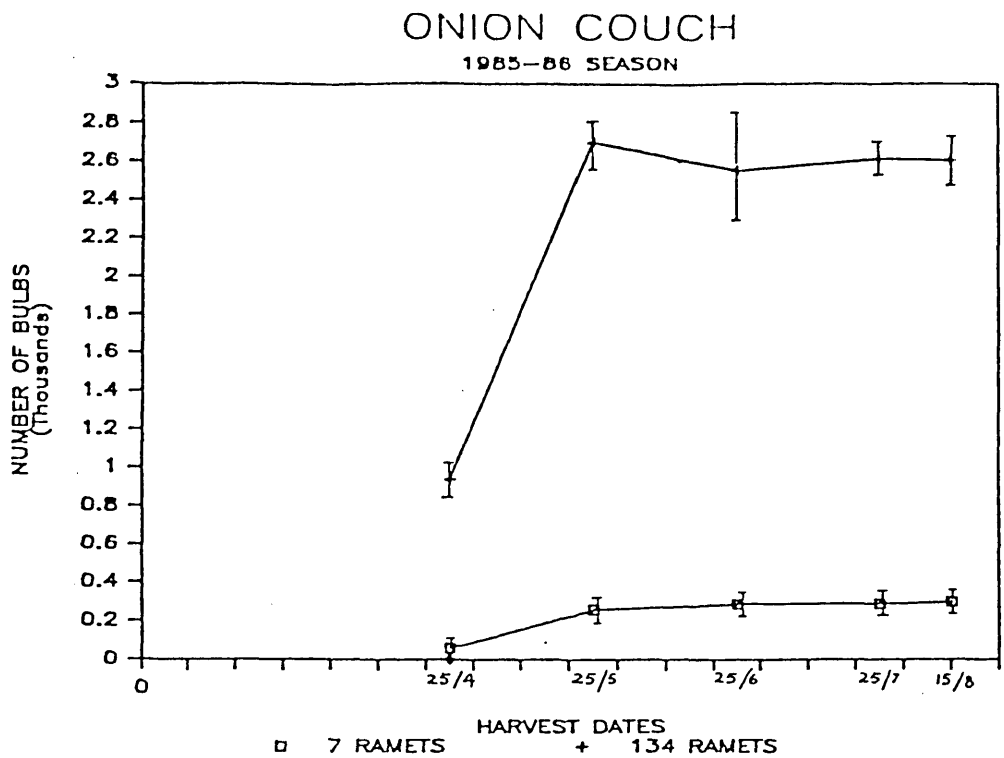
harvest, which exceeded (significantly) the number of flowering tillers present at the time of final harvest (Fig. 3.5.14).

Proportion of two and three bulb ramets in Onion Couch

The proportion of three bulb ramets was significantly greater than two bulb ramets in all plots irrespective of planting density after the second harvest (Figs. 3.5.15 and 3.5.16). Although the ramets formed in densely planted plots were greater in number they were smaller in size and thus weight as can be seen in Fig. 3.5.13, moreover, they suffered heavy tiller mortality (Fig. 3.5.4) compared to less densely planted plots. This indicates that the response of ramets to density stress is more plastic compared to aerial tillers. Most of the bulb formation was completed before aerial thining so in spite of the death of aerial tillers the basal bulb contribution remained, adding to the weight of the resulting vegetative ramets, as observed earlier.

3.5.4 Discussion

It is apparent from the results that the values of parameter β (de Wit, 1960) have given a meaningful estimate of the competitive relation between the two Arrhenatherum varieties and Wheat. The curves obtained by plotting the β values through time are in agreement with the competitive status ascertained in later sections (Chaps.3.6 and 3.7). Interpretation of the curves (in terms of de Wit, 1960; and Spitters and van den Berg, 1982) has shown that Onion Couch has the highest initial value compared to Wheat and Tall Oat-grass, this higher initial value reflects the sizes and hence dry weight of planted ramets of Onion Couch (0.80g dry weight) compared to that of seed of Wheat (0.045) and ramets of Tall



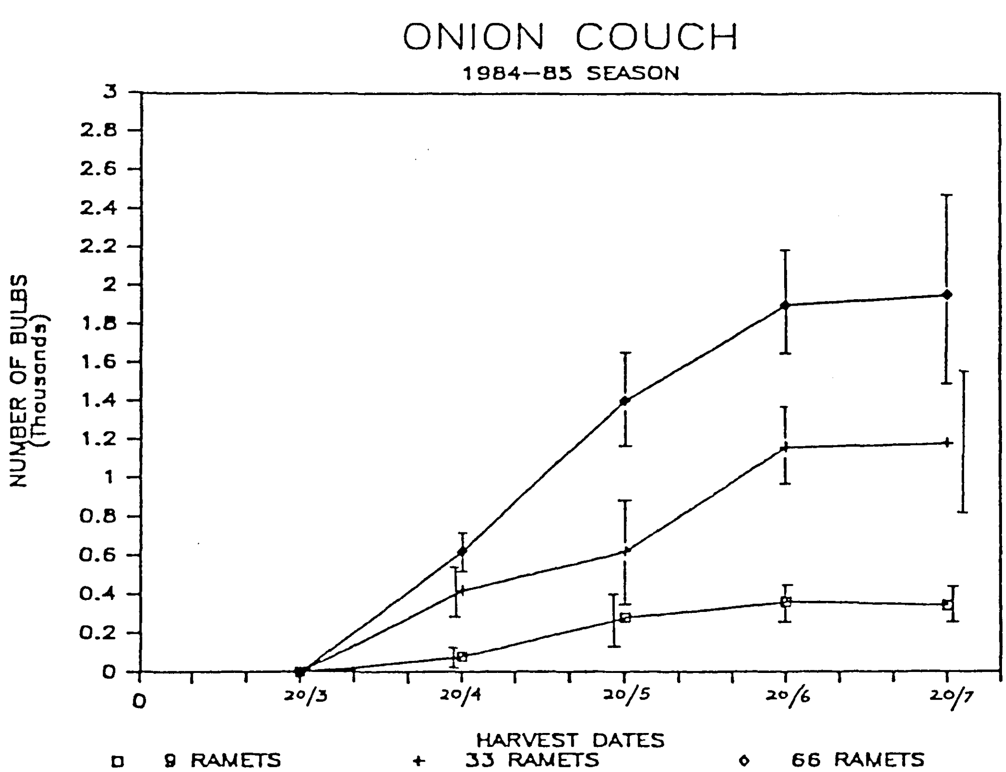
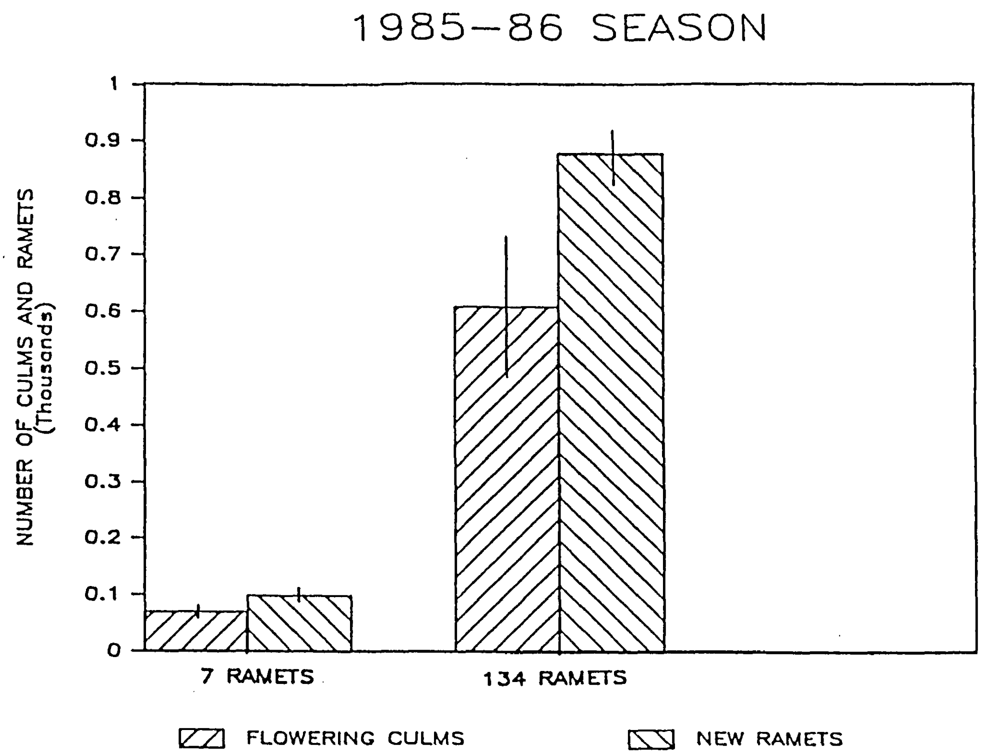


Fig. 3.5.13 Trends in mean total number of bulbs produced by ramets of Onion Couch planted at different densities on five harvest dates during the two growing seasons. With 95% confidence limit.



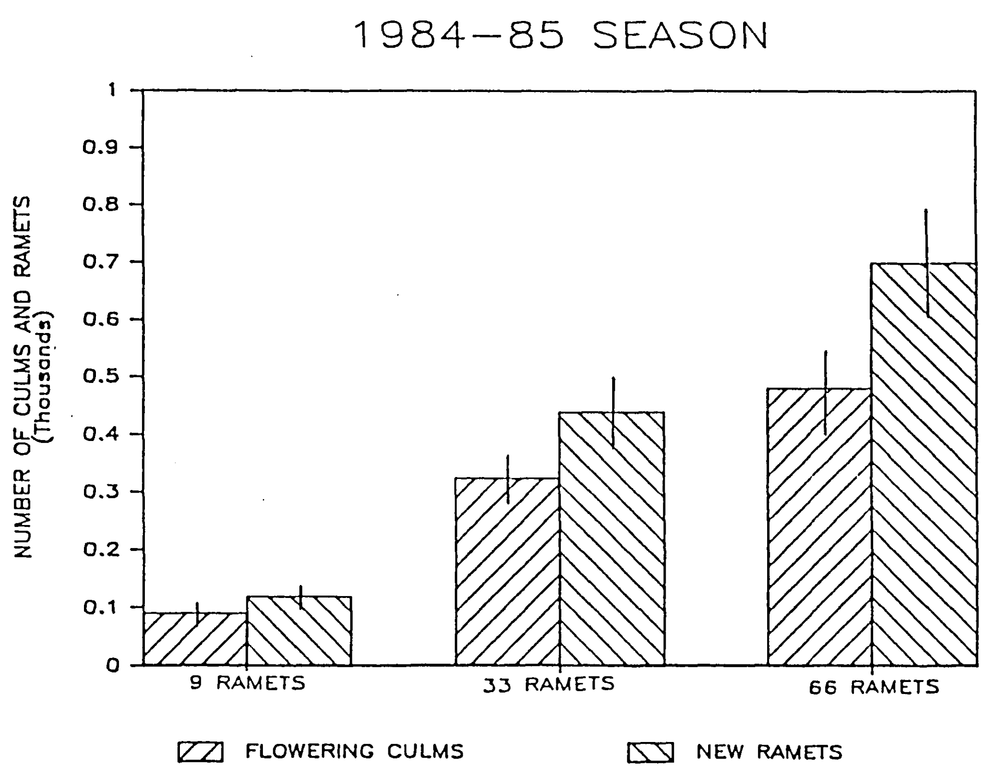


Fig. 3.5.14 Histogram showing a comparison of number of inflorescences and total number of ramets in the July harvest during the two growing seasons.

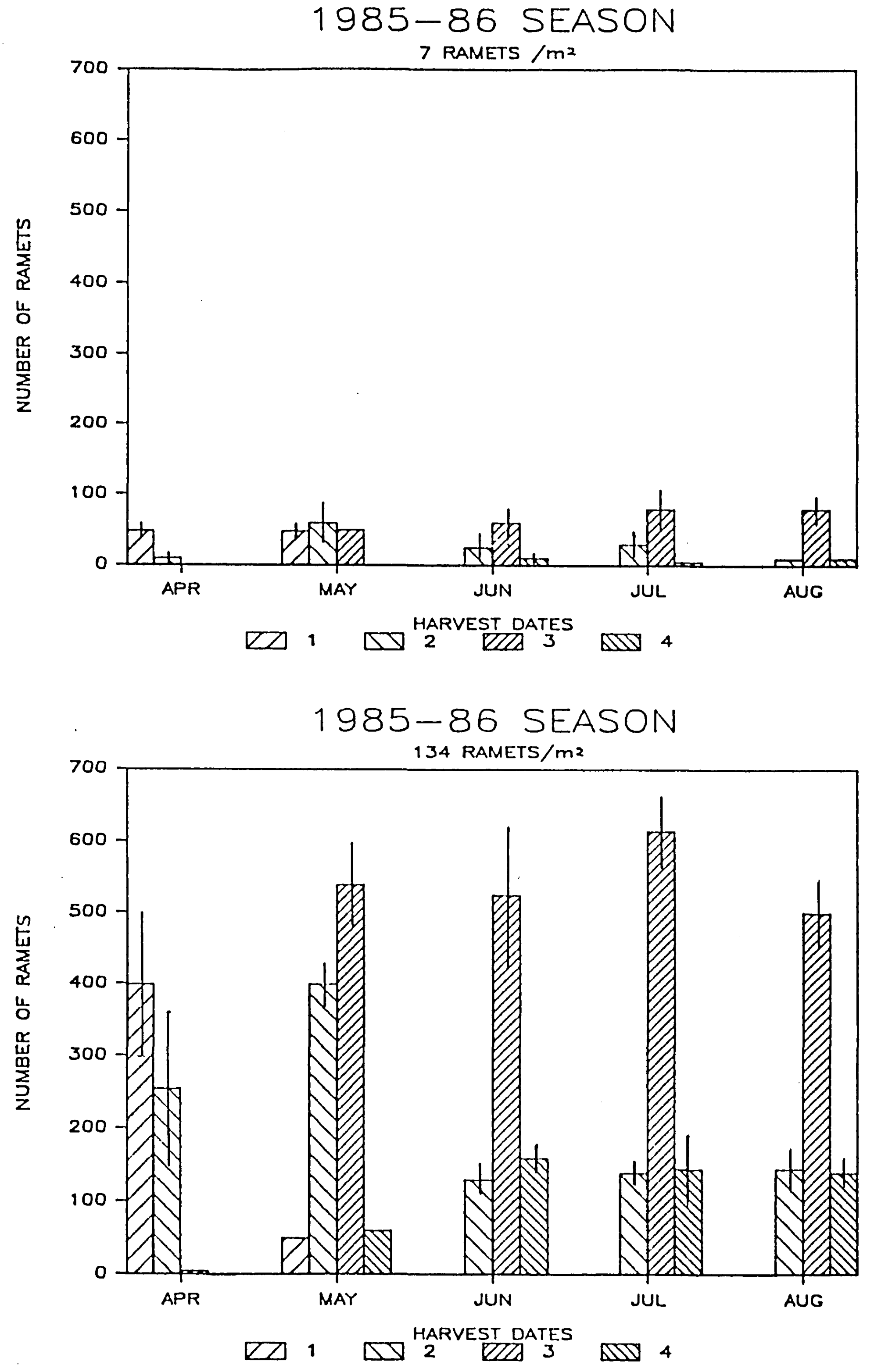


Fig 3.5.15 Histogram showing the proportion of 1,2,3,and 4 bulb ramets of Onion Couch on five harvest dates in 1985-86 season. 95% confidence limits are included.

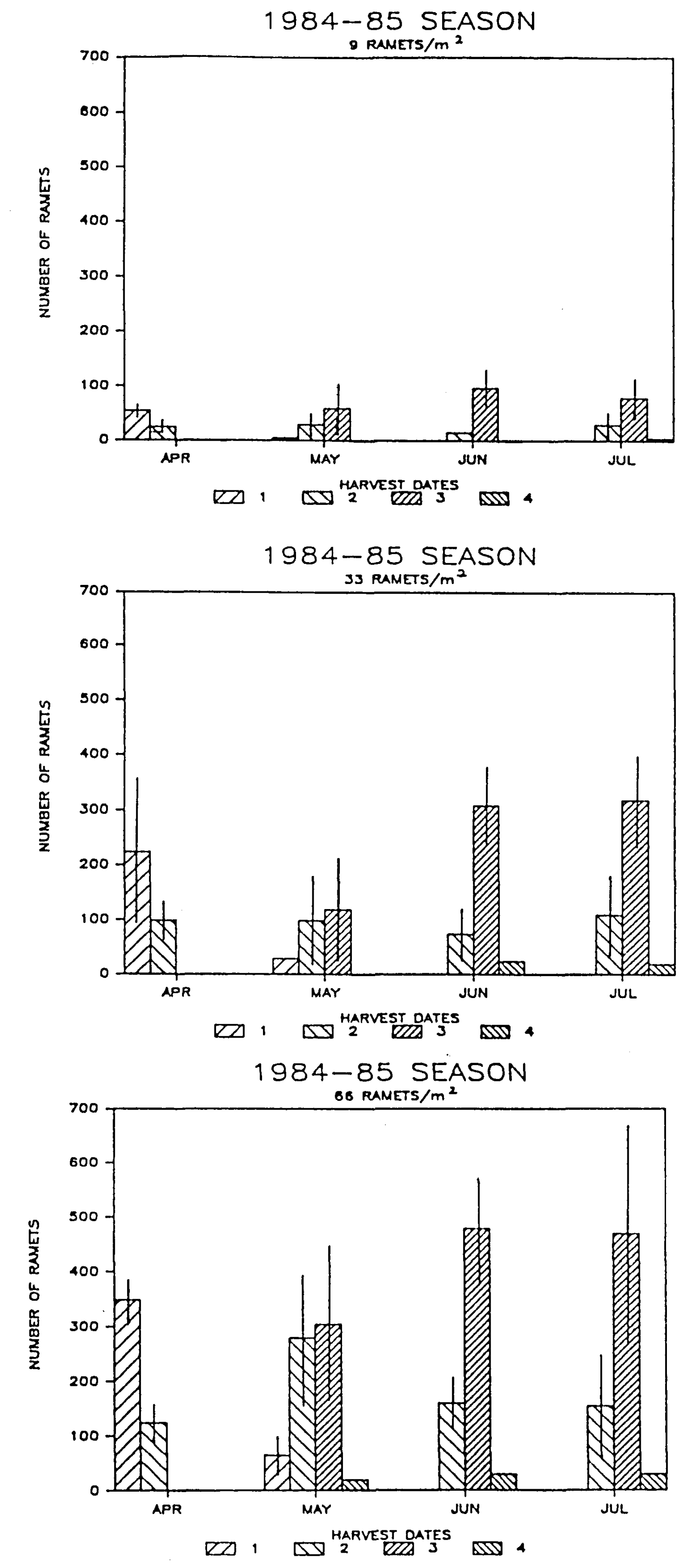


Fig 3.5.16 Histogram showing the proportion of 1,2,3,and 4 bulb ramets of Onion Couch on five harvest dates in 1984-85 season. 95% confidence limits are included.

Oat-grass (0.25g dry weight). The very low (negative) values of β for Tall Oat-grass early in the growing season probably reflect the inefficiency of the ramets as they are not natural propagules. After the initial higer values, the curve representing the β values in time for Onion Couch showed considerably slower pace (which seemed to be representing the bulb formation period) in the succeeding harvests and finally reached values similar to that of Tall Oat-grass (stem elongation period). On the other hand the β values for Wheat increased considerably in the successive harvests resulting in a steeper curvature and higher absolute growth rate compared to the two Arrhenatherum varieties. In the last harvest the curves flattened off representing a period which coincided with the flowering phase of the crop. Tall Oat-grass, after a slow start, followed a pattern resembling Wheat. The curvature of β values in time has efficiently reflected the inherent growth habit of the two Arrhenatherum varieties and Wheat. It is very obvious from Figs. 3.5.1 and 3.5.2 that the initial higher values of Onion Couch do not indicate that it occupies space prior to the crop but these values represent the growth in the field when the plants do not feel each other's presence. So it is very clear that in the case of Onion Couch the greater initial values do not determine the final outcome of competition which is actually determined by the successive β values at succeeding harvests and the resulting complete curve of β values for each species (as shown by Wheat and to lesser extent by Tall Oat-grass).

The flowering period was the same in both seasons (June-July), which shows that in spite of the delayed spring (1985-86) the flowering period was similar, an indication of response of day length and temperature as also has been reported by Pfitzenmeyer (1959).

The two Arrhenatherum varieties showed close resemblance to Wheat in the tillering, thinning and flowering phases of their growth cycle. Tall Oat-grass resembled Wheat more in the early thinning and flowering pattern compared to Onion Couch as a result of which a smaller proportion of the tillers of Tall Oat-grass, which arose during the tillering phase survived the early flowering (stem elongation) compared to Onion Couch where delayed flowering resulted in greater proportion of tillers surviving in the vegetative condition. This thining pattern is also known (Cooper, 1949; Cooper and Saeed, 1951; Langer, 1979) in several other grasses where the great bulk of green matter production by the rapidly elongating flowering culms, lowered the light intensity in the stands and thus resulted in self thining. The difference in thinning response between the Tall Oat-grass and Onion Couch seemed to be directly related to the rate and time of flowering and physiologically determind by the allocation of dry matter to the aerial tiller and basal internodes. In contrast to the stem elongation phase of Tall Oat-grass, Onion Couch showed two distinct phases during this time period. In the first phase it differentiated the basal bulbs which formed the next year's ramets (a phase also reflected by the increase in the basal bulb dry weight as a proportion of total shoot dry weight) which acted as sinks for assimilates which otherwise would have been available for shoot elongation and consequently early thinning. In the second phase it underwent stem elongation and consequently flowering. It is this inherent potential of this variety which caused delayed flowering and hence greater plasticity.

The capacity of a plant to react to competitive stress by variation in plasticity or by mortality has been shown in a large number of experimental investigations (Harper, 1977). It has been observed here, that Tall Oat-grass at a high planting density results in increase in tiller mortality with no effect on dry weight production. Onion Couch on the other hand possesed greater capacity to absorb density by producing little mortality in aerial tillers by reducing their dry weight, whereas, the basal internodes absorb this density response more efficiently by producing smaller ramets. In fact the basal bulbs of Onion Couch suffer little mortality as most of the bulb formation is completed before the commencement of thinning.

3.6 Analyses of interference between the two varieties of *Arrhenatherum* and wheat.

3.6.1 Introduction

In order to examine the extent of competition for biological space (in the sense of de Wit) between the two varieties and crop, a Replacement Series Experimental procedure developed by de Wit (1960) was used. In this type of study the species under investigation are grown together in varied proportions and their growth in mixture compared with that in monoculture. The Replacement Series has been used widely in interpreting the interaction between species of mixed populations (e.g. Hall 1974a, 1974b; Baeumer and de Wit, 1968). It was expected that this experiment would assess the usefulness of the concept in interpreting the nature and extent of interference occurring between the two varieties and a crop. In addition, two contrasting soils were used to test the influence of growing conditions on the extent of interference.

3.6.2 Methods

Three replacement series were set up:

a) Onion Couch:Wheat

b) Tall Oat-grass:Wheat

c) Tall Oat-grass:Onion Couch

The following two soil types were used:

1. John Innes compost No 3.
2. Unfertilised chalk soil from an arable field margin.

Single ramets comprising of single shoot bases of the two Arrhenatherum varieties and spring Wheat (cv.Timmo) seedlings were planted on 12.5.84 in polythene bags of 20.0cm diameter and 30.0 cm depth. Ramets and seeds were planted in evenly dispersed fashion in the mixtures so that maximum interaction could take place between them. Each bag held twelve plants, seven combinations were used for each series (12:0; 10:2; 8:4; 6:6; 4:8; 2:10; 0:12) and each combination was replicated twice.

The pots were placed in a rabbit fenced area on a large polythene sheet and watered from time to time when necessary. The experiment was harvested on 2.8.84. Aerial tillers of wheat and the two varieties of Arrhenatherum were clipped at the soil surface, basal internodes of the two varieties were dug up, washed and oven dried at 100°C for twenty four hours. The term yield refers to dry weight of aerial tillers and the term whole shoot yield refers to aerial tillers plus basal internodes of the two varieties. The raw data were plotted in the Replacement Series graphs along with the smoothed yield curves (Figs. 3.6.1 and 3.6.2). Smoothed yield curves were obtained by using a version of de Wit's (1960) model and a computer program (DEBIN), written by Dr.A.J.Morton of Imperial College, fitted the model iteratively. Estimated Relative Crowding Coefficients were used in expressing the competitive ability of the species. In addition, Relative Yield Totals based on raw data were calculated for further interpretation (de Wit,1960) of the replacement series experiments. The following observations were made at the time of the harvest:

1. Dry weight of aerial tillers.
2. Dry weight of basal internodes of the two varieties.
3. Number of tillers and flowering heads.
4. Number of new bulbs of Onion Couch.

3.6.3 Results

Inspection of the smoothed curves fitted by DEBIN (Figs. 3.6.1 A) revealed that, in John Innes compost, Wheat yielded more than the two Arrhenatherum varieties which yielded less in mixed culture than that expected by their monocultures and the initial planting proportions. Wheat had thus crowded the two Arrhenatherum varieties out of the space initially alloted. The competitive power of the plants became evident when the Relative Crowding Coefficient (K) was used to interpret the results. Wheat proved to be more aggressive when grown in mixtures with Onion Couch than with Tall Oat-grass. When the two components: aerial tiller yield and the whole shoot yield were analyzed separately, Wheat had the same Relative Crowding Coefficient for both components of Tall Oat-grass (Figs. 3.6.1a-b), but increased considerably when total shoot yield of Onion Couch was considered (Figs. 3.6.1c-d). The K of Tall Oat-grass was higher than that of Onion Couch when the two varities were grown together in the replacement series, although here K of Tall Oat-grass was slightly less when the whole shoot yield of Onion Couch was considered (Figs. 3.6.1 A, e-f).

Since the model fitted by DEBIN is based on the assumption that the species compete for the same space, Relative Yield Total (RYT) values calculated from the fitted curves, could not fail to be anything other than one, for this reason raw data (means of two replicates) were used to calculate the relative yield for each species and combinations. RYT of the three Replacement Series i.e Tall Oat-grass:Wheat, Onion Couch:wheat and Onion Couch:Tall Oat-grass, in all combination was found to be around one (Fig. 3.6.1 B).

In the Replacement Series on unfertilised chalk soil (3.6.2 A) all the species suffered a marked reduction in the monoculture and mixture yields, The plants here tillered less (Tables 3.3 , 3.4 and 3.5) and had the symptoms of nitrogen deficiency (chlorosis). K of Wheat suggests that it has lost its competitive vigour observed in John Innes compost, especially, against Tall Oat-grass. It was also observed that there was a decrease in the K of Wheat (Figs. 3.6.2 A, c-d) when the the whole shoot yield of Onion Couch was considered, which is contrary to what was observed earlier in John Innes compost (Figs. 3.6.1 A). The Relative Crowding Coeffiecient of Tall Oat-grass in mixtures with Onion Couch increased considerably on this soil (Figs. 3.6.2 A, e-f).

Fig. 3.6.1 Replacement series diagrams of plants grown in John Innes medium, a) aerial tillers of Tall Oat-grass (tog) and wheat (w). b) whole shoot of Tall Oat-grass and wheat. c) aerial tillers of Onion Couch and wheat. d) whole shoot of Onion Couch and wheat. e) aerial tillers of Tall Oat-grass and Onion Couch. f) and whole shoot of Tall Oat-grass and Onion Couch. A) Fitted curves (based on de Wit's model, 1960) are shown in solid lines and actual data points are superimposed as symbols: wheat (■), Tall Oat-grass (⌀) and Onion Couch (●). B) Showing the Relative Yield Total (RYT) of: mixtures in broken lines and the two Arrhenatherum varieties and wheat as solid lines with symbols.

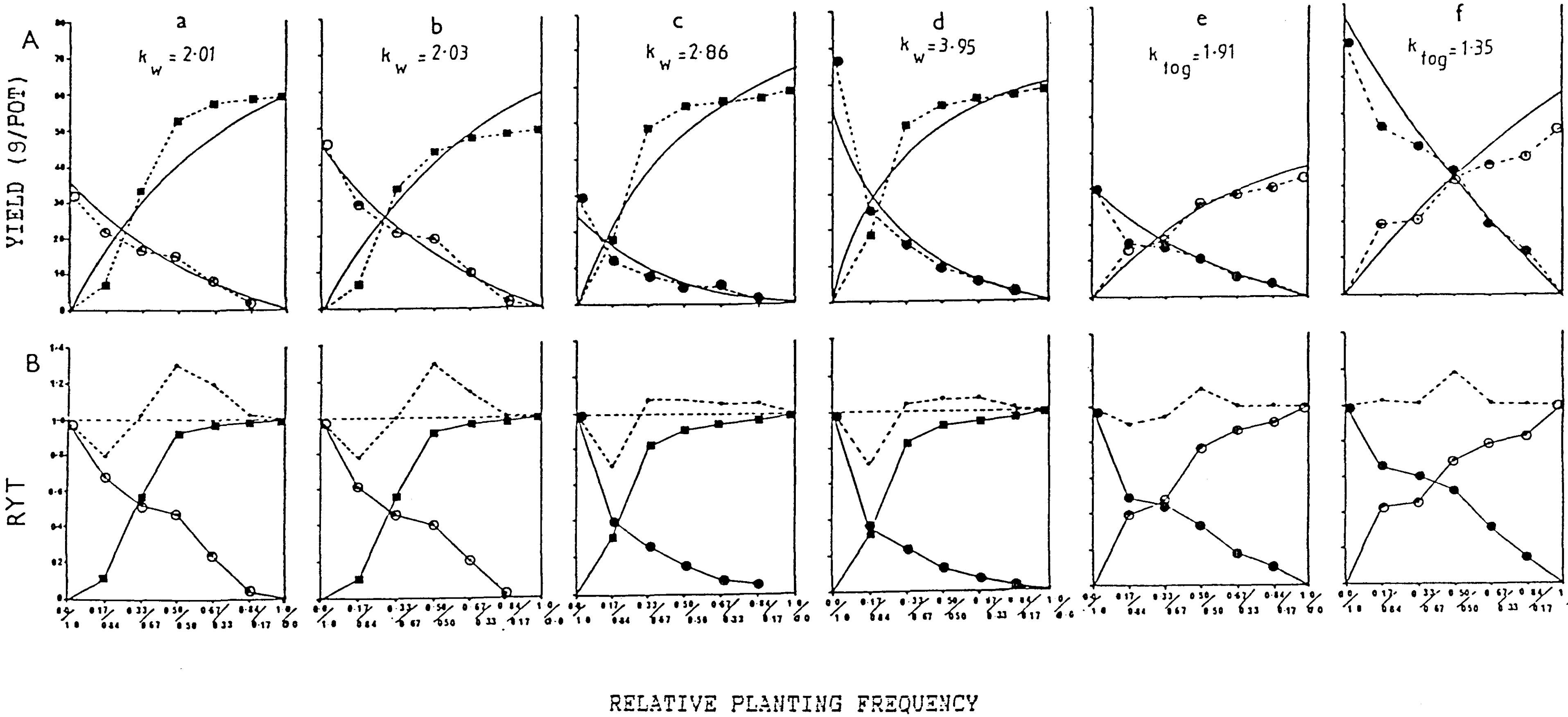
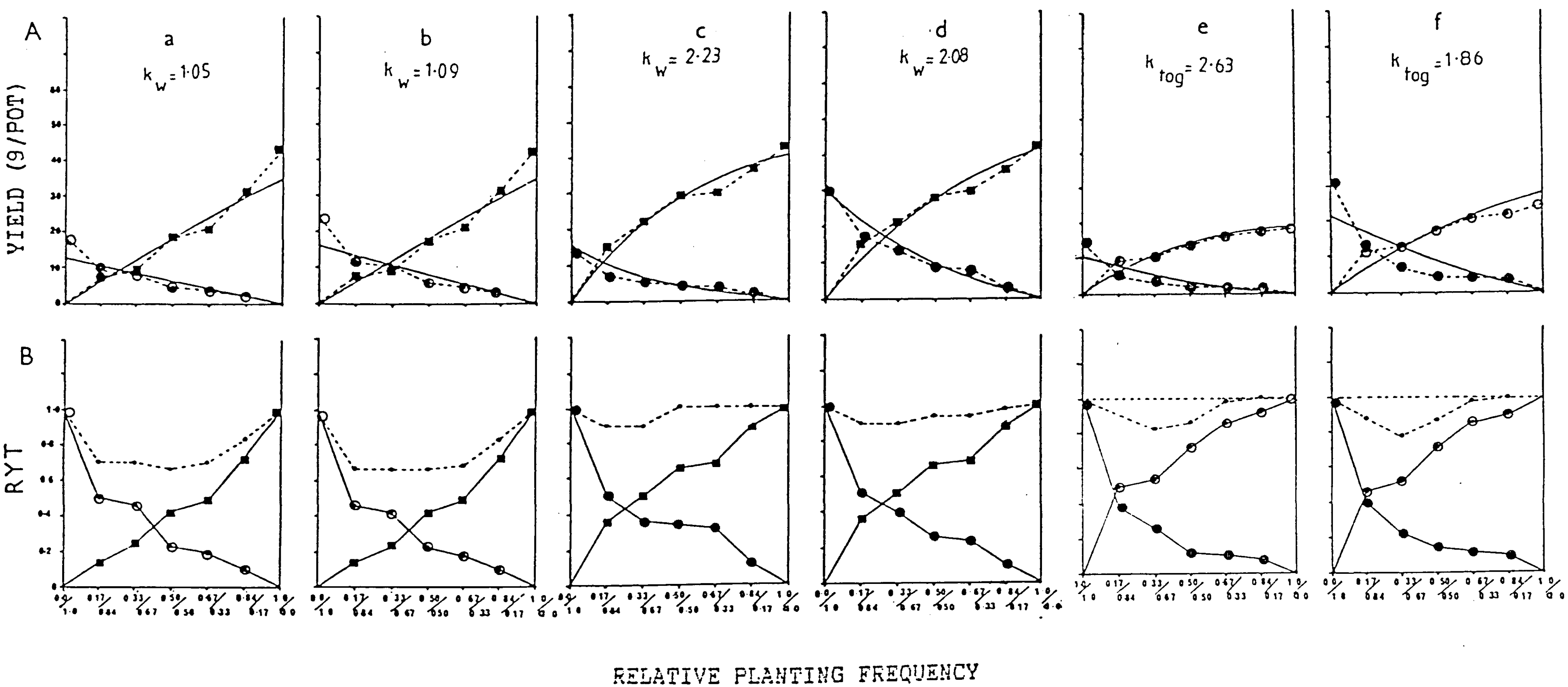

A
B
a
k_w = 2·01
b
k_w = 2·03
c
k_w = 2·86
d
k_w = 3·95
e
k_{tog} = 1·91
f
k_{tog} = 1·35
YIELD (9/POT)
RYT
RELATIVE PLANTING FREQUENCY

Fig. 3.6.2 Replacement series diagrams of plants grown in soils from the field margins, a) aerial tillers of Tall Oat-grass (tog) and wheat (w). b) whole shoot of Tall Oat-grass and wheat. c) aerial tillers of Onion Couch and wheat. d) whole shoot of Onion Couch and wheat. e) aerial tillers of Tall Oat-grass and Onion Couch. f) and whole shoot of Tall Oat-grass and Onion Couch. A) Fitted curves (based on de Wit's model, 1960) are shown in solid lines and actual data points are superimposed as symbols: wheat (■), Tall Oat-grass (o) and Onion Couch (●). B) Showing the Relative Yield Total (RYT) of: mixtures in broken lines and the two varieties Arrhenatherum and wheat as solid lines with symbols.


A
B
a
$k_w = 1{\cdot}05$
b
$k_w = 1{\cdot}09$
c
$k_w = 2{\cdot}23$
d
$k_w = 2{\cdot}08$
e
$k_{tog} = 2{\cdot}63$
f
$k_{tog} = 1{\cdot}86$
YIELD (9/POT)
RYT
RELATIVE PLANTING FREQUENCY

The RYT of Wheat:Onion Couch; Tall Oat-grass:onion Couch; was nearly one, while Tall Oat-grass:Wheat was lower than one in all combination (Figs. 3.6.2 B).

3.6.4 Discussion

It is evident from the results of the Replacement Series in John Innes compost that the two varieties of Arrhenatherum grew vigorously in monocultures but when grown in mixtures with Wheat showed a considerable contrast being characterised by low yield, especially for Onion Couch when grown in mixtures with Wheat. It seemed that the estimated Relative Crowding Coefficient (de Wit, 1960) served in this experiment as an effective index of competition and provided a quantitative and relative expression of the competitive abilities of the two varieties.

RYT derived from the raw data also served as an important reference for the interpretation (de Wit, 1960) of the Replacement Series Experiment. RYT was found to be varying around one. The RYT close to unity for the three replacement series in the John Innes medium, is an indication that the plants were crowding for the same space. It can be concluded that, in a fertile soil, Wheat would crowd and suppress Onion Couch more than the Tall Oat-grass, and it is the newly formed ramets (Table 3.3 to 3.5) of the Onion Couch which would be suppressed most. Tall Oat-grass on the other hand would compete better with Wheat on account of its growth habit and earlier occupation of space before intense competition begins (Chap.3.5). Unlike Wheat, Tall Oat-grass would suppress the tiller component of Onion Couch more than the whole shoot weight while crowding for the same space.

NUMBER OF SEEDS/RAMETS	WHEAT NO. OF TILLERS		ONION COUCH NO. OF TILLERS		ONION COUCH NO. OF BULBS	
WHEAT:ONION COUCH	JOHN INNES	FIELD MARGINS	JOHN INNES	FIELD MARGINS	JOHN INNES	FIELD MARGINS
12 : 0	36	20	-	-	-	-
10 : 2	34	16	5	4	15	12
8 : 4	29	16	10	6	56	38
6 : 6	26	15	16	10	91	60
4 : 8	21	12	20	11	125	72
2 : 10	14	6	36	16	190	100
0 : 12	-	-	95	38	400	150

TABLE 3.3 Mean number of tillers of wheat, and mean numbers of tillers and new bulbs of Onion Couch, in the Replacement Series Experiments on the two soil types.

NUMBER OF SEEDS/RAMETS	Tall Oat-grass NO. OF TILLERS		ONION COUCH NO. OF TILLERS		ONION COUCH NO. OF BULBS	
TALL:ONION OAT COUCH GRASS	JOHN INNES	FIELD MARGINS	JOHN INNES	FIELD MARGINS	JOHN INNES	FIELD MARGINS
12 : 0	106	62	-	-	-	-
10 : 2	95	58	20	5	60	12
8 : 4	85	54	40	8	108	25
6 : 6	70	50	51	10	180	34
4 : 8	40	33	60	15	230	54
2 : 10	30	20	70	23	260	85
0 : 12	-	-	95	40	400	140

TABLE 3.4 Mean number of tillers of Tall Oat-Grass, and mean numbers of tillers and new bulbs of Onion Couch, in the Replacement Series Experiments on the two soil types.

NUMBER OF SEEDS/RAMETS	WHEAT NO. OF TILLERS		TALL OAT-GRASS NO. OF TILLERS	
WHEAT:TALL OAT GRASS	JOHN INNES	FIELD MARGINS	JOHN INNES	FIELD MARGINS
12 : 0	35	20	-	-
10 : 2	33	15	12	5
8 : 4	28	14	60	9
6 : 6	25	12	78	16
4 : 8	20	10	85	18
2 : 10	10	7	90	26
0 : 12	-	-	109	62

TABLE 3.5 Mean number of tillers of wheat, and Tall Oat-grass, in the Replacement Series Experiments on the two soil types.

It seems that an explanation of the result obtained from unfertilised soils can only be given by analyses of the root component of the competing plants. It is widely believed (Pavlychenko, 1934; Donald, 1958) that competition begins as soon as the root system of one plant invades the feeding area of another and it usually takes place long before aerial tillers are developed sufficiently to exert serious competition, especially where competition is for nutrients. It has also been shown that the ability to compete for nitrogen in nitrogen deficient soils, was higher in Tall Oat-grass under shoot competition with other meadow plants and it produced larger root mass under competition (Strehlow, Salinger, Bornkamm, 1982; Mahmoud and Grime, 1976). It can be said that the hampering effect observed in Wheat:Tall Oat-grass (Fig. 3.6.2), could be the result of root competition as both the plants have proved to more aggressive (than Onion Couch). While competing for the limited amount of nutrient in the soils they might have hampered each other's above ground growth (as both failed to occupy the space lost by one) as a result of depletion in the nutrient supply.

From the results of the replacement series on unfertilised soils it seems reasonable to believe that Tall Oat-grass becomes a better competitor on such soils. This finding also reflects the habitat of the three competitors; Tall Oat-grass a variety of hedgerows and mesotrophic grasslands and relatively unfertile soils proved to be a better competitor here compared to Onion Couch and Wheat which are adapted to specialized nitches of fertilised arable soils.

It can also be sugested that by maintaining a high level of fertility in the farmland would not only reduce competition for nutrients but would also improve crop yield in Onion Couch infested farms by stimulating the Wheat growth which would in turn suppress the amount of ramet (or vegetative propagule) reserves (due to greater investment in aerial tillers) and hence future infestations.

3.7 Extent of Crop yield reduction by the presence of the two varieties of Arrhenatherum.

3.7.1 Introduction

An additive experimental design, keeping the density of the crop constant and varying the densities of the two varieties of Arrhenatherum was used here to investigate the practical importance of a weed infestation in terms of yield loss. The experiment was initiated to: (a) Supplement the results obtained from the Replacement Series (Chap.3.6); (b) Predict the crop losses due to increasing densities of the two Arrhenatherum varieties with the help of a model.

3.7.2 Methods

The experiment was conducted at Silwood Park on agricultural land which had similar soil characteristics to that used in the previous experiment (Chap.3.5). Twenty eight $1m^2$ plots were laid out separated by paths of 0.50m width. Single ramets of the two varieties were washed and separated from larger aggregates derived from populations described in Chap.3.1. Single ramets of Onion Couch and Tall Oat-grass were planted in twenty four of the plots at a density of 3, 7, 11, 15, 22, 33, 54, 66, 92, 108, 125 and 134, on 28 and 29.10.85. Winter Wheat (cv.Hustler) was sown on 31.10.85 in twenty eight plots at a rate of $350m^{-2}$. Four of the plots represented weed free controls. The plots were laid out as a fully randomized experiment. The method of sowing, planting and amount of fertilisers applied per plot was the same as described in the Chap.3.5. The experiment was performed under a net as a previous attempt with spring Wheat was foiled by Jackdaws which attacked the crop seedlings.

No emergence was observed during the month of November because of severe ground frost but by the middle of December both Wheat and the two varieties of _Arrhenatherum_ had emerged. The harvest was made on 15 to 18 July 1986. Two harvests were made per plot: the central $0.25m^2$ and the outer edges separately to estimate any edge effect. Tillers of Wheat and the _Arrhenatherum_ were clipped at the soil surface, basal internodes of the two varieties of _Arrhenatherum_ were recovered by digging the plots. Basal internodes were washed before oven drying for 24 hours at 100°C and then weighed.

The following measurements were made at the time of harvest.

For the two varieties of _Arrhenatherum_:

1. Number of tillers.
2. Dry weight of tillers.
3. Dry weight of basal internodes
4. Number of bulbs and proportion of two and three bulb ramet in Onion Couch.

For wheat:

1. Number of tillers.
2. Dry weight of tillers plus ears

Two models and a derivative were fitted to the data. In both models weed population was expressed as number of tillers and number of ramets m^{-2}, and crop as percentage reductions of the whole shoot dry weight from weed free control.

The computer programs for the two models (and a derivative) were written and adpated by Dr. A.J.Morton of Imperial College, Silwood park. The two models, and a derivative of one of them used for fitting the curves are described below:

1. RECHYP1. This program fitted the hyperbolic model of weed-crop competition proposed by Cousens et al (1984). Crop yield loss in this model is described by the equation:

$$YL=Id/(1+Id/A)$$

where YL is % crop yield loss, d is weed density, I is % crop yield loss per weed plant per unit area as weed density approaches zero, and A is % yield loss as weed density approaches infinity. RECHYP1 fitted the equation by non-linear optimization based on minimum sums of squares deviation. Constraints were applied to the two parameters A and I; the value of A was set between 0 to 100 and I was set between 0 to 10 in the program used here.

1a. RUNHYP. This approach (or algorithm) was based on the equation described in RECHYP1, but here a NAG routine EO4DF was used for non-linear optimization and no constraints were applied on the parameters.

2. RECHYP2. This program fitted the model of weed-crop competition used by Watkinson (1980, 1981) and Firbank _et_ _al_(1984) and is based on a reciprocal equation which describes an asymptotic yield-density relationship. Crop yield per unit area (Y) in this model is described by the equation below, which makes the assumption that yield per unit area is independent of density:

$$Y= c(1+ \alpha N_w / N_c)^{-1}$$

where c is the weed-free yield, N_c is the density of the crop, N_w is the density of the weed and α describes the competitive equivalence of the average weed plant to the average crop plant.

Yield loss is thus: $YL = \alpha N_w (N_c + \alpha N_w)^{-1}$

Mathematically the two model are similar: an assumption of an asymptote of 100% for the equation described in RECHYP1 would transform it into a form resembling that described in RECHYP2 , that is:

$YL = Id/(1+Id)$.

In addition, the parameter I (of Cousens _et_ _al_.,1984) is based on percentage loss, whereas a (RECHYP2) is based on proportion. The relationship between the Watkinson parameter α and the Cousens parameter I is thus:

$\alpha = N_c\ I/100$

The main difference between the two models is the assumption in the Watkinson model that the asymptote of crop yield loss is 100%. This model was fitted by non-linear optimization based on minimum sums of squares deviation (program RECHYP2).

3.7.3 Results

Initially RECHYP1 and RECHYP2 were run with weed population expressed both as number of ramets originally planted and tiller density at harvest (Figs. 3.7.1 and 3.7.2). The values of A obtained in both cases are higher for Tall Oat-grass than Onion Couch. The value of I is considerably higher for Onion Couch than Tall Oat-grass when the crop yield loss data based on the number of ramets planted is analyzed. It seems that data based on the number of ramets originally planted failed to take into account the mortality of ramets (killed before producing any regrowth), especially in Tall Oat-grass at lower planting densities (evident from the reduced number of tillers compared to Onion Couch, especially in Tall Oat-grass planted at 54 ramets m^{-2} and 66 ramets m^{-2}). On the other hand, crop yield loss data based on tiller density seemed more appropriate as it is based on the number of tillers present at the time of harvest (representing regrowth from the surviving ramets).

On comparing the values obtained by fitting the models (Table 3.6), RUNHYP shows lowest residual sum of squares but values of A for some of the data were unrealistically high, particularly when the asymptote was not well defined in the raw data. RECHYP1 and RECHYP2 which both constrained the asymptote appeared to be biologically more reasonable and it is the results of these which will be

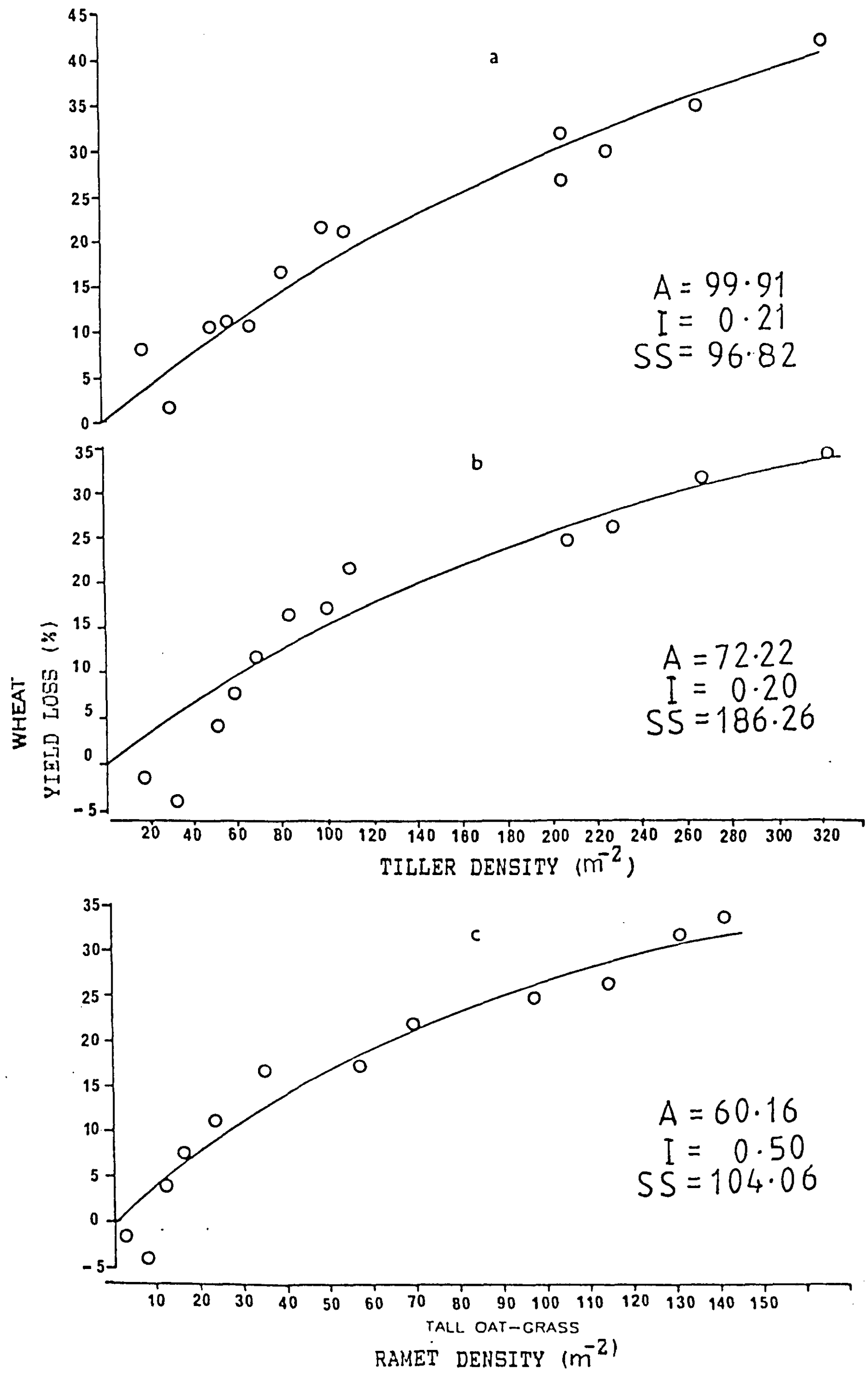


Fig. 3.7.1 RECHYP1 applied to percentage crop yield loss and Tall Oat-grass tiller density: a) 0.25 m^2 plots, b) 1 m^2 plots, and c) percentage crop yield loss and planted ramet density (0.25 m^2 plots).

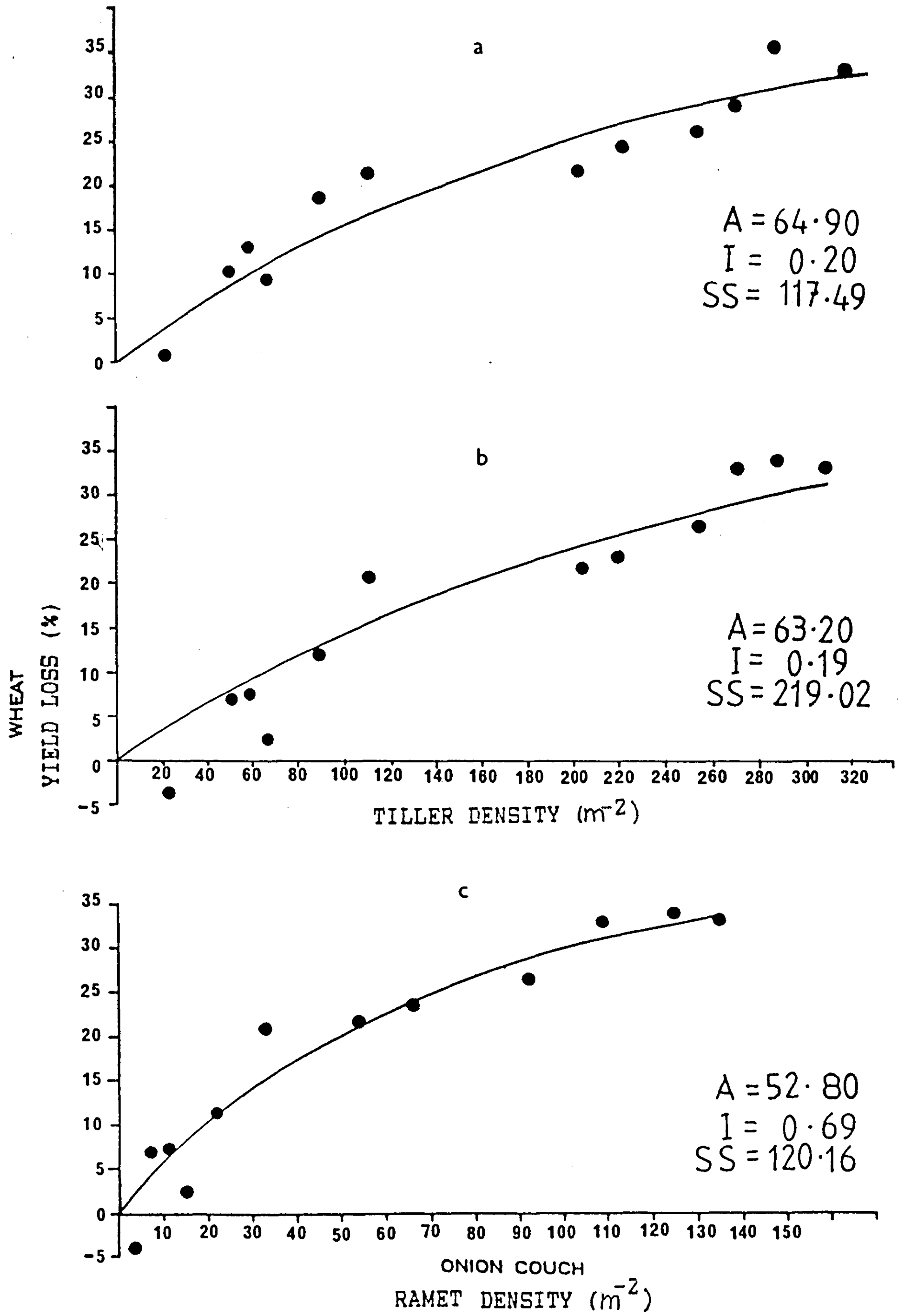


Fig. 3.7.2 RECHYP1 applied to percentage crop yield loss and Onion Couch tiller density: a) 0.25 m^2 plots, b) 1 m^2 plots, and c) percentage crop yield loss and planted ramet density (0.25 m^2 plots) = c.

discussed here. The curves obtained after applying RECHYP1 were used to interpret the results of the experiment between the crop and the two varieties of <u>Arrhenatherum</u> (Figs. 3.7.1 and 3.7.2).

The crop yield and the tiller number from the central ($0.25m^2$) was 415g and 160 respectively, and from the whole $1m^2$ was 1250g and 485 respectively. This indicates there has been no edge effect on yield in spite of the expectation. It seems that absence of edge effect has been offset by a tendency of planting and fertilising towards the centre of plots. After analysing the two harvests per plots, it seemed that the data from the central $0.25m^2$ harvest is more representative of the field situation as competitive stress of the crop would be expected to be more intense because of higher tiller density. The shape of the curves (in spite of higher R.S.S) also indicate that yield loss data from the central plots gave more satisfactory fit compared to the whole plot as the two <u>Arrhenatherum</u> varieties (especially, Tall Oat-grass) seems to become more aggressive towards the edges (Table 3.6).

At low weed density the value of competitive ability (I) for the two varieties was very similar, whereas parameter A shows that at very high density the presence of Tall Oat-grass caused greater yield loss compared to Onion Couch (Fig. 3.7.1 and 3.7.2). The α values based on RECHYP2 show the same order of competitive ablity (Table. 3.6).

Although Onion Couch produced more tillers at higher densities, dry weight of aerial tillers was higher in Tall Oat-grass than Onion Couch and dry weight of basal internodes was found to be much higher

PROGRAM	PARAMETER	WINTER WHEAT AND TALL OAT GRASS		WINTER WHEAT AND ONION COUCH	
		$0.25m^2$	$1m^2$	$0.25m^2$	$1m^2$
RUNHYP	A	70.15	79.86	212.42	54.06
	I	0.19	0.24	0.13	0.24
	SS*	185.59	90.25	163.30	109.72
RECHYP1	A	72.22	99.91	63.20	64.90
	I	0.20	0.21	0.19	0.20
	SS	186.26	96.82	219.02	117.49
RECHYP2	α	0.58	0.64	0.53	0.56
	SS	197.48	96.99	175.12	153.12

* = SUM OF SQUARES

TABLE 3.6 Results of applying the three programs to competition experiments between winter wheat and the two *Arrhenatherum* varieties.

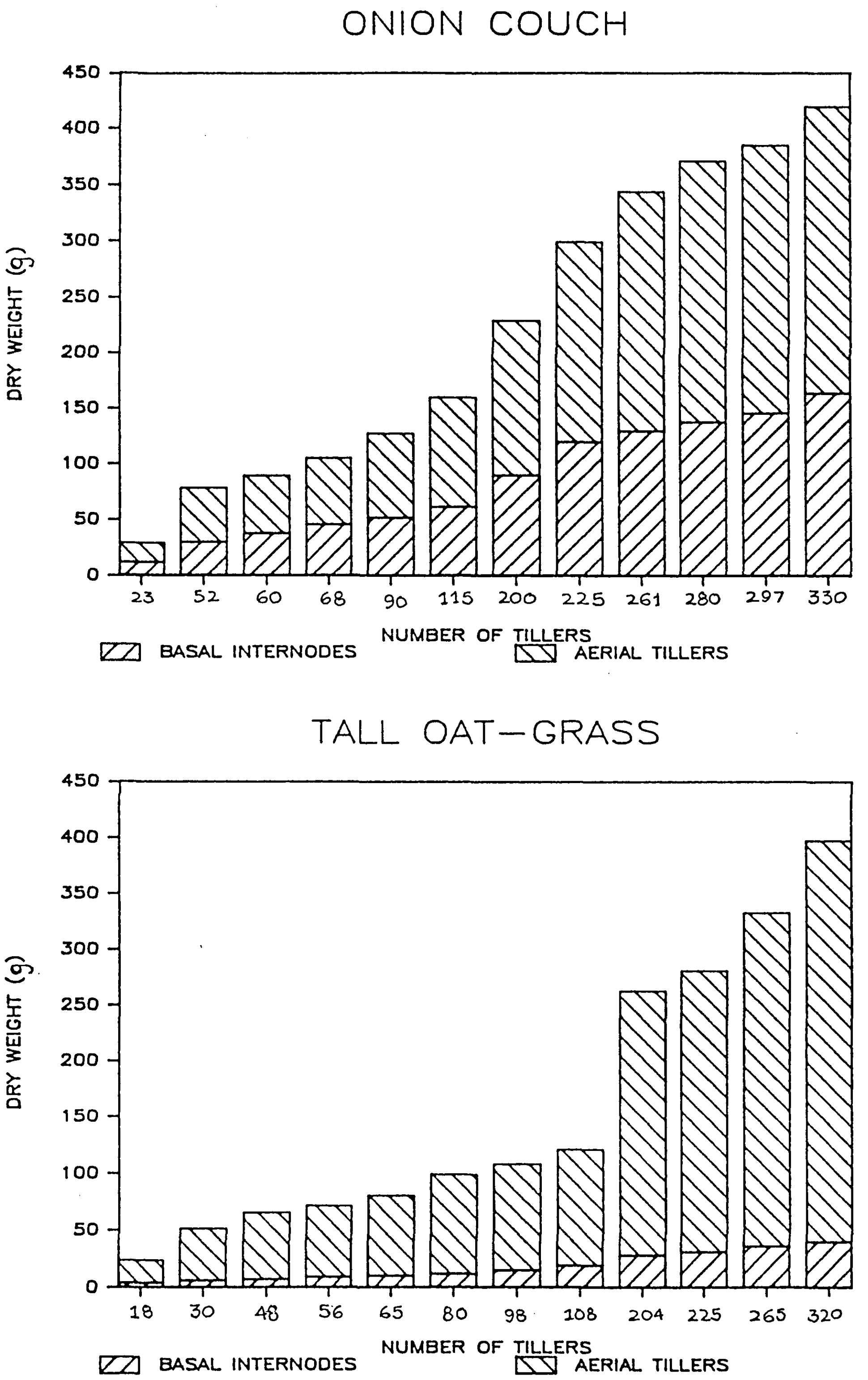


Fig. 3.7.3 Histogram showing dry weight of aerial tillers and basal internodes of the two varieties growing in competition with wheat.

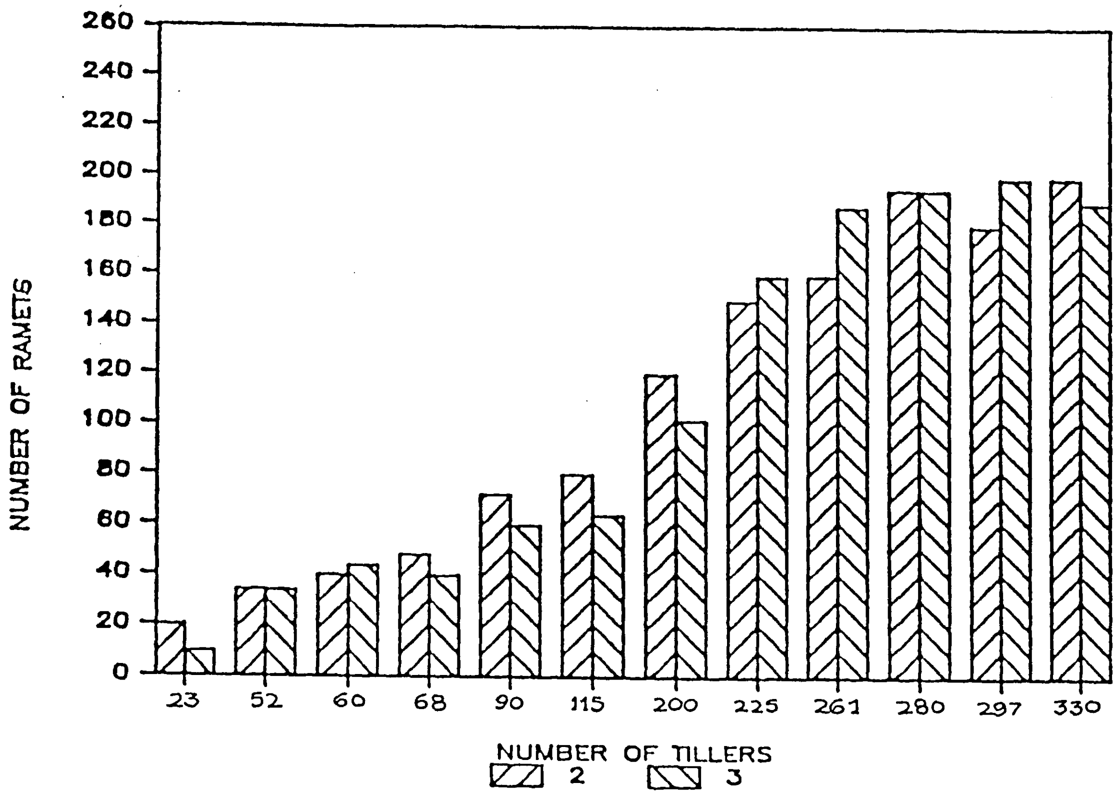


Fig. 3.7.4 Histogram showing proportion of 2 and 3 bulb ramets of Onion Couch growing in competition with winter wheat.

in Onion Couch compared to Tall Oat-grass (Figs.3.7.3). The proportion of two and three bulbs ramets produced in Onion Couch was the same over all densities (Fig.3.7.4).

3.7.4 Discussion

As the two methods are mathematically similar the resulting goodness of fit as judged by the residual sum of squares was quite similar. Either model of yield loss-weed density i.e. RECHYP1 or RECHYP2 could be chosen for predictive purposes as they provided a reasonable description of data from artificially planted ramets of the two varieties of Arrhenatherum in these experiments. The Cousens model (program RECHYP1) seems to be more realistic of the two models because instead of assuming a crop yield loss of 100% at high weed density as assumed in the Watkinson model (program RECHYP2), its parameter A provides a better estimate of crop yield loss as weed density approaches infinity. It can be argued that different weeds vary in their aggressiveness at very high densities, and that parameter A of the Cousens model gives a useful index of this aspect of competitive ability.

It is also evident from the results based on RECHYP1 that the number of replicates planted at high densities in this experiment was not enough to produce a really clear asymptote. In order to make more accurate predictions more plots at high densities and some plots at higher density than used in this experiment would be required to produce a clearer asymptote. However, the values of A indicate that at very high density, Tall Oat-grass would suppress the crop more than Onion Couch. On comparing the competitive abilities (based on I and A) of the two varieties of Arrhenatherum with other weeds

(Cousens _et al_, 1984), the order of competitive ability, as given by I, is _Galium aparine_ (2.65) > _Bromus sterilis_(0.82) > _Avena fatua_ (0.75) > Tall Oat-grass (0.21) > Onion Couch (0.20), and at high weed density given by A, is Tall Oat-grass (99.91) > _Avena fatua_ (96.79) > Onion Couch (64.90) > _Bromus sterilis_(62.75) > _Galium aparine_ (55.96). The comparison shows clearly that Onion Couch is not as competitive in a crop situation (winter wheat) as Tall Oat-grass and some other weeds.

The results show that the two varieties of _Arrhenatherum_ underwent considerable modification and their growth was very much limited by competition from the crop. The results also show that at low weed densities the competitive abilities of both varieties are very low, and at higher densities Tall Oat-grass reduced the yield of wheat more than Onion Couch did. The results agree with the outcome of the Replacement Series Experiment (Chap.3.6) which showed that wheat suppresses the two varieties when competing for the same space and that Tall Oat-grass was a better competitor with the crop than Onion Couch. The competitive stress exerted by a vigourously growing cereal on the vegetative propagules of Onion Couch was also reflected in the decrease in the proportion of three bulb ramets and the decrease in the dry weight of the vegetative propagules compared to when the vegetative propagules obtained from a similar population were grown in monocultures (Chap. 3.5).

It seems that it is the growth habit, especially the partitioning of resources (Chap.3.5) into aerial tillers and basal internodes that makes Tall Oat-grass a better competitor when in a crop situation. In the experiment, Tall Oat-grass overtopped the wheat in the early grain filling phase (May and June) and thus competed for growth requirements at an early phase compared to Onion Couch which overtopped the crop late during the grain filling period (July) and thus grew during the growth cycle of the crop as a subordinate species, producing slower aerial growth but storing greater reserves in the basal internodes. These bulbous internodes so produced act as vegetative propagules, and it is this strategy (rather than the competitive ability) which contributes to the success of Onion Couch as a weed of arable land. The question that now arises is whether these swollen internodes, formed as a result of the specialized growth habit of Onion Couch, are particularly tolerant to cultivation or other arable practices.

3.8 Effect of burial on regeneration from perennating organs of the two varieties of *Arrhenatherum* .

3.8.1 Introduction

The main purpose of this experiment was to evaluate the relative effect of burial of the perennating organs (shoot bases) of the two varieties of *Arrhenatherum* in order to investigate their potential success in arable fields. Single ramets and aggregates of two ramets (comprised of two connected shoot bases) and aggregates of three ramets (comprised of three connected shoot bases) were planted at different depths to simulate the effect of fragmentation and burial by cultivation.

3.8.2 Materials and Methods

The planting material used in this experiment for both varieties was obtained from the populations described in Chapter 3.1. Perennating organs formed during the summer of 1984 were separated into the required number and sizes to be planted in replicates. The details of planting material, size of containers and the number of ramets are given in Table 3.7.

Accurate planting depths were achieved by placing the planting material on a levelled surface of John Innes No.3. compost in the bags and then filling the bags to the required depths. The ramets or aggregates were laid horizontally and were placed at equidistant intervals from each other in a circular fashion away from the side walls in order to prevent any regrowth emerging against the side walls of the bags. The bags were arranged in a randomized block on a bench in the green house which was illuminated for 18 hours by means of high pressure Metal-halide lights at 25 $\mu E.s^{-1}\ m^{-2}$. Average temperaure was 12°C in Feburary and March and 25°C during April and May. The soil was kept moist by watering and drainage was allowed through holes in the containers.

The experiment was started on 20.2.85 and was harvested on 25.5.85. During the first six weeks, the number of emerged shoots was counted at weekly intervals. At harvest, all the plants were dug up carefully and were kept intact as far as possible to facilitate classification of the parts.

The originally planted ramets or aggregates were classified either as having survived by producing aerial tillers or as having died. The latter were not always recovered in the experiment, as the effect of burial treatment under John Innes compost and humid green

DEPTH OF PLANTING (CM)	TOTAL NUMBER RAMETS/ AGGREGATES		NUMBER OF RAMETS PER UNIT	SIZE OF CONTAINER (AREA DEPTH) (CM ^{2} × CM)		NUMBER OF CONTAINERS USED
	ONION COUCH	TALL OAT GRASS				
0.0	18	18	1	255	22	2
	14		2			
	12	12	3			
2.5	27	27	1	453	28	3
	21		2			
	18	18	3			
7.5	27	27	1	453	28	3
	21	-	2			
	18	18	3			
15.0	27	27	1	453	28	3
	21	-	2			
	18	18	3			
20.0	18	18	1	453	28	2
	14	-	2			
	12	12	3			

Table 3.7 Material and containers used for the experiment.

house conditions often resulted in complete decay of the originally planted material and their numbers were then determined by substraction from the numbers of ramets or aggregates originally planted.

The following measurements were made at the time of harvest:

1. Number of planted ramets or aggregates producing at least one shoot reaching above the soil surface.
2. Number of aerial tillers and new bulbs formed per planted ramet or aggregate.

3.8.3 Results

Effect of various burial treatments on the mortality of planted ramets or aggregates

Fig. 3.8.1. shows the percentage of ramets with one or more aerial shoots from various depths at the time of harvest. Nearly half of the ramets and aggregates of Onion Couch placed on the soil surface dried out before any sign of bud activity had appeared. The mortality seemed to be slightly more pronounced in the aggregates, probably as a result of their orientatation on the soil surface, where surface contact was less than observed in single ramets and aggregates of two ramets. The ramets and aggregates of Tall-Oat grass failed to produce any regrowth at all when placed on the soil surface. At a shallow planting depth of 2.5cm no mortality was observed in the ramets or aggregates of Onion Couch, whereas 60% of single ramets and 40% of aggregates of Tall Oat grass died when buried at this depth. When buried at a depth of 7.5cm, 62% of single ramets of Onion Couch died, however, most of the aggregates (two and three ramets) of Onion Couch survived and produced aerial growth

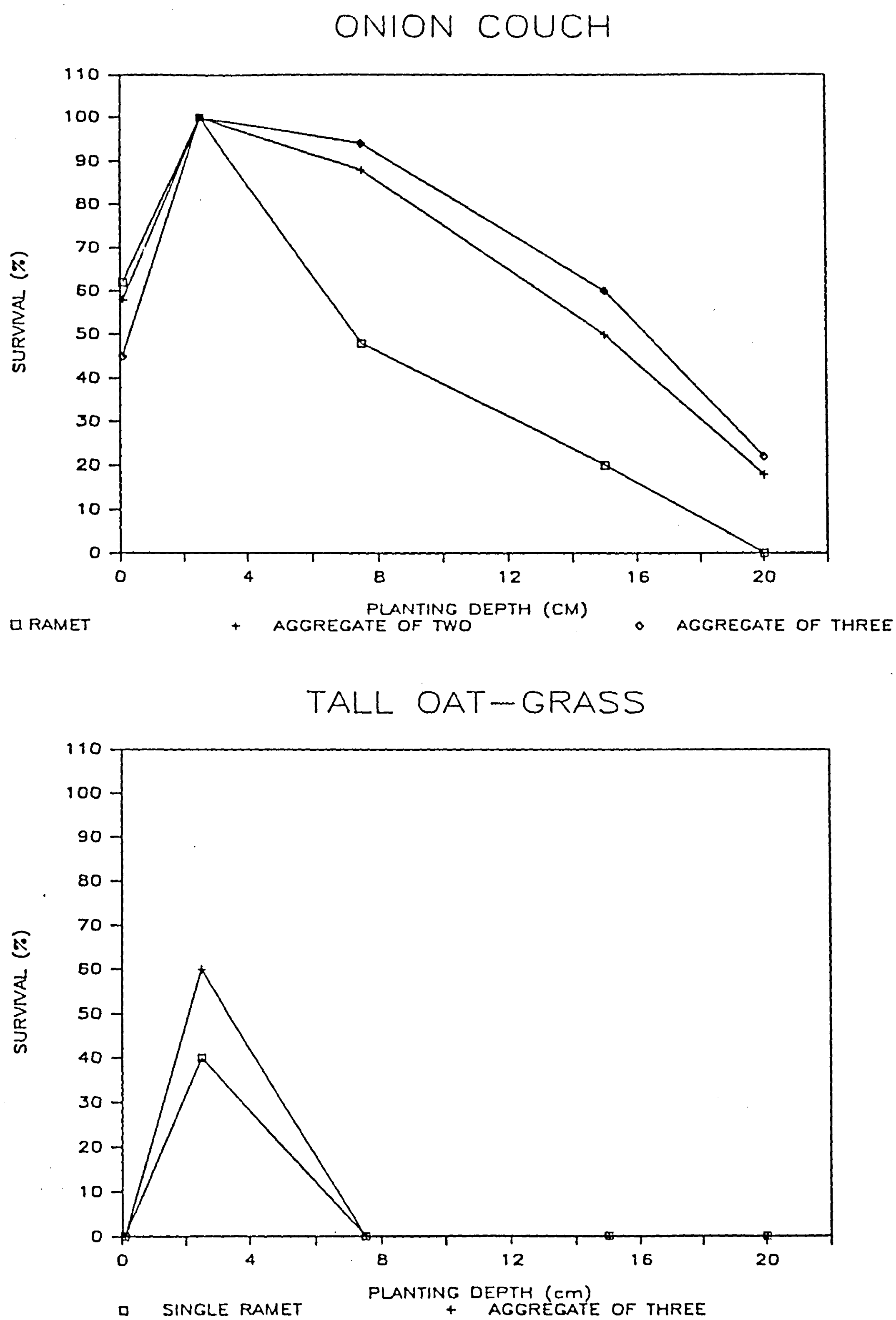


Fig. 3.8.1 Effect of burial on the survival of the planted ramets and aggregates of the two <u>Arrhenatherum</u> varieties.

from this depth. None of the Tall Oat-grass ramets survived below a planting depth of 2.5cm. When buried at a depth of 15cm, 75% of single ramets of Onion Couch died. Aggregates of two and three ramets also showed increased mortality at this depth; nearly half of them died. Mortality at 20.0cm depth was 100% in ramets and about 80% in aggregates of two and three ramets of Onion Couch.

Time and number of tiller emergence in different treatments

The number of tillers emerging (per bulb planted as ramets or aggregates per treatment) above the soil surface on various days after planting is shown in Fig. 3.8.2. The time of first emergence was unaffected by the size of the planted material at the shallow depths of 0.0cm and 2.5cm. The first shoots in all the bags at these depth appeared on the first day of recording, that is, 7 days after planting. The delay in emergence progressively increased with the depth and the decreasing size of the planted material. It was 14 days after the emergence from the shallow depths that the first shoots appeared in the single ramets buried at a depth of 7.5cm and another 7 days elapsed before single ramets buried at 15.0cm produced any tillers above the soil. There does not appear to be much difference in the emergence timing between aggregates of two and three ramets compared to the single ramets, so they are referred to here as aggregates. The aggregates buried at 7.5cm produced the first shoot above soil by the first day of recording, those buried at 15.0cm produced shoots 7 days after planting and the ramets buried at 20.0cm produced their first shoot 20 days after planting. The only depth from which Tall Oat-grass ramets or aggregates produced any regrowth was 2.5cm, no emergence from any other depth was recorded.

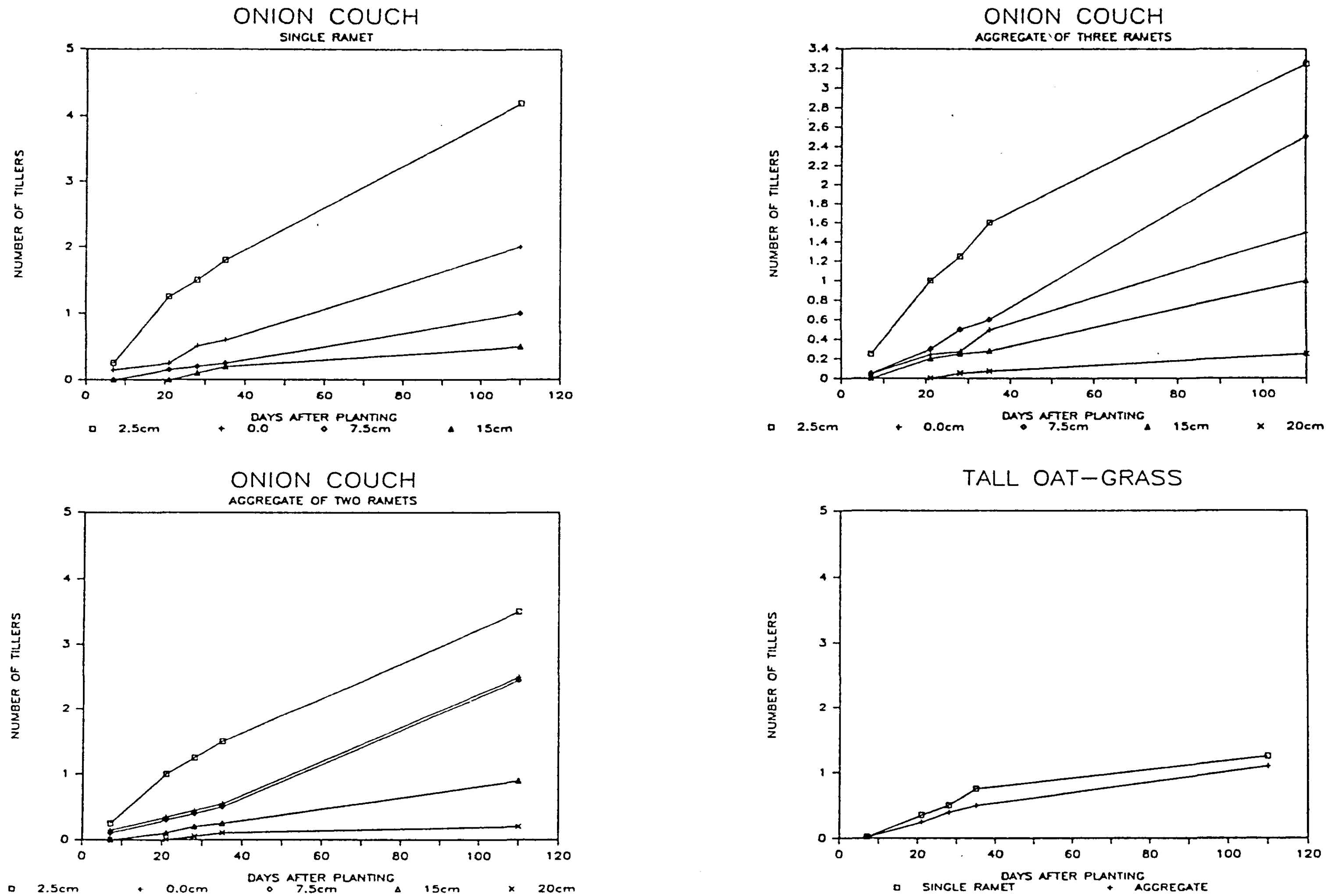


Fig. 3.8.2 Number of tillers emerging above the soil surface (per number of bulbs planted in each burial treatment) on various days after planting of ramets and aggregates of the two *Arrhenatherum* varieties.

On the last recording it was observed that at the shallow depth of 2.5cm, the number of aerial tillers per bulb planted as ramet or aggregate (per treatment) was greatest in treatments with single ramets then in aggregates of Onion Couch which suggests bud dormancy due to correlative dominance in the connected ramets. At greater depths, that is 7.5cm and 15.0cm, more aerial tillers per bulb planted were produced by aggregates compared to single ramets, which is probably due to lower shoot vigour and higher mortality associated with the decrease in the size of the ramets and increasing depth of burial.

Number of shoots and bulbs produced per ramet or aggregate in different treatments

In order to assess the amounts of tillers and bulbs produced by surviving ramets individually per treatment, the results that follow are based on means and 95% confidence limits (Fig. 3.8.3). The mean number of aerial tillers per ramet or aggregate where they were exposed on the soil surface was generally variable, but less variable in the single ramets and aggregates of two ramets which had more surface contact with the growth medium than the aggregates of three ramets, where most of the ramets in the aggregate, because of their orientation when placed on the soil surface, did not have sufficient contact with the soil and thus dried before contributing towards any tiller production. The greatest number of tillers was produced when ramets were buried at a shallow depth of 2.5cm and the number of aerial tillers increased with increase in the number of ramets in the aggregate (Plates 4 and 5). The number of tillers per ramet was significantly reduced with increase in depth and decrease in the number of ramets in the aggregate, as shown in Fig. 3.8.3

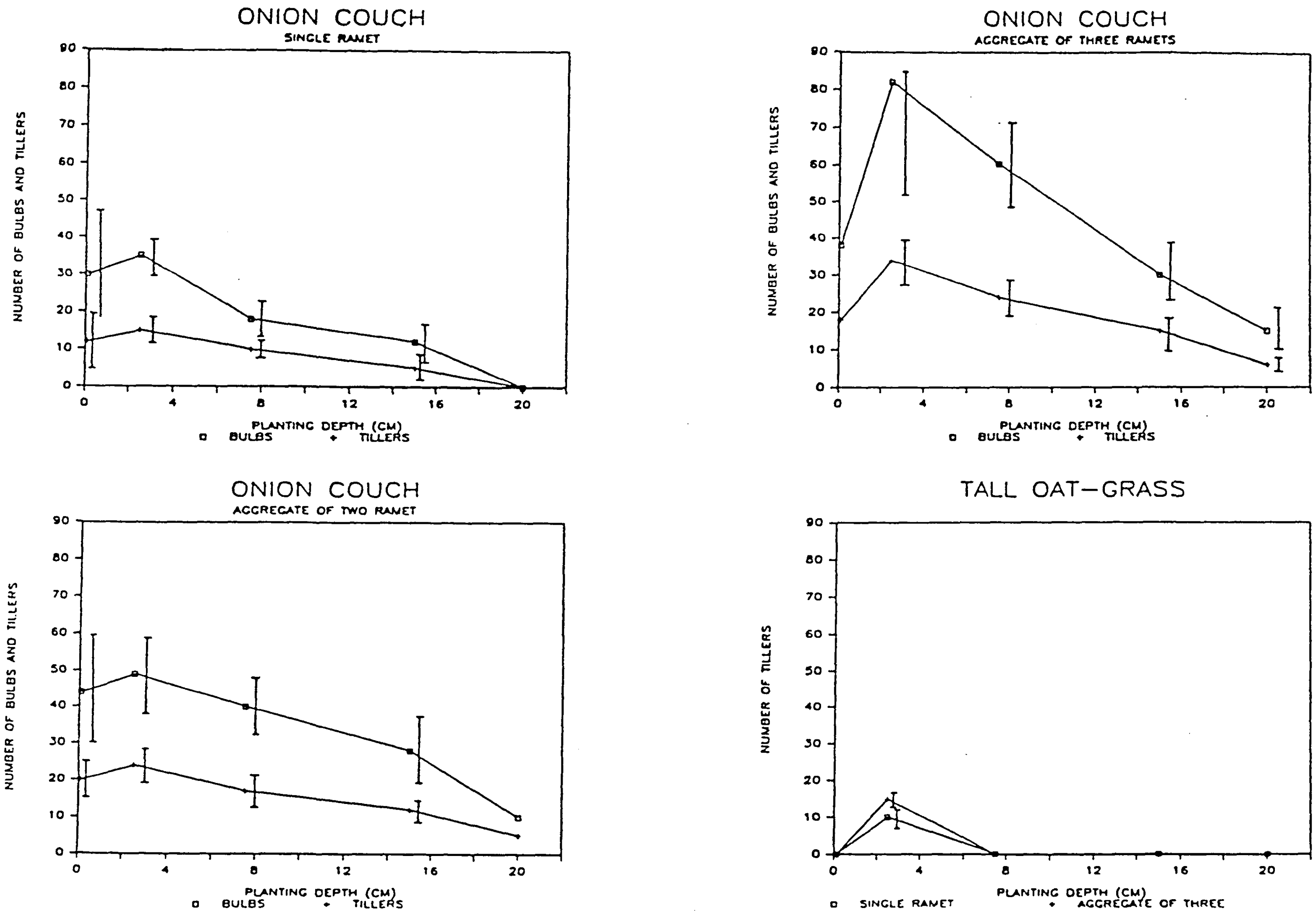


Fig. 3.8.3 Mean number of tillers and bulbs produced by ramets and aggregates of Onion Couch, and mean number of tillers produced by ramets and aggregates of Tall Oat-grass, in each burial treatments. With 95% confidence limit.

Plate 4 Regeneration from a single ramet (left) and an aggregate (right) buried at a depth of 2.5cm.

Plate 5 Regeneration from single ramets buried at a depth of 2.5cm (left) and 7.5cm (right).

Plate 6 Regeneration from aggregates buried at a depth of 2.5cm.

Plate 7 Regeneration from aggregates buried at 15cm (left) and 7.5cm (right).

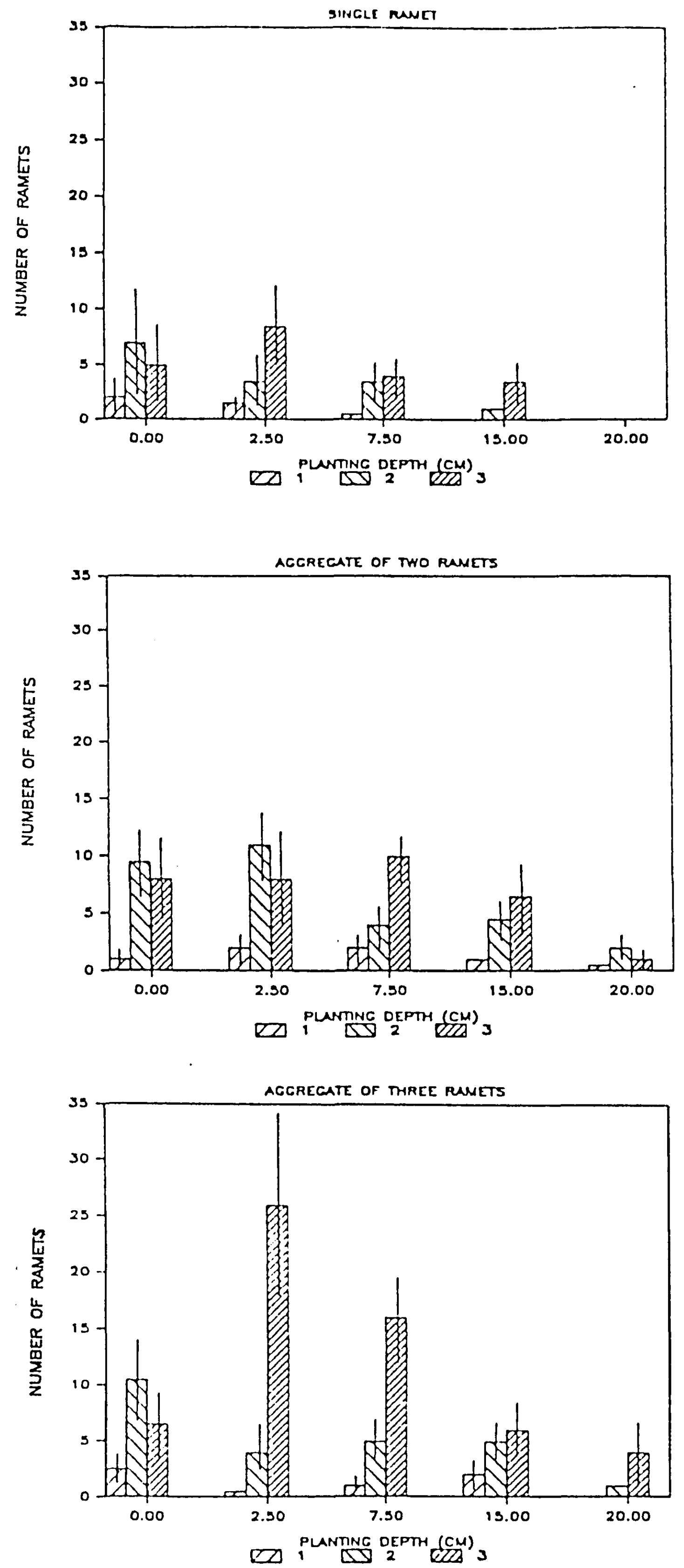


Fig. 3.8.4 Mean number of 1, 2, and 3 bulb ramets produced per ramet and aggregate (originally planted) of Onion Couch, in each burial treatment.

(Plates 4 to 7). The mean number of bulbs formed per ramet or aggregate followed the same pattern as observed in the tiller production (Fig. 3.8.3). A trend of more bulbs per tiller was observed by ramets or aggregates planted at greater depths, which seems to be some sort of compensatory measure where a smaller number of tillers produced is offset by more vigorous shoots (Fig. 3.8.4).

The only burial class from which ramets or aggregates of Tall Oat-grass produced tillers was 2.5cm. The number of tillers per planted ramet or aggregate here also increased with the increase in the number of ramets or connected shoot bases in an aggregate (Fig. 3.8.3).

3.8.4 Discussion

Although the conditions in the green-house and the medium of growth were very different form the field situation, the results in this experiment show clearly what the two varieties can achieve under good growing conditions. The results of the experiment indicate the greater capacity of emergence from perennating organs of Onion Couch when exposed on the soil surface and at all depths of burial compared with the equivalent perennating organs of the Tall Oat-grass. The greater tolerance of burial of the perennating organs of Onion Couch is probably due to the greater amount of food reserves (Fig. 3.8.5) in them. The results also show that increasing the depth of burial was more detrimental to the survival of single ramets than aggregates. Further evidence of the amount of reserves in the ramets and aggregates and the resulting regrowth comes from the fact that the mean number of tillers and bulbs increased and emergence time decreased with increase in the number of ramets in

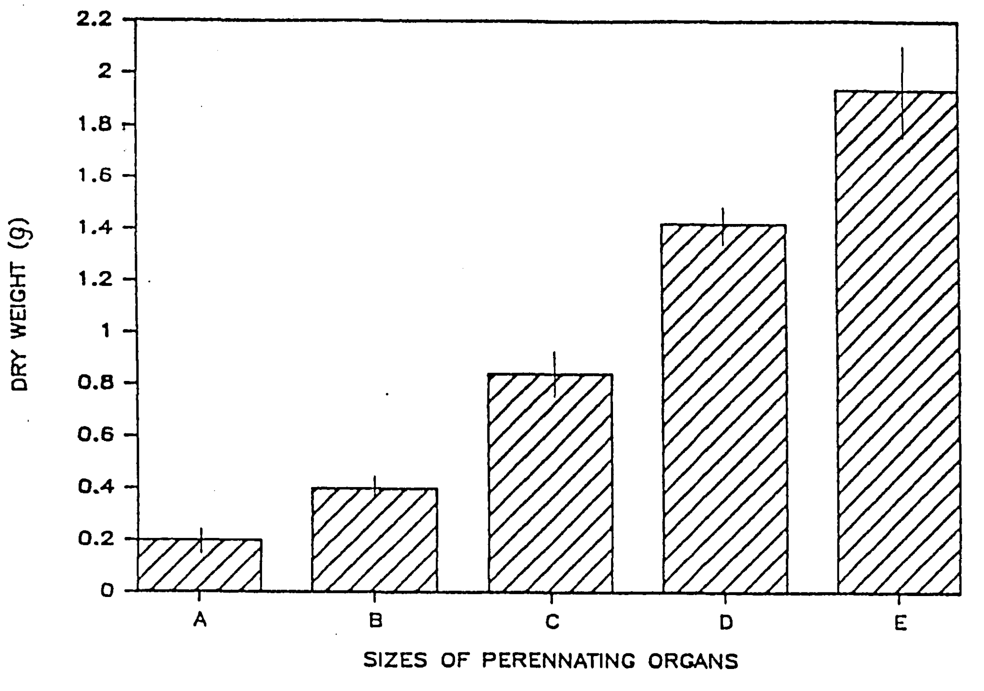


Fig. 3.8.5 Mean dry weight of the ramets and aggregates of the two Arrhenatherum varieties. With 95% confidence limit.

a) single ramets of Tall Oat-grass.

b) aggregate of three ramets of Tall Oat-grass.

c) single ramets of Onion Couch.

d) aggregate of two ramets of Onion Couch.

e) aggregate of three ramets of Onion Couch.

the aggregate.

These results are also in agreement with the available evidence from the literature (Vengris 1962, Hakansson 1976) about other perennial grasses, which suggests that the vegetative propagules with smaller reserves are probably limited in regrowth from depth mainly by the available food reserves. Ramets of Onion Couch also show slight bud dormancy due to correlative dominance in the aggregates, as a result of which a growing shoot from these aggregates can manipulate the stored nutrient from the connected ramets and the aggregates acts as one unit rather than as individual ramets and thus survives burial with little or no mortality.

3.9 Conclusions

Significant and consistent differences were found between the two varieties of Arrhenatherum for most of the attributes measured. These differences between the two varieties seem to be largely due to genetic factors which determine the bulbosity (chapter 3.3) of the variety and thus in turn reflect the adaptive significance of morphological and physiological differences between Tall Oat-grass and Onion Couch.

The two Arrhenatherum varieties differed in vegetative characteristics, pattern of growth and development, space occupation and response to thinning. Onion Couch was higher yielding and allocated a greater proportion of its whole shoot biomass to the development of basal internodes during the earlier part of the growth cycle and this was also reflected in delayed flower initiation. Tall Oat-grass, on the other hand, allocated these reserves in producing vigorous aerial tillers which underwent rapid elongation and produced flower earlier in the season (chapter 3.5). Tall Oat-grass, on the basis of its early growth and flowering capability, competed better with Wheat, probably by offering competition for both nutrient and light early in the life cycle of the crop, compared to Onion Couch which developed as a subordinate plant in the crop situation, allocating a larger proportion of photosynthate to basal internodes thus producing larger ramets (chapters 3.5 and 3.7) which benefit this variety during subsequent disturbance associated with agricultural practices. Like Wheat, Tall Oat-grass also suppressed Onion Couch but, unlike Wheat, it suppressed aerial tillering more than the basal internodes on a fertile medium. On unfertilized soils from the field margins Tall Oat-grass proved to be the better competitor as demonstrated in the Replacement Series Experiments (chapter 3.6).

The widespread occurrence of Tall Oat-grass indicates that the colonization of new areas by seeds is far more efficient in Tall Oat-grass than Onion Couch. This could be because, firsly, as the two varieties interbreed freely and pollination is by wind, there is less probability of the resulting seeds (due to cross pollination) producing the Onion Couch variety, which is homozygous for bulbosity (chapter 3.3), and secondly, Onion Couch cannot compete with Tall Oat-grass and other grasses (chapter 3.2) in a grassland situation.

The absence of dormancy in the seeds of Arrhenatherum give little chance of the seedlings surviving the agricultural practices in an arable system. One mechanism of regeneration in which the two Arrhenatherum varieties differ seemed to be accounting for most of the differences in the ecology observed between the two varieties. This is the inefficiency of the ramets of Tall Oat-grass which do not possess the potential for vegetative propagation when fragmented and exposed or buried under a cultivation regime, although in a natural habitat these unfragmented ramets are responsible for the vegetative expansion which allows it to form large patches. In contrast, ramets of Onion Couch act as vegetative propagules and on the basis of stored reserves can survive agricultural practices (chapter 3.8). Like Tall Oat-grass, the ramets formed by Onion Couch could not disperse vegetatively more than very short distances without soil disturbance and even under cultivation they frequently occur as aggregates (several connected ramets). Although the aggregates produced fewer tillers per ramet and hence fewer new bulbs at shallow depths, probably due to correlative dominance, they possess a greater potential for surviving cultural measures, with little or no mortality compared to single ramets (chapter 3.8).

The comparative studies described in this chapter indicate that the two Arrhenatherum varieties exhibit two distinct types of growth pattern response to different stresses (competitive and density dependent) and disturbances (infrequent cutting, and burial):

a) Intensive tillering and lateral growth of Tall Oat-grass during the establishment phase resulted in a stock of axillary buds above ground, and gave it a tussocky appearance and also made it less sensitive to infrequent cutting to which it responded by rapid re-establisment. Onion Couch developed few tillers during the establishment phase, resulting in a smaller number of axillary buds which are partially buried in the soil, and exhibited a very slow rate of recovery from repeated cutting and thus became particularly susceptible even to infrequent cutting (chapters 3.2 and 3.4).

b) Rapid growth, and response to density dependent stresses by mortality(a characteristic which it shares with the more aggressive Wheat), make Tall Oat-grass a more competitive variety. Onion Couch, on the other hand shows features relatively adapted to stress tolerance and disturbance (root severence and burial) as it: tends to grow slowly and conserves nutrients in the basal internodes, this pattern of growth conferring an additional advantage on the swollen internodes, which act as vegetative propagules and survive burial in the event of disturbance (cultivation). It responds to density stress in a more plastic fashion in monocultures and the shoots of Onion Couch are more productive (dry weight) in monocultures than in mixtures (with a crop or Tall Oat-grass), where it suffers greater loss in production compared to Tall Oat-grass.

The comparative growth patterns and responses to stress and disturbance, of the two Arrhenatherum varieties differ considerably in magnitude and appear to be characteristic for Tall Oat-grass and Onion Couch. The growth pattern and the response to stresses and disturbance (in the form of infrequent cutting) as exhibited by Onion Couch may not have any survival value under a productive grassland situation, where such factors are constant features of the environment, but growth pattern and responses to stresses and disturbance (in the form of root severence and burial) inherited in Onion Couch could become of considerable importance in an arable system where disturbance (fragmentation, burial and dispersal of ramet by cultivation) is regular but does not occur during the growing season of the crop. The factors responsible for selecting the two different pattern of growth and response to environmental factors in Tall Oat-grass and Onion Couch and allow them to survive and persist in their habitats bear a close resemblance to the two factors for selection of adaptive strategies recognised by Grime (1979), i.e. 'selection for competitive ability in undisturbed environments' and 'selection for adaptability to disturbed conditions' respectively. It seems therefore, that obvious intraspecific variation exists with respect to the growth strategies (Grime, 1979) adopted by the two varieties of Arrhenatherum. Tall Oat-grass of grassland situations, represents a potentially fast growing plant which has evoloved by selection for high competitive ability (C-selection) maximising the capture of resources in productive, relatively undisturbed conditions (infrequent cutting or grazing and absence of cultivation). Onion Couch, which is the prevalent variety in the arable fields has evolved in habitats experiencing moderate intensities of stress (arising from competition with a vigorously growing crop), and disturbance (especially towards the end of its growth cycle, i.e. cultivation). The growth strategy adopted by Onion Couch resembles the secondary adaptive strategy (Grime, 1979) of 'stress-tolerant ruderal'.

The inability to exist in nature without man's interference can be regarded as a feature of crop mimicry (Barrett, 1983) and it is very evident in the Onion Couch variety of Arrhenatherum. It is probable that:

a) The presence of fewer tillers and more erect growth habit of Onion Couch during the establishment phase could have resulted from the selection pressure of the dense competitive conditions which prevail in a crop canopy, compared to the prolific tillering and more decumbent growth form of the Tall Oat-grass.

b) The slow occupation of space and accumulation of reserves in basal internodes is a strategy of considerable survival value in arable situations, where it experiences intense competition from the crop and where its continuity depends on the production of large sized ramets which survive cultivation. This strategy would prove to be disadvantageous in a natural grassland where partially buried ramets and fewer tillers during the establishment phase would present open areas and poor competition to invading grasses.

c) Phenotypic plasticity is considered (Bradshaw, 1967) to be an adaptive mechanism in plants. Onion Couch shows a higher carrying capacity of tillers m^{-2} and hence plasticity compared to Tall Oat-grass. The Tall Oat-grass was more plastic in the juvenile stage (establishment phase) but less plastic in panicle development, and like annual crops it underwent considerable self thining. Onion Couch, on the other hand shows higher plasticity during the panicle development stage by modifying the mode of growth and energy allocation in response to a dense crop environment. This represents the two adaptive strategies of the two _Arrhenatherum_ varieties: adaptation of Onion Couch to a crop situation; where competion is more intensive than encountered by Tall Oat-grass in a natural grassland.

d) The high susceptibility to cutting during the active growing period is another feature of Onion Couch which made it more specifically adapted to crops which are not cut or grazed during their growth period, in contrast to grassland.

e) The absence of any mechanism of dispersal of the vegetative ramets from the aggregates make them dependent for their dispersal on soil cultivation and mechanical disturbance (an integral part of arable land), in the absence of which the large aggregates become spot-bound and less productive (Chap.2).

f) The lower competitive ability and performance on unfertilized soils is another feature which restricts the Onion Couch variety to fertile arable fields.

It seems that the above mentioned features of the Onion Couch variety of Arrhenatherum represent a high degree of specialization which it has undergone in order to avoid the competitive stresses of the crop and the disturbances associated with the agricultural practices. This has resulted in a restricted distribution of this variety to a specialized niche of farmland in contrast to the Tall Oat-grass variety which shows a much broader ecological tolerance.

It can be concluded, on the basis of these experiments that the adaptive strategies of the Onion Couch variety of Arrhenatherum could have evolved as a result of selective forces imposed by the crop and the associated agricultural practices.

CHAPTER 4

ADDITIONAL EXPERIMENTAL WORK WITH ONION COUCH IN THE CONTEXT OF ITS GROWTH AND DEVELOPMENT IN ARABLE SITUATIONS.

4.1 Introduction

Experiments described in chapter 3 have identified some of the attributes of Onion Couch which make it a successful weed of arable land. The possession of vegetative propagules which withstand cultivation a common feature of the World's worst weed (Holm et al, 1977) emerged to be the most important weedy attribute of this variety. This method of vegetative propagation where perennating organs of Onion Couch become highly specialised to act as vegetative propagules has influenced the growth cycle of the variety and it has undergone substantial morphological adaptations and also changes in the physiological processes controlling its growth and development, and these adaptations in turn enable Onion Couch to persist as an agricultural weed. There is still a lack of information regarding its behaviour in natural infestations, especially regarding the prevalance of Onion Couch infestations on certain soil types only, and the status of the vegetative propagules in natural infestations where they tend to form aggregates and decrease the efficiency of most weed control practices (Ayres, 1985).

Experiments and observations described in the following sections were conducted to consolidate the knowledge gained from artificially planted plots (Chap. 3) and at the same time to realise any discrepancy between artificially planted ramets (also assumed to be simulating intense cultivation, where aggregates are broken down to single ramets) and naturally occuring aggregates (more frequent in an arable system). It was hoped that the results from this work would be of great importance: a) in understanding the agro-ecology of Onion Couch; b) for practical agricultural considerations, especially, types of control; c) in providing some details (quantitative) to develop a more realistic structured model of control and spread of Onion Couch.

4.2 Regeneration from vegetative propagules of Onion Couch buried at different depths in four soil types.

4.2.1 Introduction

Onion Couch is regarded as a weed which tends to show preference for chalky and light soils where it has been reported to exist as a consistent and successful weed of arable land (Chap.2). This experiment was performed in the hope of shedding some light on why Onion Couch is generally restricted to some soils and not others. It was also planned to use the information so obtained to simulate the effect of cultivation practices in the context of interaction with the soil type on the success of regrowth from the vegetative propagules of Onion Couch buried at different depths.

4.2.2 Methods

To investigate the effect of soil textures, four soils of differing texural characteristics (Table. 4.1) were collected from arable situations. Two of these soils i.e chalk loam and clay-with-flint

SOIL TYPE	SAND (%)	SILT (%)	CLAY (%)
CLAY-WITH-FLINT	56.4	27.0	16.6
CHALK LOAM	68.4	15.0	17.6
SAND	84.4	10.4	5.2
CLAY	45.4	29.0	25.6

Table 4.1 Texural characteristics of the four soil types (determined by the soil hydrometer method).

were collected from fields infested with Onion Couch, the other two i.e clay and sandy soils were collected from fields with no infestation. The plant material used for the experiment was obtained from the plots maintained at Silwood Park; the material here was transplanted from the population described in Chap.3.2. The size and number of vegetative propagules, and containers used for planting are given in Table 4.2. On the 10.8.85 the material was planted in a manner similar to that followed earlier for a similar experiment (Chap. 3.8). The bags were fertilized after planting with a small amount of NPK fertilizer. On the 25.11.85, after three weeks of frost, the containers were transeferred to a green-house with 12 hours of light from Metal-halide lamps at 245 $\mu E\ s^{-1}\ m^{-2}$ and average temperature of 12 C to simulate spring conditions. The experiment was harvested on 1.1.86. The number of shoots emerging per treatment was recorded on 20, 80, and 110 days after planting. At harvest, plants in all bags were dug up carefully and were kept intact as far as possible to facilitate classification of parts. All vegetative propagules originally planted were examined at the time of harvest and the dry weight was taken after drying of at 100°C for 24 hours. The originally planted ramet or aggregates were classified either as having survived by producing aerial tillers or as having died. Dead ramet or aggregates were found intact with little or no signs of decay.

The following determination were made for each treatment at the time of harvest:

1. Number of ramets or aggregates producing at least one shoot above the soil surface.

2. Number of buds on the ramets or aggregates that developed into

DEPTH OF PLANTING (CM)	TOTAL NUMBER RAMETS/ AGGREGATES	NUMBER OF RAMETS PER UNIT	SIZE OF CONTAINER (AREA DEPTH) (CM^2 CM)	NUMBER OF CONTAINERS USED
0.0	8 6	1 3	453 28	1
1	8 6	1 3	453 28	1
3	8 6	1 3	453 28	1
9	8 6	1 3	453 28	1
18	8 6	1 3	453 28	1

Table 4.2 Material and containers used for the experiment.

aerial shoots, and number of vertical shoots that failed to reach the soil surface.

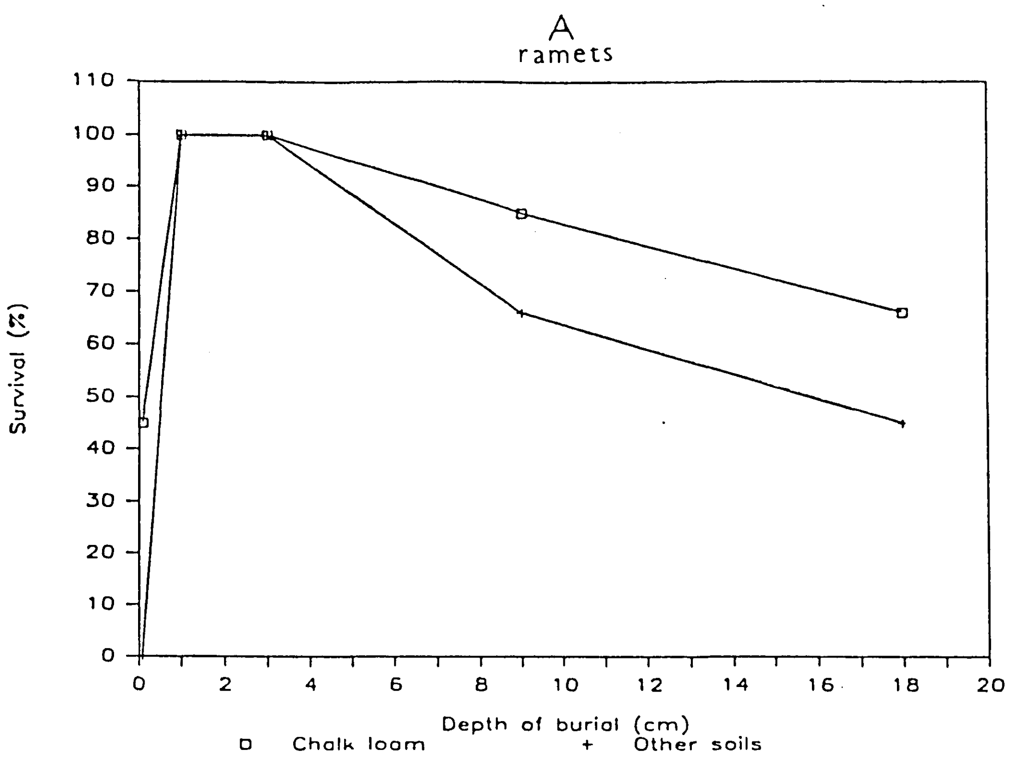
4. Number of aerial tillers and bulbs, and their dry weight per planted ramet or aggregate.

5. Height of the tillers in each treatmment.

4.2.3 Results

Effect of burial on the mortality of planted ramets and aggregates in the four types of soils.

Fig. 4.2.1 shows percentage of vegetative propagules producing one or more aerial shoots at the time of harvest. None of the vegetative propagules placed on the surface of sand, clay or clay-with-flint produced any signs of regrowth, in fact they dried out in four to five days after placing them on the soil surface before any signs of bud activity had appeared. On the chalk loam soil 45% of single ramets and 30% of aggregates survived. The mortality observed in the experiment seemed to be higher than that observed in the field situations. This high mortality of the vegetative propagules in the experiment seemed to be due to the state of the material used for planting. Freshly formed bulb chains were used with no sign of bud activity or regrowth, and they were thoroughly washed free of soil particles before placing them on the soil surface; a state in which they are unlikely to occur in an arable situation. In spite of the unfavourable state of the planting material, the survival of some of the vegetative propagules on the surface of the chalk soils seems to be due to the crumbly texture of the soil, which provides some sort of protective micro-environment for regrowth compared to the other soil types. On chalk loam soils, as observed in Chap. 3.8, the mortality of vegetative propagules on the soil surface was higher in



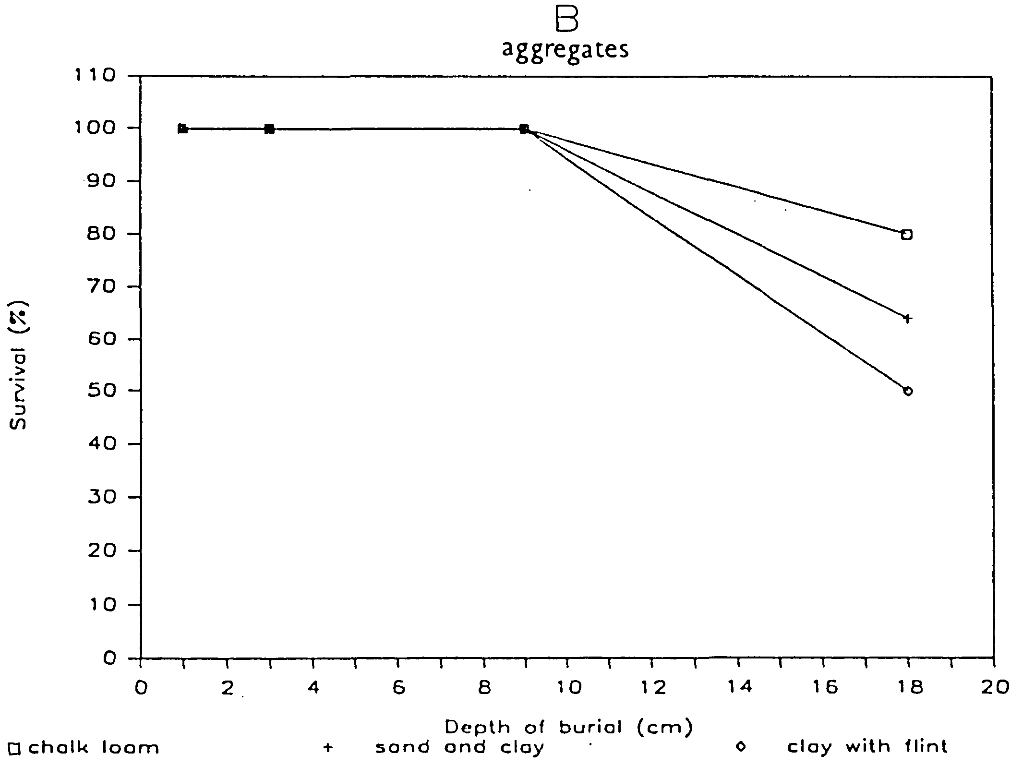


Fig. 4.2.1 Effect of burial on the survival of planted ramets and aggregates in the four soil types.

aggregates compared to the single ramets.

Although vegetative propagules buried in chalk loam soils at all depths showed less mortality compared to the other soils, the overall pattern of mortality of vegetative propagules with increasing depth seemed to be very similar in all soil types. The description that follows therefore refers to the effect of burial on the single ramets and aggregates in all soil types. No mortality was observed in any vegetative propagules buried at the shallow depth of 1.0cm and 3.0cm. When buried at a depth of 9.0cm, all the aggregates succeeded in producing aerial shoots from this depth whilst nearly 40% of single ramets failed to produce an aerial shoot from this depth. At a depth of 18.0cm mortality increased considerably especially in single ramets, although it was slightly less in the aggregates.

Time of tiller emergence

The change with time in the number of tillers emerging above the soil surface in each treatment on various days after planting is shown in Figs.4.2.2 and 4.2.3. Each line on the graph is based on tiller emegence per bulb planted as ramets or aggregates at different depths in four type of soils. As in the previous experiment (Chap. 3.8), the time of emergence was unaffected by the size of the planted material at shallow depths of 1.0cm and 3.0cm. The first shoots appeared by the first day of recording. The delay in emergence in all soil types progressively increased with the depth and the size of the planted material. Few single ramets when buried at a depth of 9.0cm produced shoots above the soil, whilst many aggregates buried at the same depth had emerged on the first

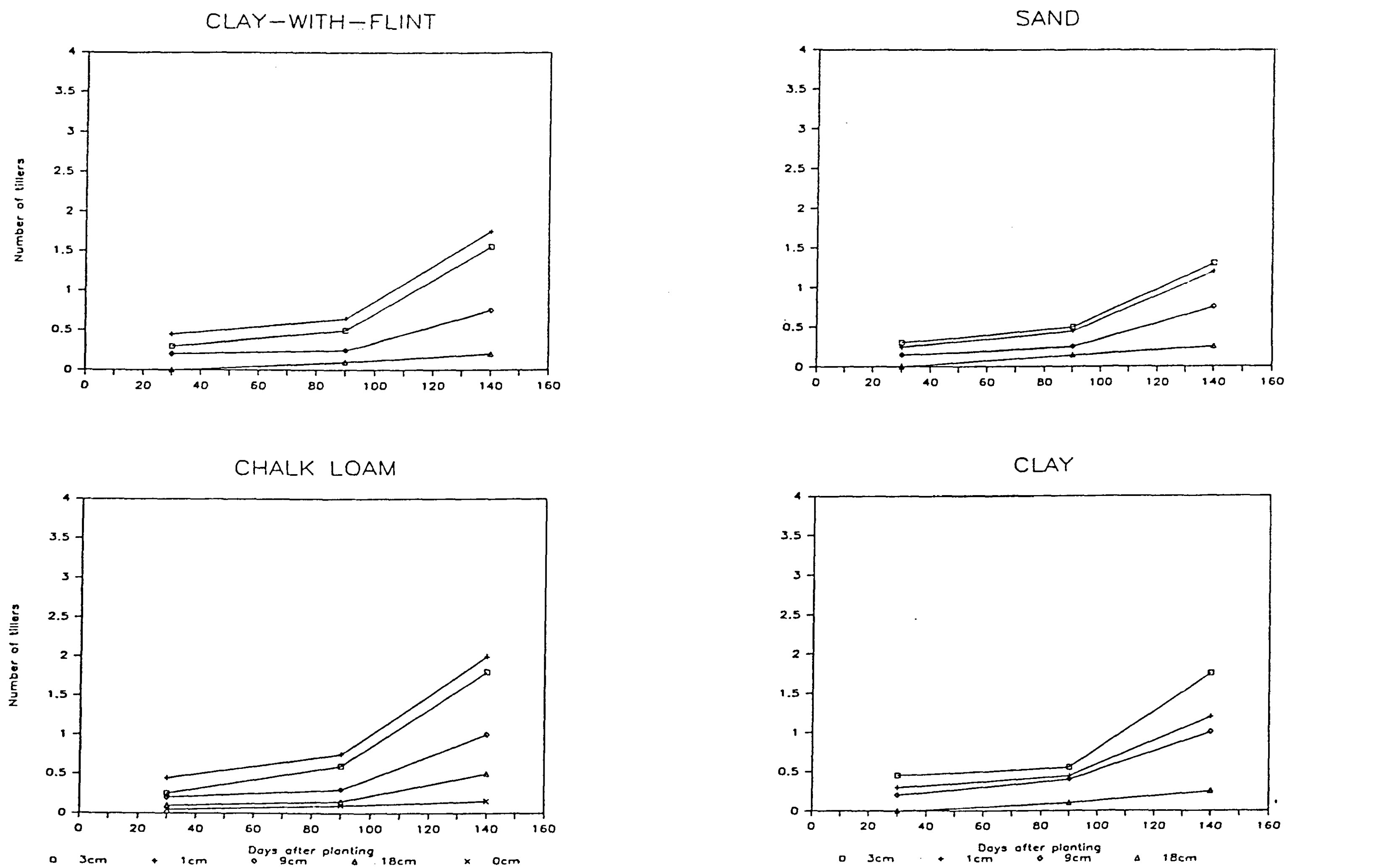


Fig. 4.2.2 Number of tillers emerging above the soil surface (per number of bulbs planted in each burial treatment) on various days after planting of single ramets, in the four soil types.

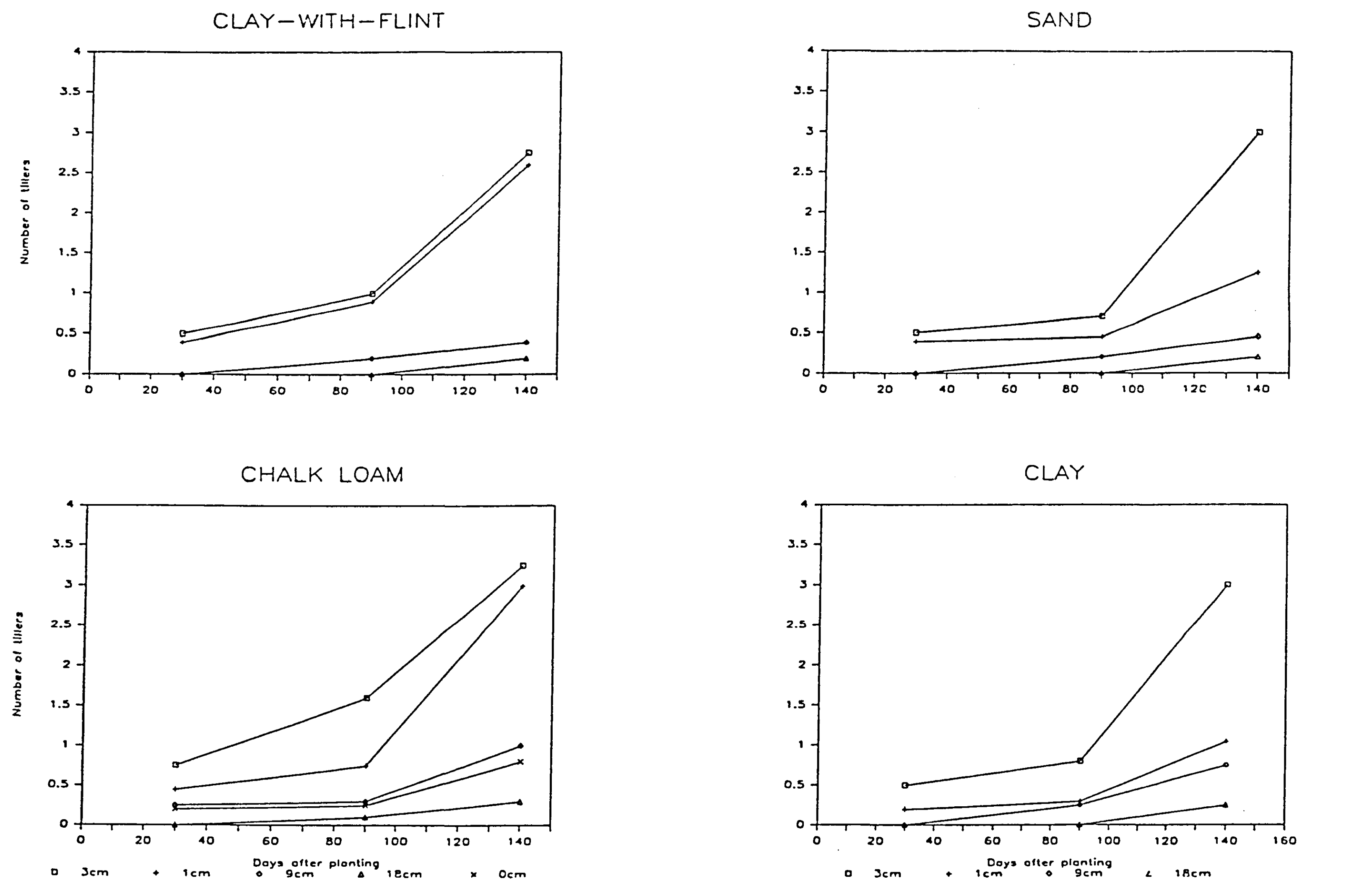


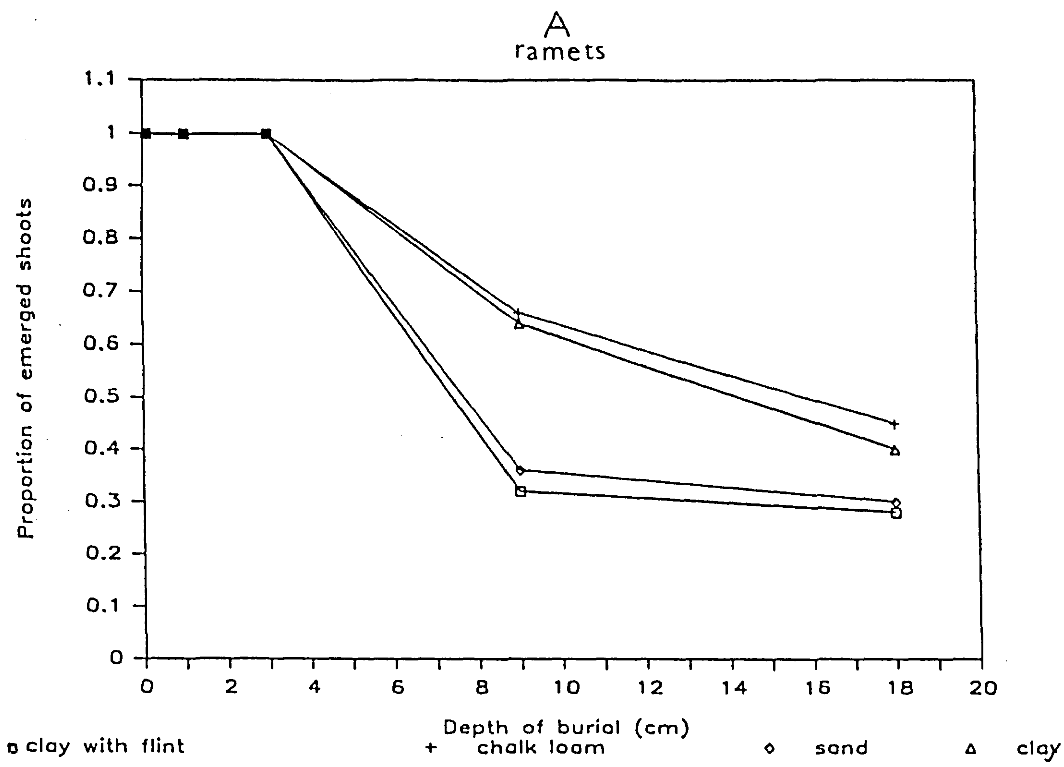
Fig. 4.2.3 Number of tillers emerging above the soil surface (per number of bulbs planted in each burial treatment) on various days after planting of aggregates, in the four soil types.

occasion of recording. None of the single ramets buried at a depth of 18.0cm in any of the soil types produced any shoots above the soil until the bags were moved to the green-house for more than a fortnight, whereas some shoot emergence was registered in the aggregates buried at this depth before moving them to the green-house. It is obvious from Figs. 4.2.2 and 4.2.3 that the amount of tiller emergence was relatively less from vegetative propagules buried at very shallow depths of 1.0cm in sand and clay compared to chalk loam and clay-with-flint, whilst tiller emergence from vegetative propagules buried at or below 3.0cm, was high in clay and chalk loam compared to sand and clay-with-flint.

The observations made on tiller emergence are in agreement with the results of the experiment described in Chap. 3.8. In addition, the ratio of aerial tillers to the number of bulbs planted per treatment was greater in single chain ramets than in aggregates at shallow depths, and with increase in depth of burial this ratio was displaced towards the aggregates, suggesting the greater vigour of the aggregates.

Proportion of emerged to total number of shoots

Fig.4.2.4 shows the proportion of emerged to total number of shoots (emerged + unemerged shoots) from the buds at the nodes of the vegetative propagules at the time of harvest. As the experiment was carried out under comparatively much lower temperature and humidity compared to the experiment described in Chap. 3.8, the burial treatment in this experiment did not cause any decay of the originally planted vegetative propagules. This made it easier to observe the effects of burial on the bud activity of vegetative



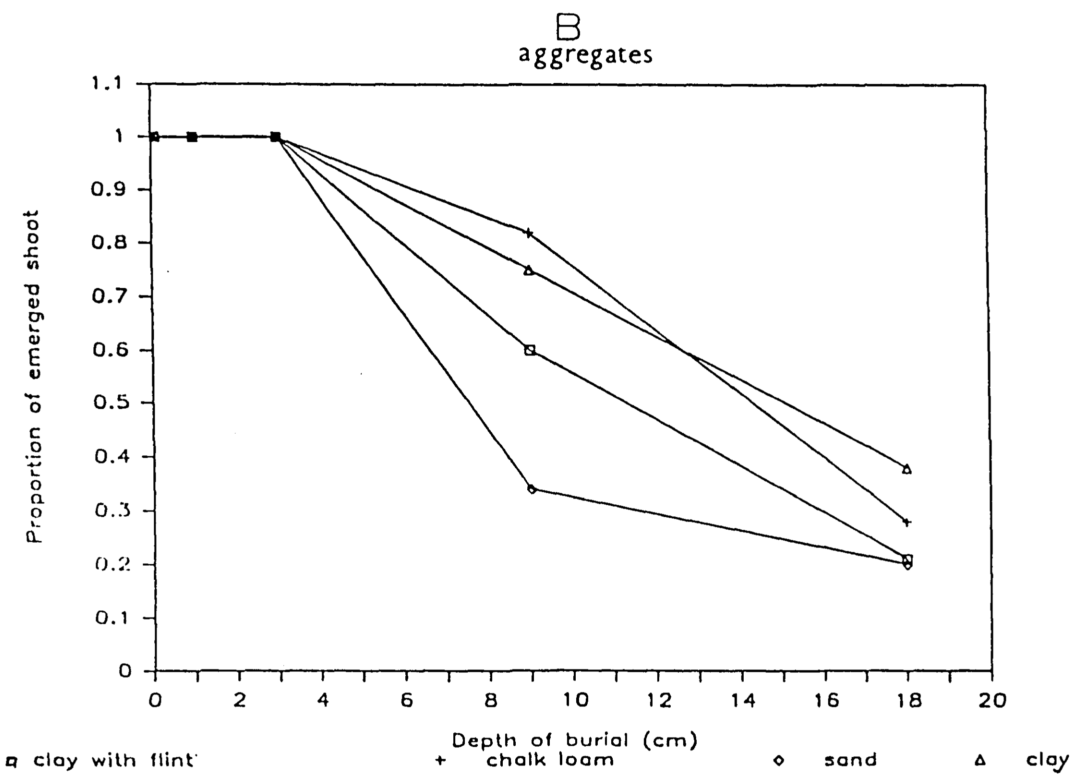


Fig. 4.2.4 Mean proportion of emerged to total shoots produced by ramets and aggregates, under different burial treatments in the four soil types.

propagules planted at varying depths.

In the planted vegetative propagules, most of the regrowth was observed to be coming from the buds at the nodes of the basal two bulbs of the ramets in spite of the fact that they were placed horizontally at the time of planting. Soil type does seems to have a modifying effect on the bud activity because the percentage of emergent to total shoots was higher in chalk loam and clays compared to sand and clay-with-flint in both sized vegetative propagules. However, the general pattern of bud activity is similar in all the soil types. At shallow depths of burial, all vegetative propagules produced shoots which emerged. Vegetative propagules buried at a depth of 9.0cm showed a decrease in the proportion of emerged shoots and the proportion of emerged shoots becames considerably reduced in the vegetative propagules planted at a depth of 18.0cm, resulting in the production of large numbers of unemerged shoots (shoots which failed to reach the soil surface). At this depth, 50% of the vegetative propagules produced shoots none of which emerged above the surface and the vegetative propagules were classified as dead. The presence of a greater proportion of emerged shoots from chalk loam and particularly clay soils seems to reflect the textural charateristics of the two soil types (Table 4.1). It is also evident from Fig. 4.2.4 that the number of buds becoming active to produce shoots, expressed as proportion of total number of nodes (or buds), is greater in single ramets than in aggregates, which indicates that there is a tendency in aggregates to have a high proportion of inactive buds or, in other words, it points to the existence of correlative dominance in the connected ramets.

Mean yield from ramets and aggregates buried at different depths

The yield of the vegetative propagules is shown in the form of number of shoots and bulbs and their dry weights in Figs.4.2.5 and 4.2.6. Although the statistical reliability of the experiment does not look very convincing because of the small number of replicates and the varying amount of regrowth from the buried vegetative propagules, in order to demonstrate any modifying effect of the soil types the results that follow are based on means with 95% confidence limits.

The mean number of shoots produced by vegetative propagules buried at different depths generally followed the pattern observed earlier (Chap. 3.8). Mean number of tillers and their dry weight increased significantly with an increase in the number of ramets in the aggregates and there was a significant decline with increasing depth in the number of tillers and their dry weights. The results described below for each soil type refer to both ramets and aggregates, as they showed a more or less similar pattern of shoot production from their respective burial depths.

In the bags with chalk loam soils, greatest mean production was registered by the vegetative propagules planted at a depth in the range of 1.0cm to 3.0cm. Vegetative propagules buried at a depth of 9.0cm to 18.0cm produced significantly less, respectively. In the bags with clay-with-flint soils, greatest production of shoots was observed after planting at a depth of 1.0cm and 3.0cm, the production progressively declining with further increase in the depth of planting. In the bags with the sandy soils, greatest mean production was registered by the vegetative propagules planted at a depth of 3.0cm, those buried at a shallow depth of 1.0cm producing

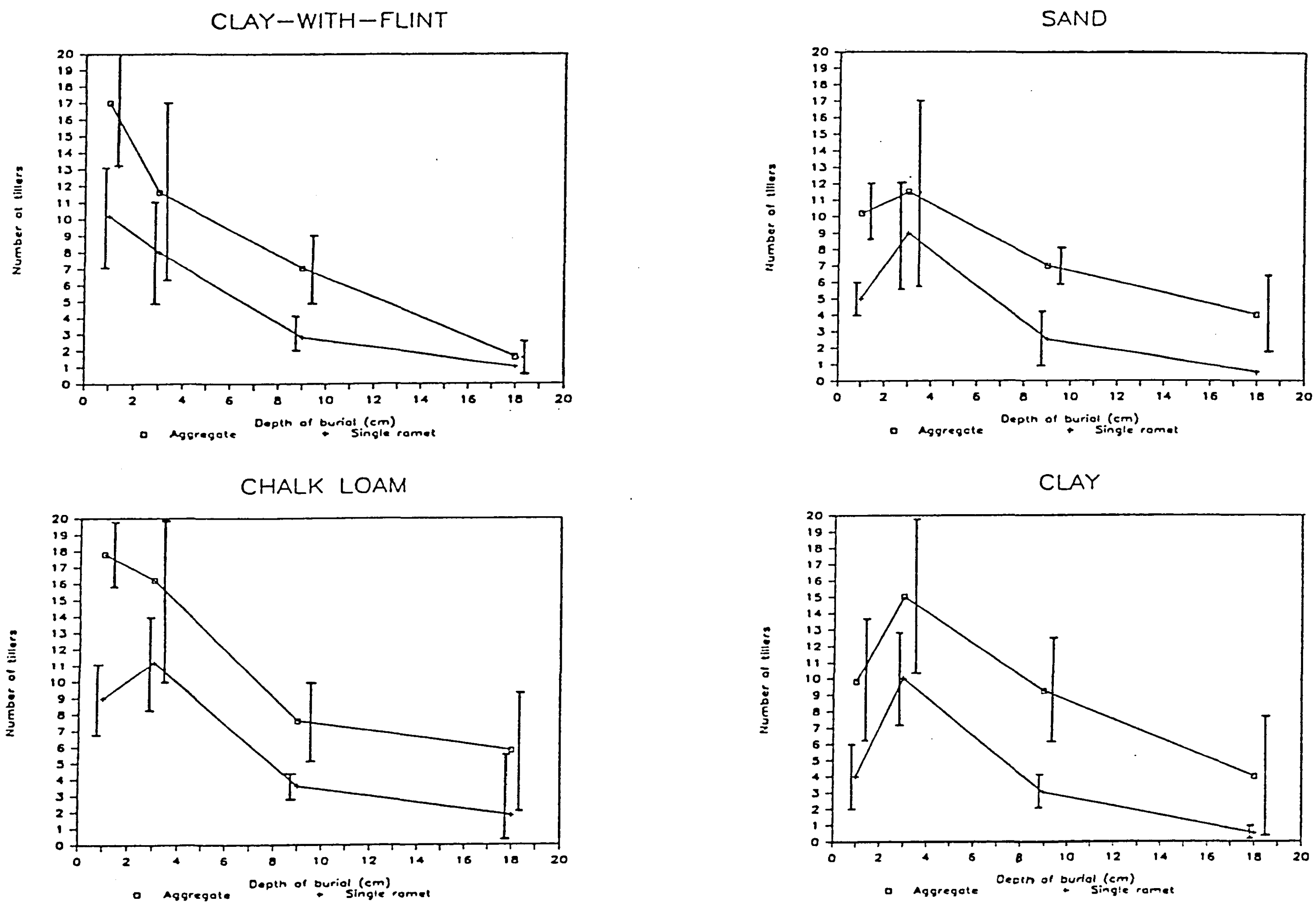


Fig. 4.2.5 Mean number of tillers produced by ramets and aggregates under different burial treatments in the four soil types.

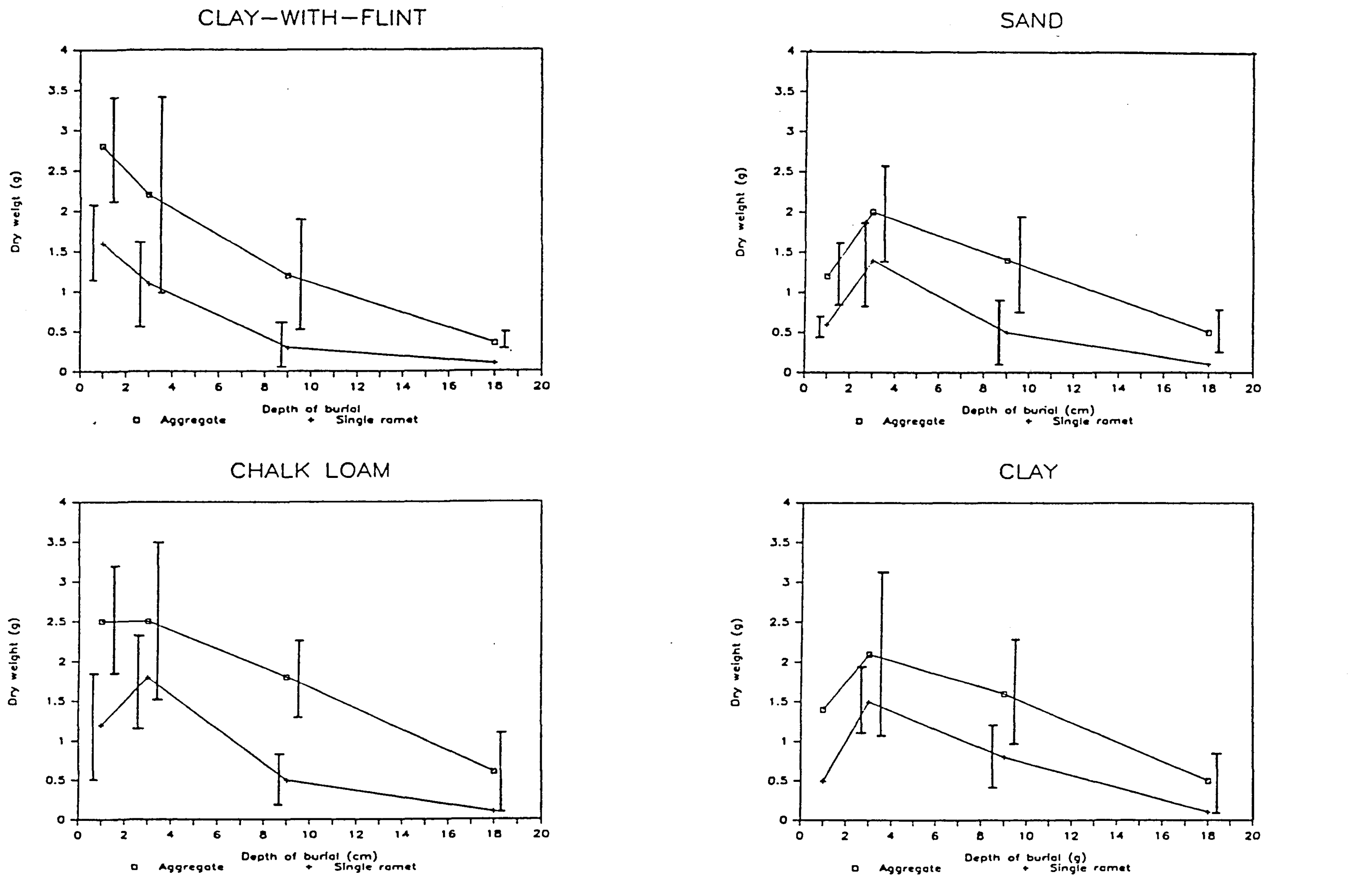


Fig. 4.2.6 Mean dry weight of tillers produced by ramets and aggregates under different burial treatments in the four soil types.

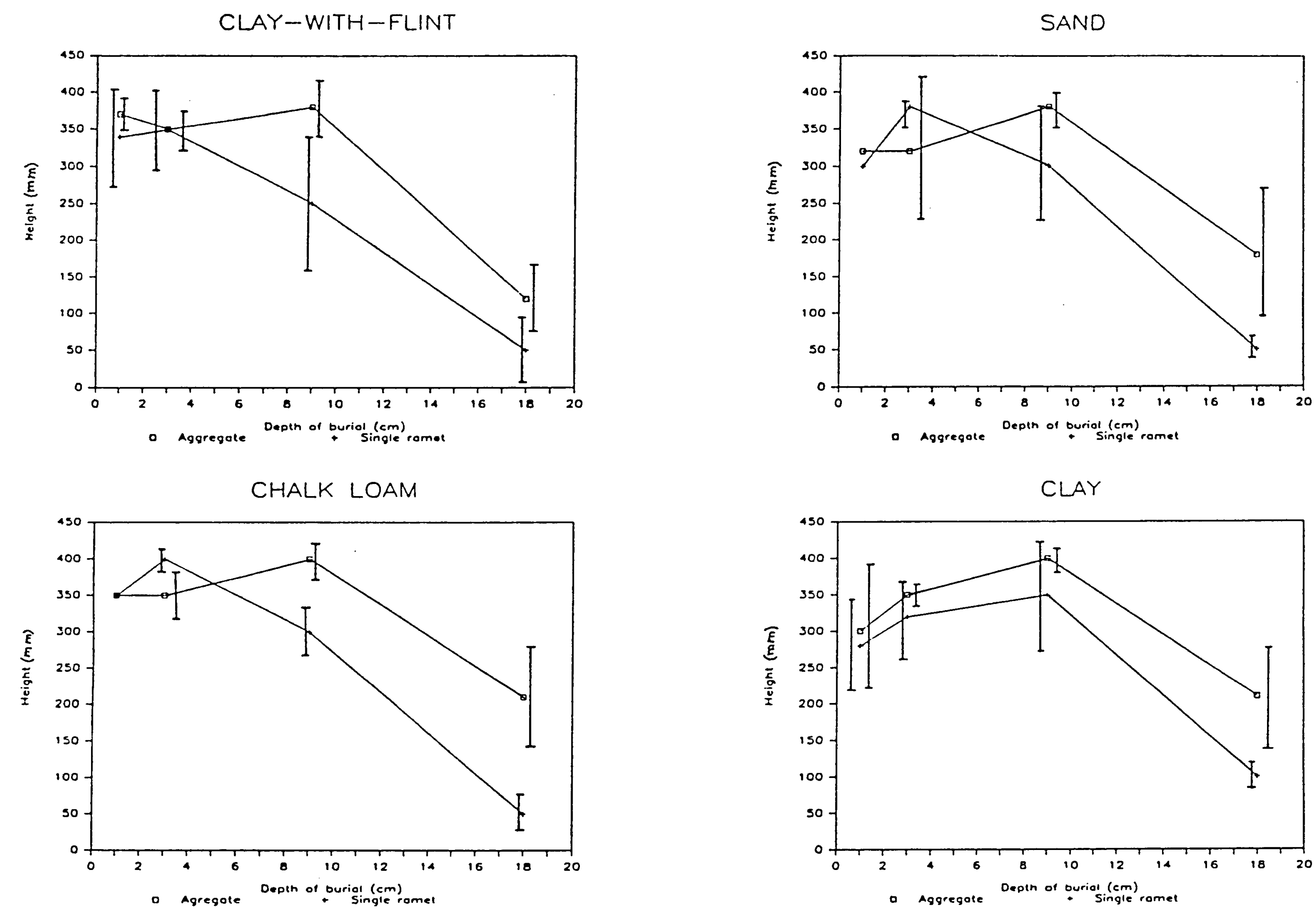


Fig. 4.2.7 Mean height of tillers produced from ramets and aggregates at the time of harvest, under different burial treatments in the four soil types.

significantly less, and the ones buried at depths of 9.0 to 18.0cm followed the same general trend of progressive decline in production. In the bags with clay soils, greatest mean production was observed at a depth of 3.0cm. There was significantly decreased production at a depth of 1.0cm (as noticed on the sandy soils) and the pattern from other depths was similar to the already described soil types.

Further evidence of greater regeneration from clay and chalk soils is reflected in the mean height of the tillers emerging from different burial classes (Fig.4.2.7). The single ramets produced tallest tillers when buried at the depth of 3.0cm, followed by a significant decrease in mean height from the burial depth of 9.0cm. In the clay soil, however,even the vegetative propagules buried at 9.0cm produced tall tillers, which indicates the diminished effect of burial in the clay soil (due to the appearence of cracks on drying which facilitate emergence). In aggregates the tallest tillers are produced at 3.0cm and 9.0cm depths, and here again the tallest tillers comes from the vegetative propagules buried in chalk loam and clay.

4.2.4 Discussion.

The results are in agreement with the experiment described in Chap. 3.8 and have clearly demonstrated that the regrowth from the planted vegetative propagules will depend on both the number of ramets in the vegetative propagules and the depth to which they are buried. In addition, the results have clearly shown that exposure of vegetative propagules on the soil surface could be quite effective in reducing the regrowth from the vegetative propagules. It is apparent from the results that the vegetative propagules of Onion Couch in the bags with chalk soil have shown more production in all treatments compared to the other three soil types. This is probably due to the crumbly texture of the soil and the porous tilth which provided not only a protective micro-climate for the exposed vegetative propagules, but also allowed easier emergence from the buried vegetative propagules. The vegetative propagules in the clay-with-flints soil produced more tillers at shallow depths, where presence of flint, apart from the resistance it provides to erosion by wind and water and to evaporation from the soil surface also benefits Onion Couch by providing protective cover from adverse environemental conditions (drying, frost,etc). At greater depths, the decline in the production of tillers seems to be due to the rather more compact structure of the clay-with-flint soil, which being less crumbly compared to chalk loam, made the emergence from greater depth more difficult. Sandy and clayey soils, on the other hand, produced significantly lower and more variable yield at a depth of 1.0cm which seems to be due to the drier surface soil (resulting from the drainage and moisture retaining characteristics of the two soils respectively). At a greater depth of burial, the production declines more sharply in the sandy soils, probably because of the presence of more homogenously distributed particles compared to clayey soil where the appearence of cracks in the soil on drying allowed free passage of vertical shoots and diminished the effect of burial to a greater extent.

The results of this experiment suggest that Onion Couch could easily spread resulting in large scale infestations particularly on a chalk loam and clay-with-flint. The reason for suggesting this is mainly due to the fact that the new ramets which are formed at the bases of the current shoots are normally present in the top centimetre of the soil. The bulb chains formed at the bases of new tillers and connected to the old vegetative propagules by a caudex (whose length varies with the depth of burial) are very brittle at this connection, especially in large chain aggregates which even with cultivation implements operating at a fairly shallow depth results in high degree of breakage into smaller aggregrates. This means that virtually any cultivation practice would be enough to break the large aggregate and spread and bury them to some shallow protective depth. Since the experiment described here indicated that the most vigorous regrowth from very shallow depths comes from the bags with chalk loam and clay-with-flint, it suggests that soils with such texture provide greater protective environment essential for bud survival and regrowth compared to predominantly sandy and clayey soils.

4.3 Growth and development of Onion Couch from single ramets and aggregates in two crop situations in a natural infestation.

4.3.1 Introduction

In natural infestations a higher frequency of aggregates compared to single ramets is encountered and in a crop situation competition from the crop can influence the regrowth both morphologically and physiologically from these ramets and aggregates. The aim of this work which was conducted by destructive sampling of vegetative propagules of Onion Couch of approximately similar sizes, in natural infestations was: 1) to investigate the performance of vegetative propagules of varying sizes (single ramets to large aggregates) during the crop growth cycle, especially trends in tiller and bulb production and allocation of dry matter to these two components and 2) to investigate whether any density dependent relationship exists in the attributes measured, between single ramets (or small aggregates) and large aggregates.

4.3.2. Methods

The experiments were conducted in natural infestations for two years. During the 1984-85 season, two field situations were selected for fortnightly harvests: 1). Winter wheat on a clay-with-flint soils at Hungerford, Berkshire. The land was cultivated (shallow tine) annually and had been under continuous winter wheat for some years. The field was well managed and gave an annual yield of 8 t ha^{-1} (Chap.2.6). The field was light to moderately infested with Onion Couch which formed small patches (Plate 8). 2) Winter oat on a chalk loam soil at Shalbourne, Wiltshire. The field was usually ploughed but was currently harrowed and ploughed. The field had been under winter cereals for five years and before that the field was down to grass. The field looked marginal and gave an annual yield of 5 t ha^{-1} (see Chap.2.6). The field was strongly infested with Onion Couch, which formed very large patches (whole field infestation). during the 1985-86 season, one field with winter wheat on clay-with-flint soil (an intensively sown crop with a moderate infestation of Onion Couch) at Hungerford (Plate 9) was selected for monthly harvests. Data collected from the 1985-86 season were combined with data collected from a similar situation (wheat) in the 1984-85 season because there was not much difference, apart from late tillering due to a delayed spring. In addition, data obtained

Plate 8 Small patches of Onion Couch infestation in a wheat field.

Plate 9 Large patches of Onion Couch infestation in a wheat field.

from the regrowth of individual ramets sampled at monthly intervals from a plot planted with 9 ramets m^{-2} in monoculture (see Chap.3.5) were used here to represent a crop free control, to compare the performance of similar sized ramets from the two farm situations.

All harvests involved destructive sampling; single ramets and aggregates present in the top 3cm of the soil were dug up carefully at each harvest and brought to Silwood Park where they were washed and further selection was made on the number of bulbs per aggregate. The number of bulbs in the aggregates varied (slightly higher in the wheat field), so it was thought more appropriate to select aggregate sizes on the basis of number of bulbs per aggregate, rather than, number of ramets per aggregate. The aggregate size selected for regular harvest was the one more frequently encountered in the farm situation. The following approximate numbers of bulbs per aggregate were selected at each harvest: (1) 3 bulbs (single ramet); (2) 11 bulbs per aggregate (3-4 ramets); (3) 20 bulbs per aggregate (8-10 ramets); (4) 45 bulbs per aggregate (16-20 ramets); (5) 250 bulbs per aggregate (80-90 ramets).

Five replicates for each single ramet and aggregate were selected for the first four size categories. The data collected for the fifth category were based on two replicates, as these sizes were later found to be very infrequent in Wheat fields although they were quite frequent in the oat field. In addition, height and tiller numbers of 15 crop plants were monitored at each harvest.

The following measurements were made at each harvest:

For Onion Couch:

1. Dry weight of aerial tillers and basal internodes (after oven drying for 48 hours at 100°C)
2. Number of aerial tillers.
3. Number of new bulbs.
4. Number of bulbs per ramet or aggregate (previous year's).
5. Average height of tillers.

For crops:

1. Number of tillers per plant and their height.

The first harvest was made on 10.10.84 before crop seeds were sown. The second harvest was made on 25.3.85 followed by six harvests at fortnightly intervals, the final harvest being on 15.7.85.

4.3.3 Results

The results are mostly based on means of five replicates per harvest, confidence limits are included where possible.
Figs. 4.3.1 and 4.3.2 shows the trends in the growth and development of single ramets growing in three different situations. The trends of growth and development of Onion Couch harvested from the oat field bear significant similarities in most of the characteristics to the growth observed from single ramets in the crop free control plots. On the other hand, growth from single ramets in the wheat field shows trends which significantly differ from the trends of growth observed in the oat field and crop free control plots, especially in total number of tillers and bulbs, allocation of dry weight to the two components and proportion of two and three bulbs ramets.

This pattern of growth from single ramets (Figs. 4.3.1 and 4.3.2) in

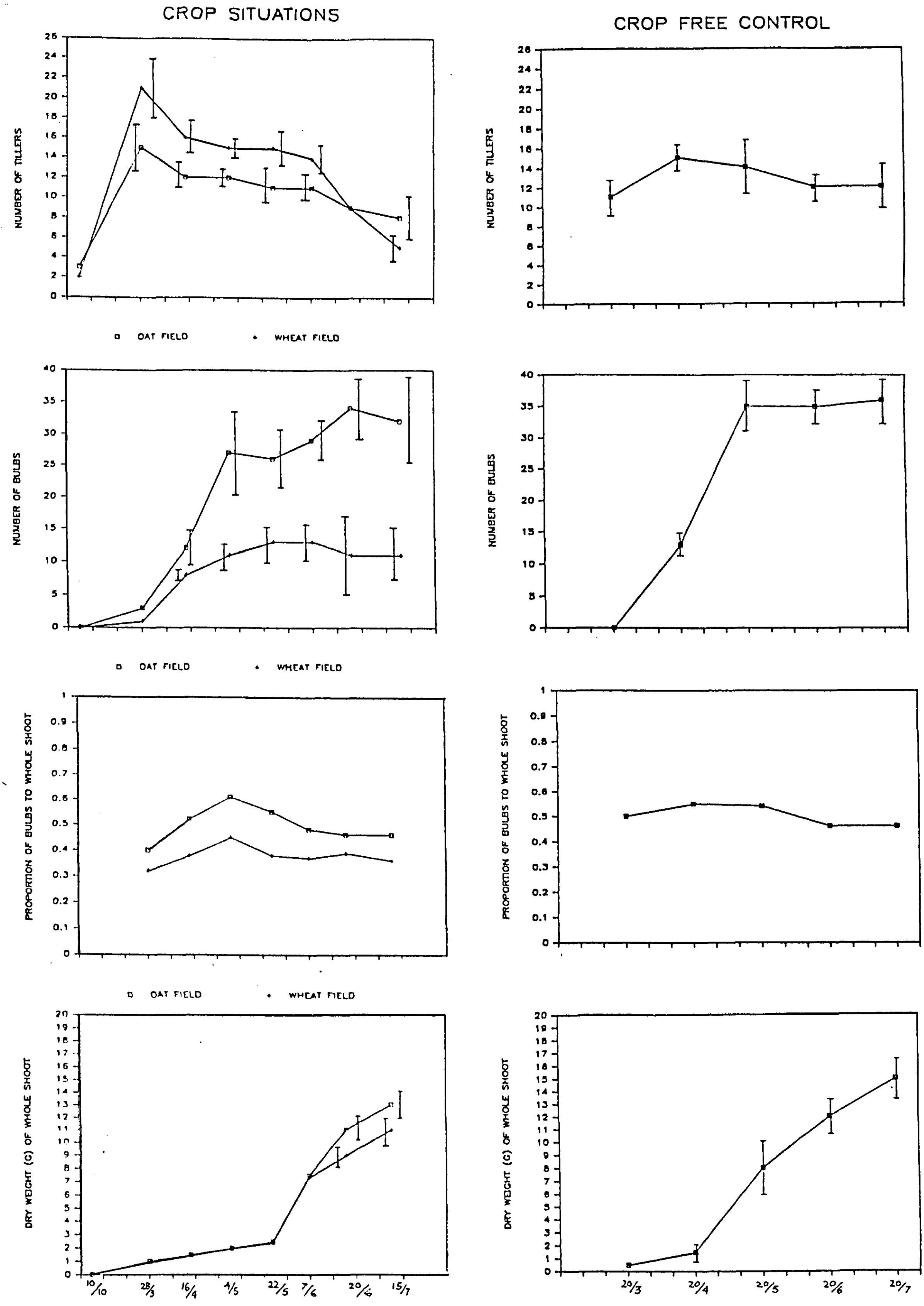


Fig. 4.3.1 Comparison of trends in growth characteristics of various attributes of Onion Couch developing from single ramets in a natural infestation and a crop free control.

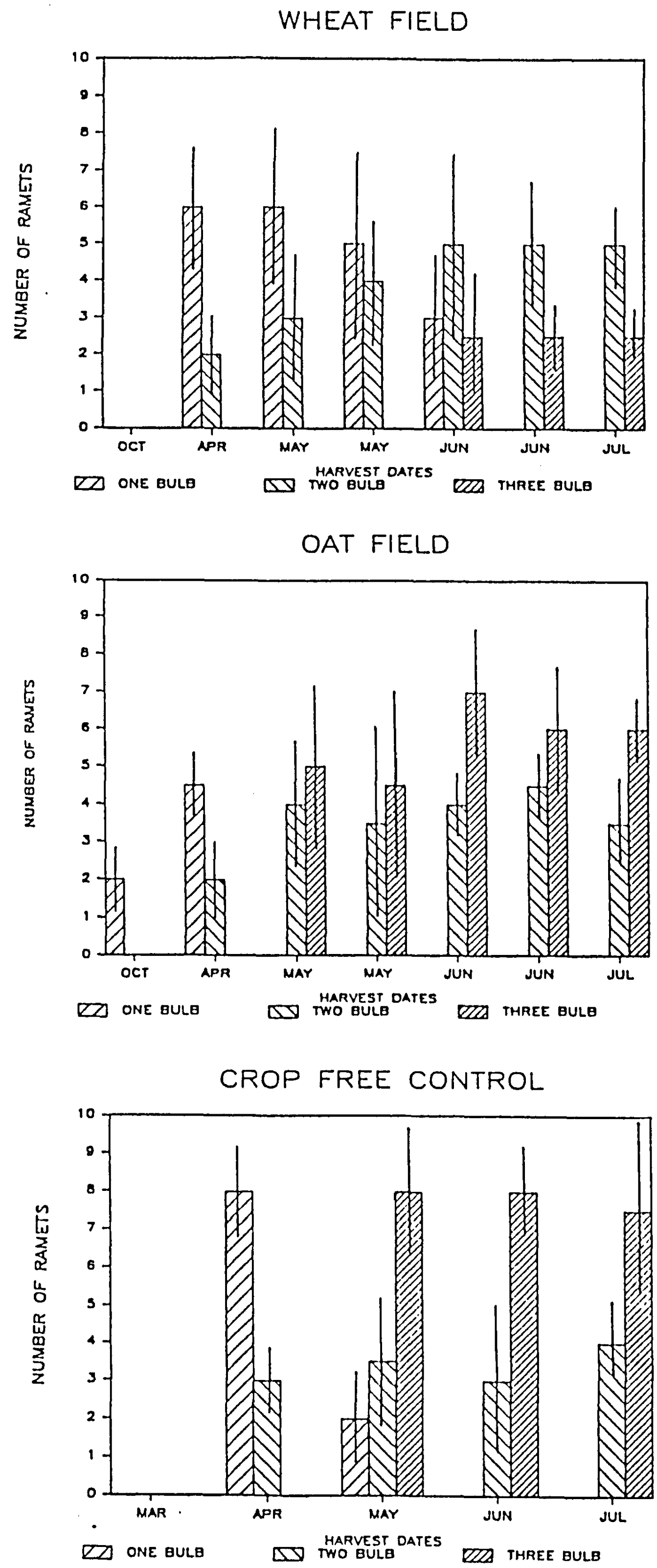


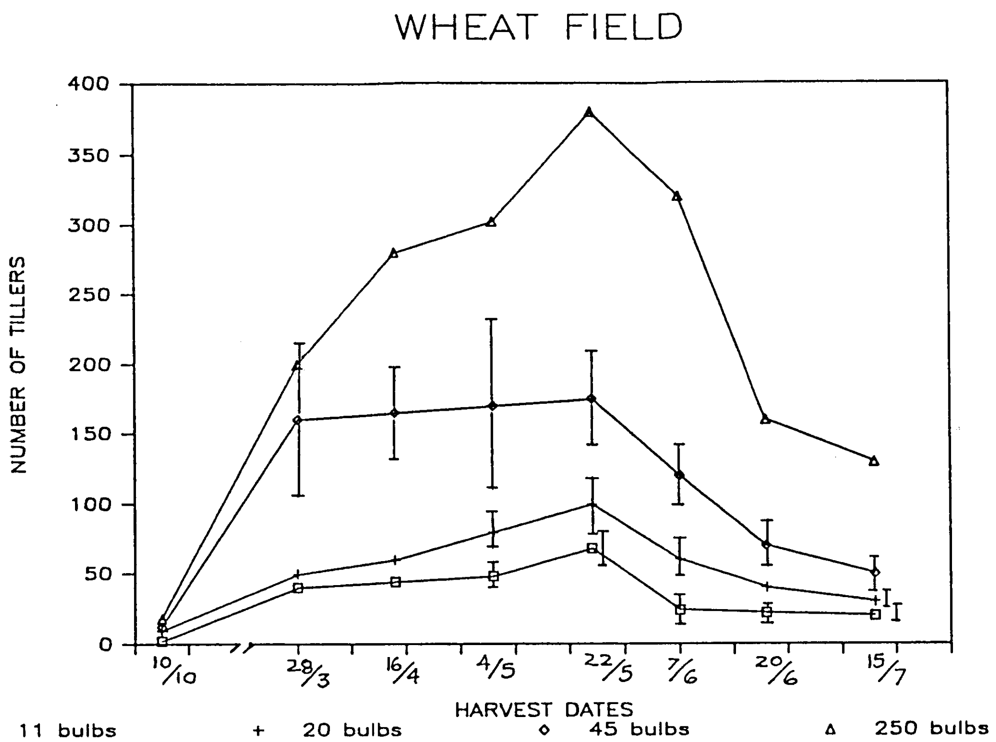
Fig. 4.3.2 Comparison of trends in bulb production form single ramets in natural infestations, and a crop free control.

the two crop situations is retained by aggregates developing (Figs. 4.3.3-4.3.9) in the two crop situations .

Fig. 4.3.3 shows the trends of tillering and self thinning on a fortnightly basis. Tillering initiated in autumn reaches its peak in the following spring (April). Numbers of tillers were generaly higher in larger aggregates compared to smaller aggregates. The growth from larger aggregate underwent significantly greater self thinning during the stem elongation phase (June), this being presumably an effect of increasing number of ramets per aggregate. Tillering and self thinning generally appear to be higher in all aggregates regenerating in the wheat field than in the oat field. After the thinning phase, the tillers developing from aggregates of four different sizes (2-5) in both crop situations appeared to be stabilizing at approximately similar numbers: 18, 30, 45, 120 respectively.

Fig. 4.3.4 shows the trends in the production of whole shoot weight. The whole shoot weight of Onion Couch developing from aggregates of the same sizes was similar in the two crop situations. This indicates that the smaller number of tillers which developed from aggregates in the oat field during the early phase of growth, were stronger than the tillers developed from aggregates in the wheat field.

The trends in allocation of dry weight to aerial tillers and basal internodes (Figs. 4.3.5 and 4.3.6) were significantly different in the shoots developing from aggregates in the two crop situations. Shoots of Onion Couch developing in the wheat field invest



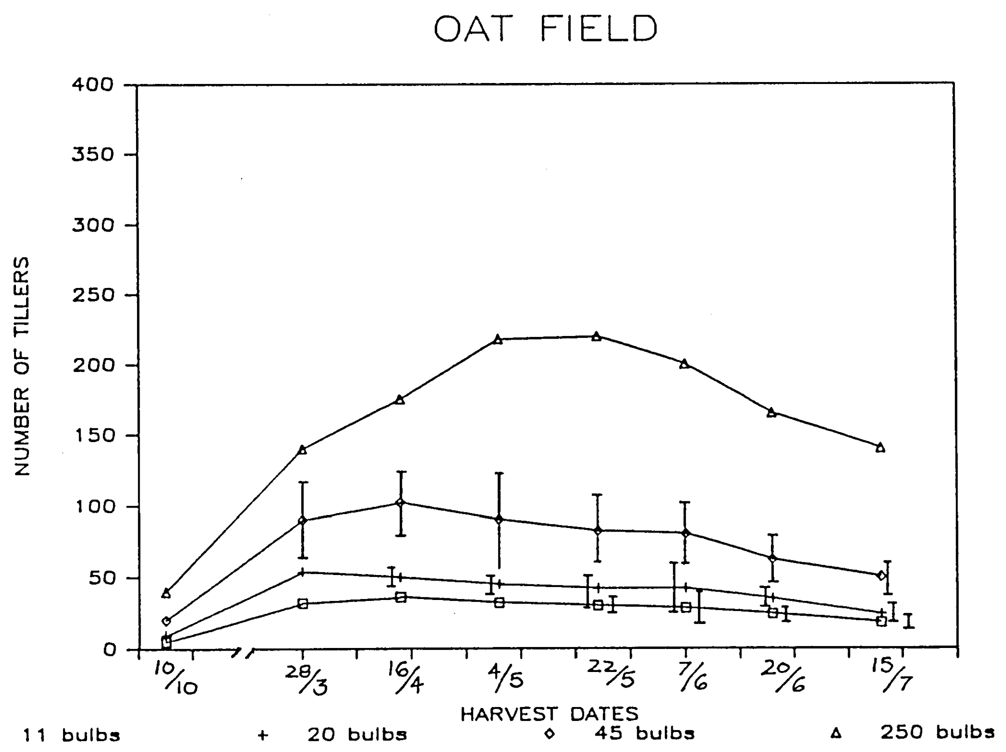
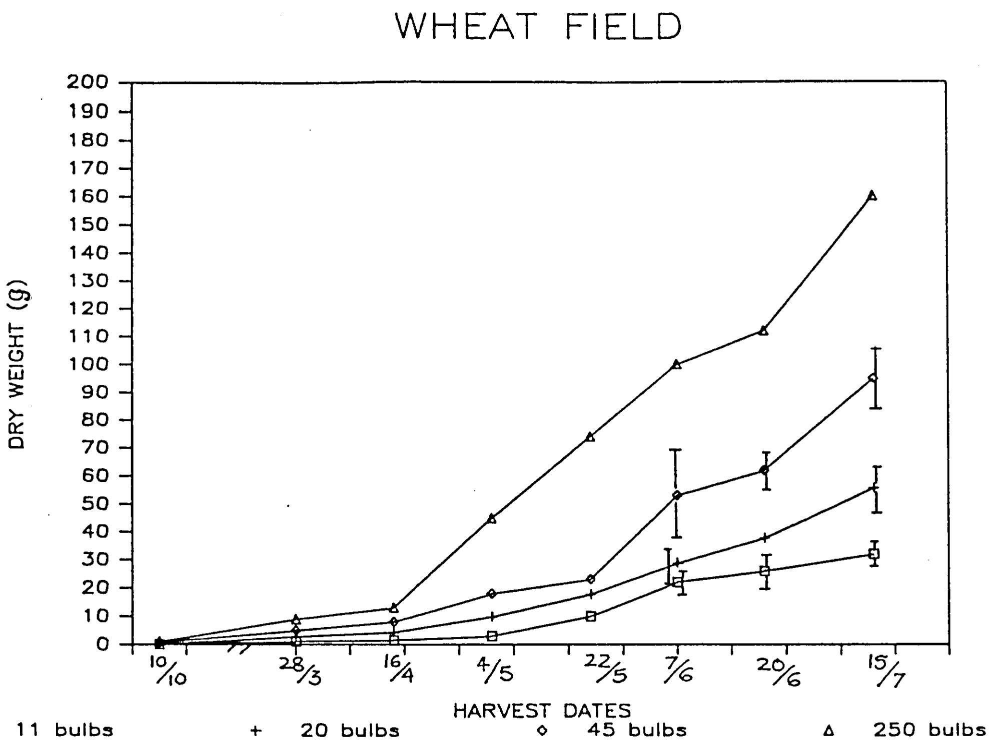


Fig. 4.3.3 Trends in tiller production in Onion Couch from aggregates of varying sizes, in competition with wheat and oat. With 95% confidence limits



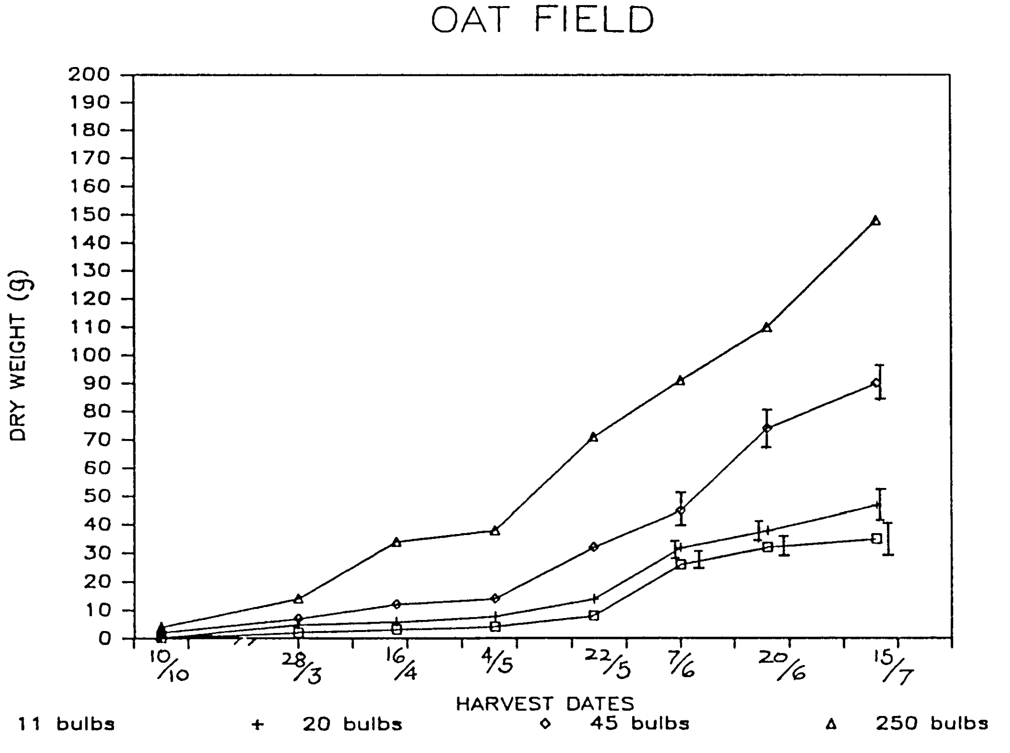


Fig. 4.3.4 Trends in allocation of dry weight to the whole shoot in Onion Couch from aggregates of varying sizes, in competition with wheat and oat. With 95% confidence limits

significantly greater amount of reserves in the aerial tillers than basal bulbs, whereas shoots of Onion Couch in the oat field invested equal amounts of reserves in basal bulbs and aerial tillers. These trends are also reflected in the basal bulb dry weight as a porportion of whole shoot (Fig. 4.3.7). This proportion was about 0.60 and 0.45 for Onion Couch in the oat and wheat fields respectively during the early phases of growth (coinciding with bulb formation), and then dropped to 0.48 and 0.34 in the oat and wheat fields respectively (coinciding with tiller elongation).

Fig. 4.3.8 shows that bulb initiation started earlier in the plants developing in the oat field but the bulk of bulb formation took place during the month of May in both situations. Fig. 4.3.8 also shows that total number of new bulbs formed per aggregate (of all sizes) was significantly higher in the oat field. A greater proportion of the tillers formed during the tillering phase in Onion Couch developing in the oat field contributed to the total number of newly formed ramets, whereas, only a small proportion of Onion Couch developing in the wheat field contributed to the total number of ramets at the time of harvest (because most of the one bulb tillers become unrecognisable at the time of final harvest). Fig. 4.3.9 shows that the proportion of three bulb ramets in Onion Couch developing in the oat field was higer than Onion Couch developing in the wheat field. It is also clear from Fig. 4.3.8 that although the larger aggregates have a higher number of new bulbs than the smaller ones the relationship between the two sizes (concerning the total number of new bulbs) of aggregates is non-linear.

Fig. 4.3.10 shows that the wheat tillers grew faster and dominated

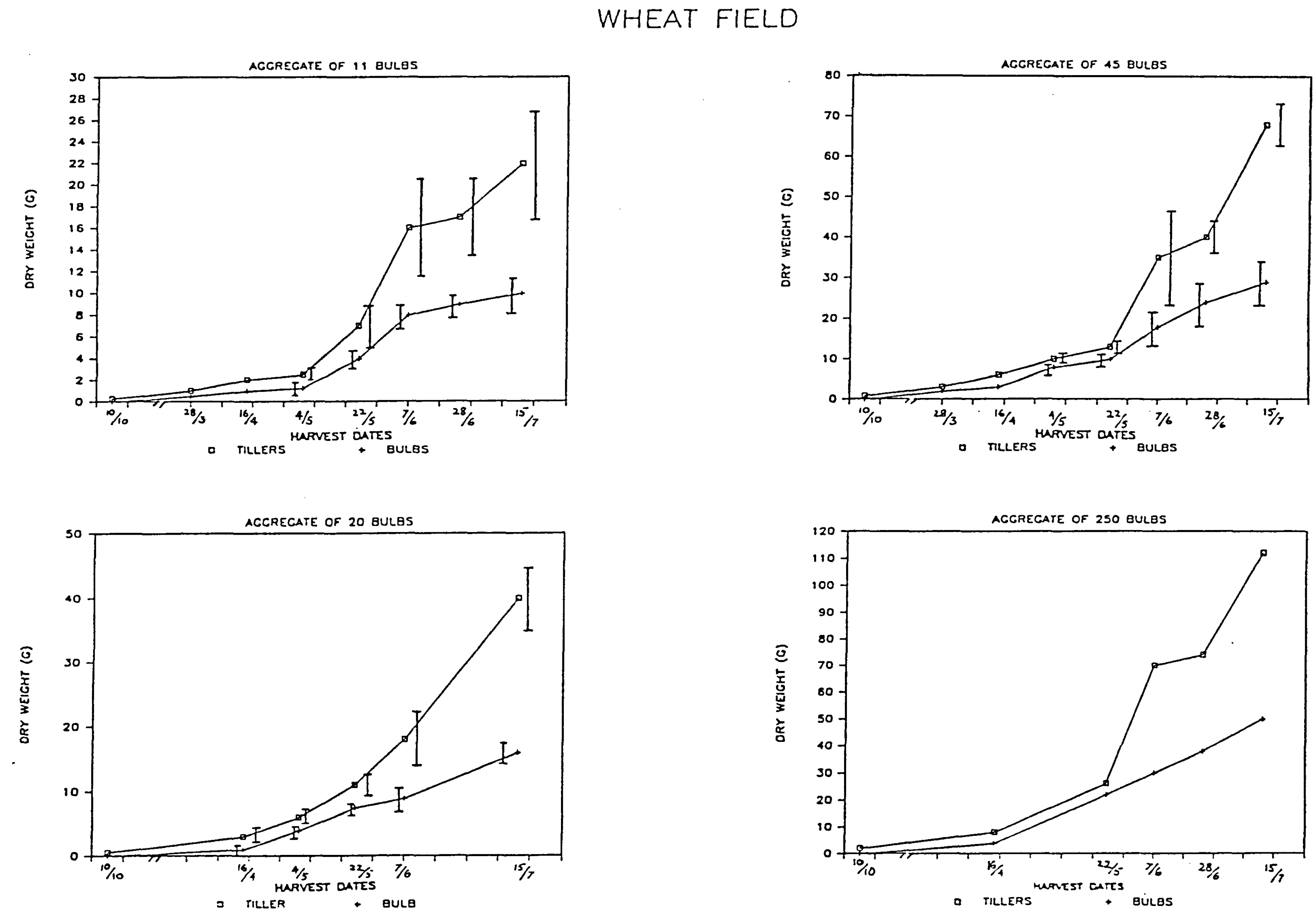


Fig. 4.3.5 Trends in allocation of dry weight to aerial tillers and basal bulbs in Onion Couch developing from aggregates of varying sizes, in competition with wheat. With 95% confidence limits.

OAT FIELD

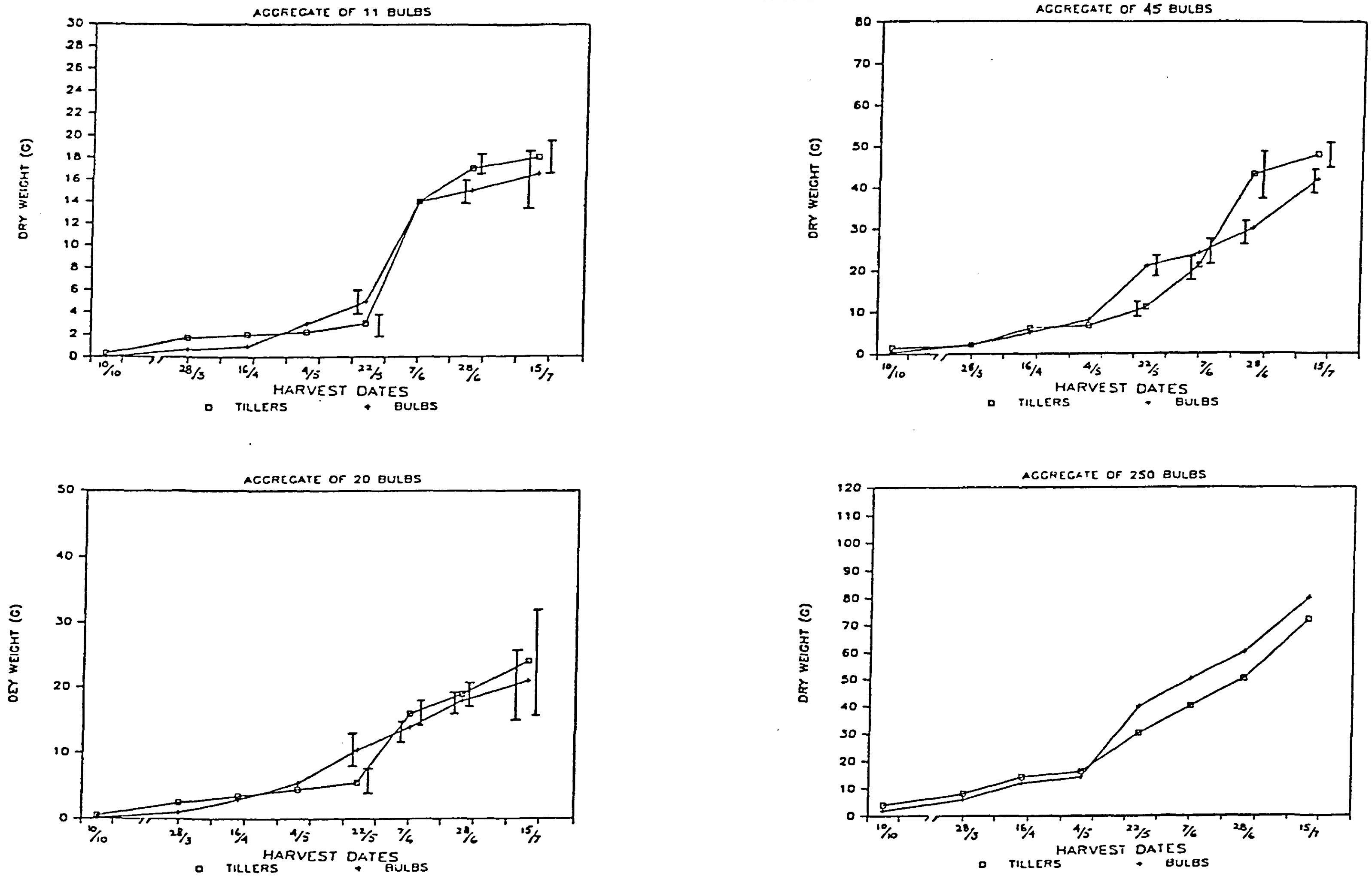


Fig. 4.3.6 Trends in allocation of dry weight to aerial tillers and basal bulbs in Onion Couch developing from aggregates of varying sizes, in competition with oat. With 95% confidence limits

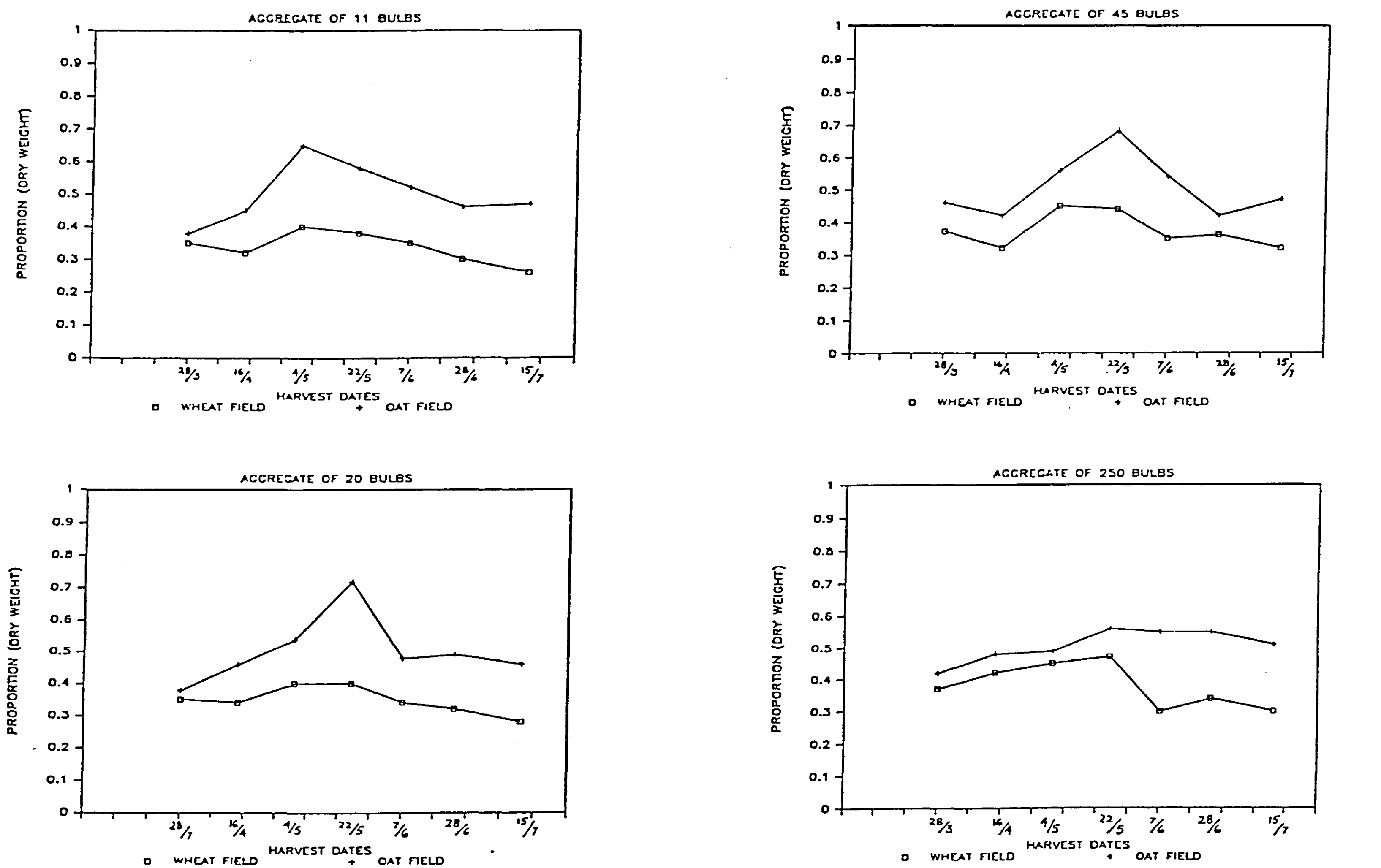
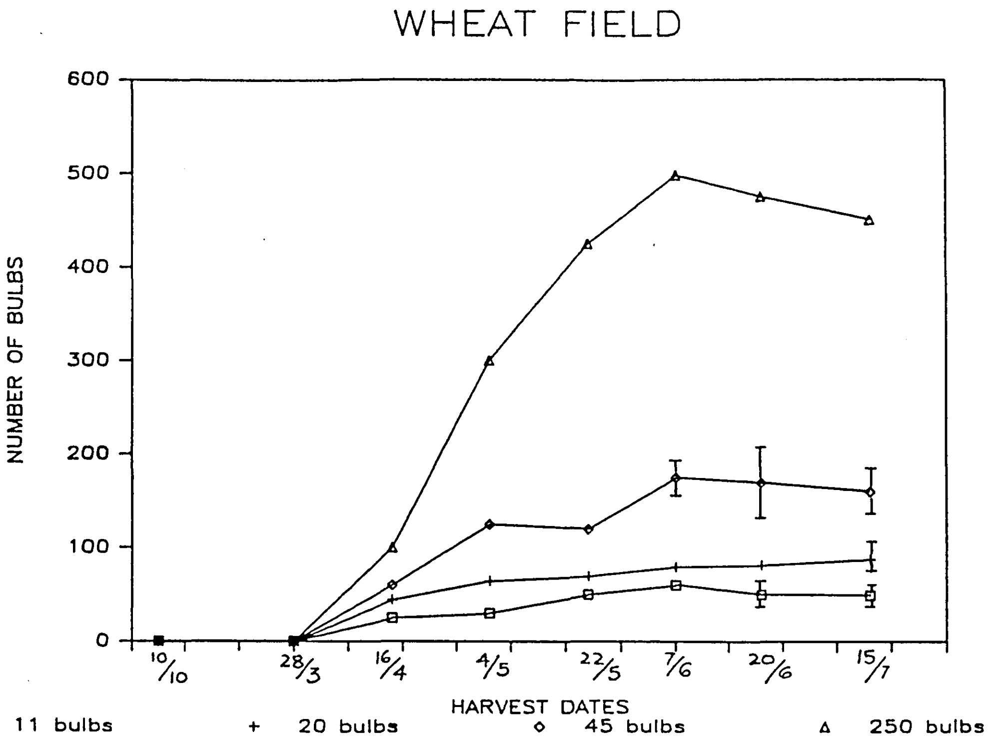


Fig. 4.3.7 Trends in dry weight of basal internodes as a proportion of whole shoot in Onion Couch, regenerating from aggregates of varying sizes, in competition with wheat and oat.



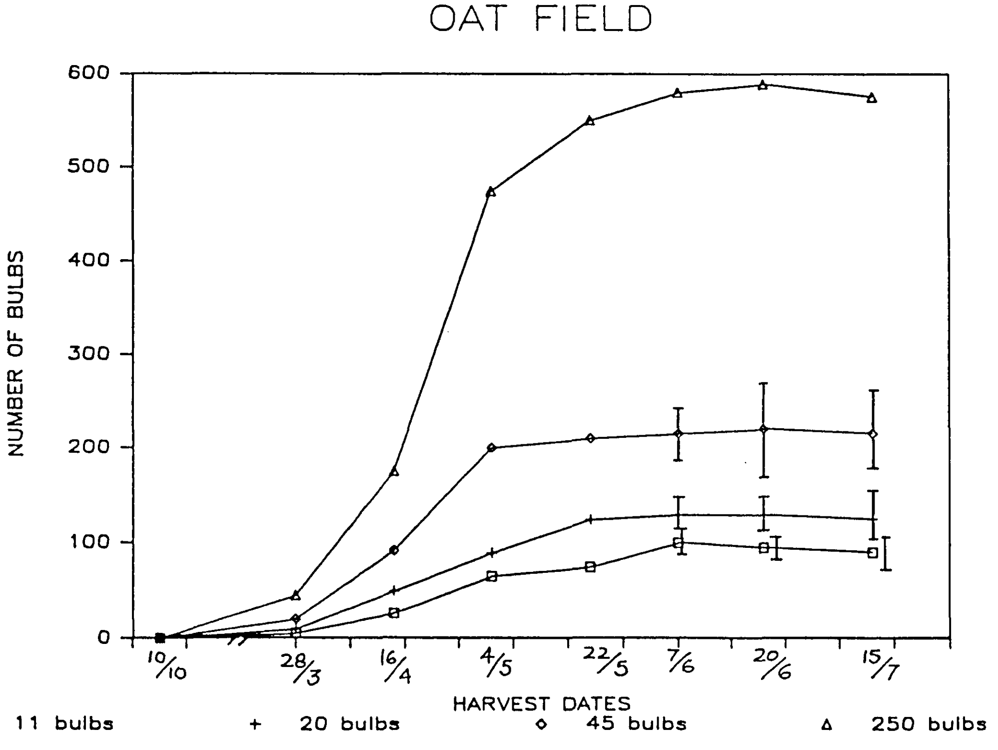


Fig. 4.3.8 Trends in bulb production in Onion Couch from aggregates of varying sizes, in competition with wheat and oat.

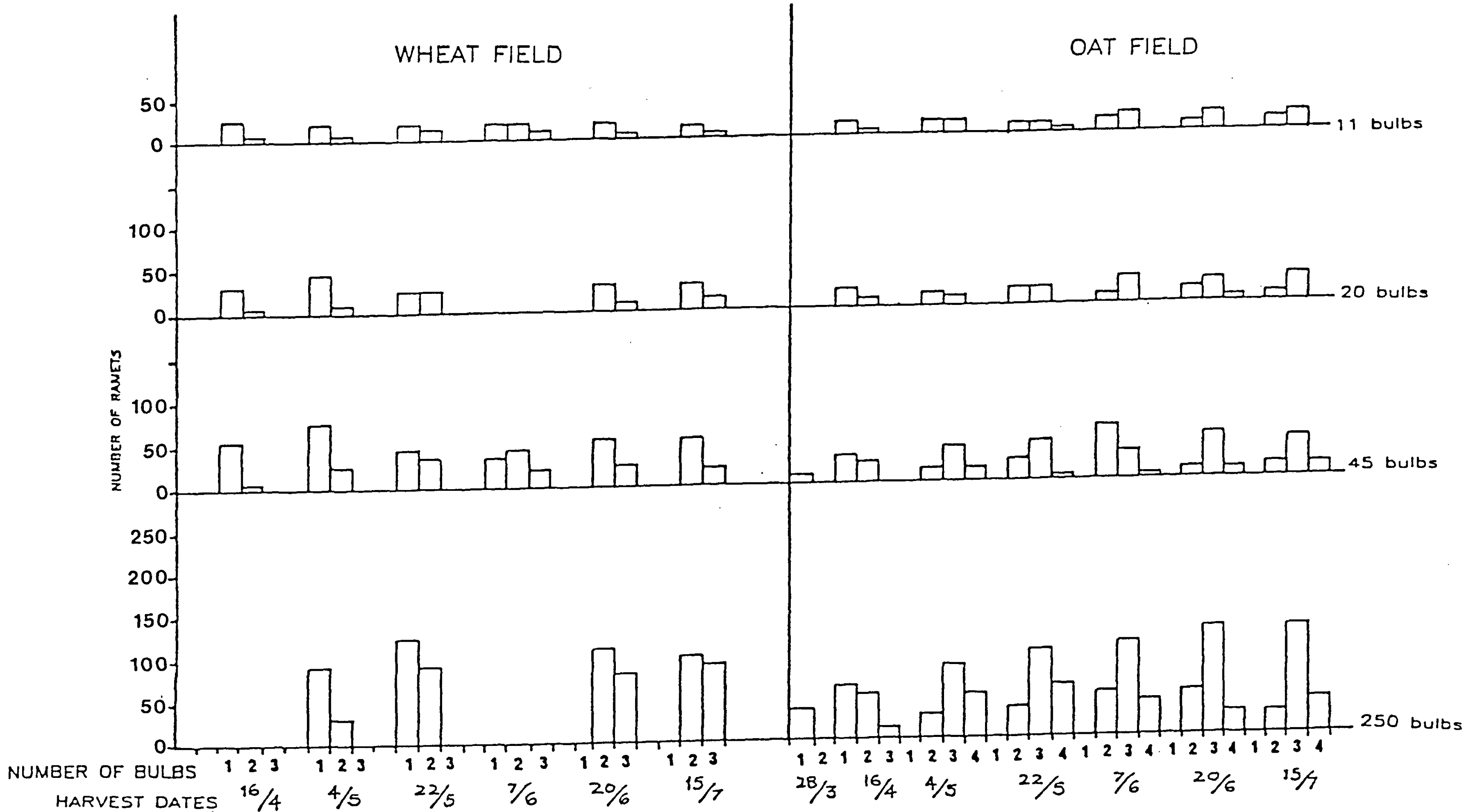
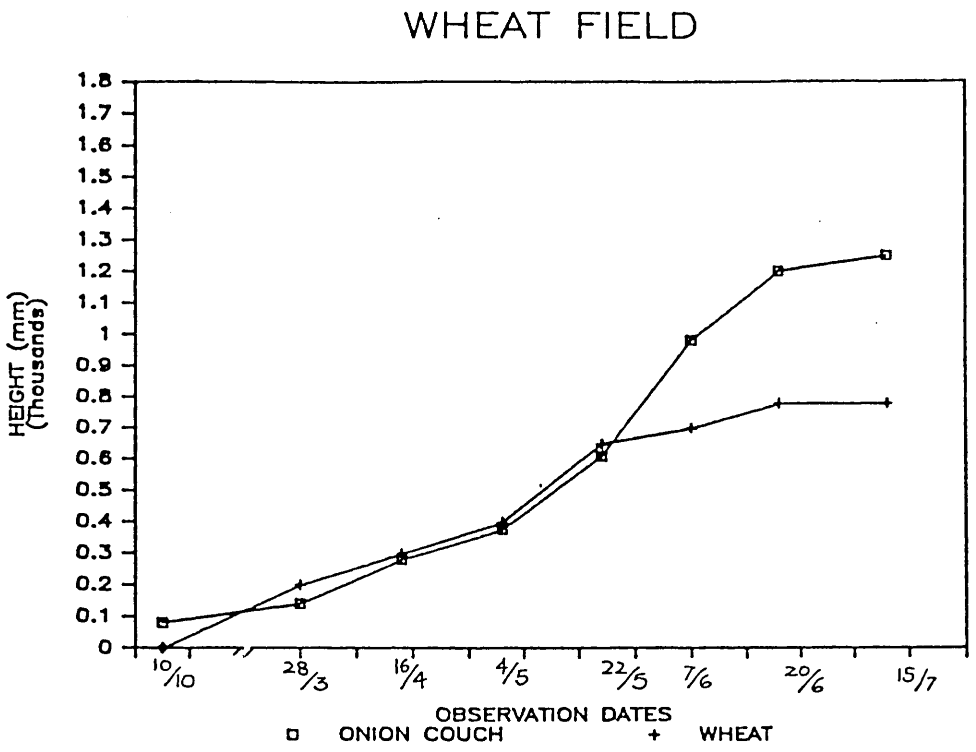


Fig. 4.3.9 Trends in the proportion of 1, 2, 3, and 4 bulb ramets in Onion Couch produced from aggregates of varying sizes, in competition with wheat and oat .



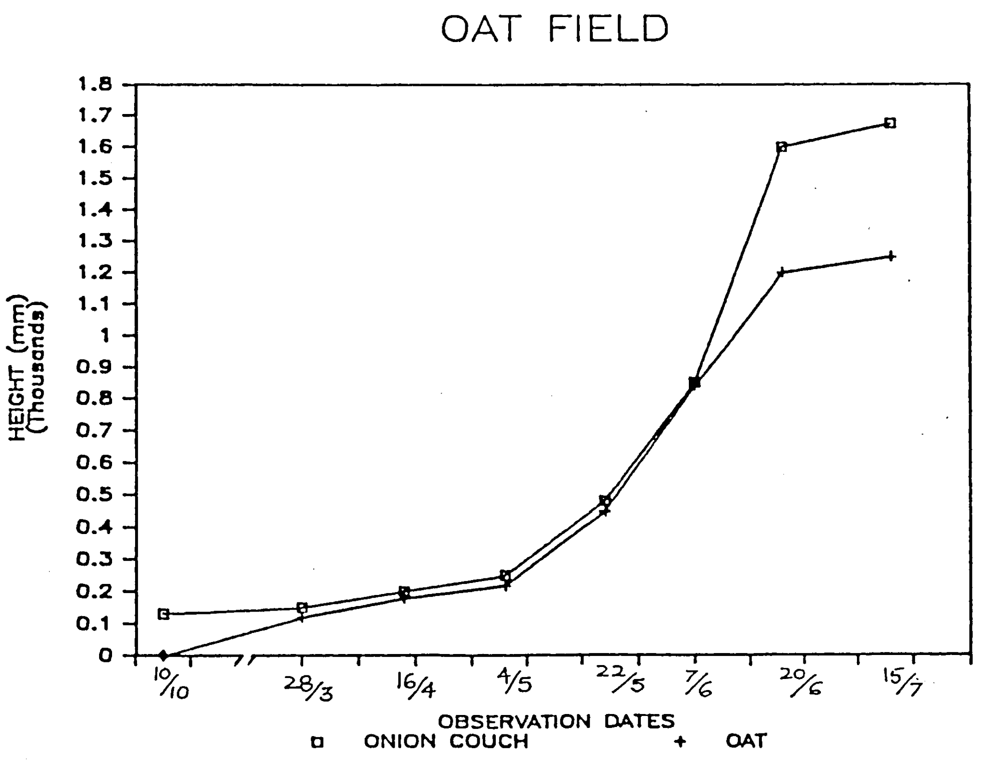


Fig. 4.3.10 Trends in increase in height of Onion Couch, and associated crops.

in height the tillers of Onion Couch until the end of May, when wheat enters into its grain filling phase, and only then the Onion Couch tillers were observed to emerge above the crop canopy. The oat tillers remained slightly shorter than Onion Couch until the end of May, after which both oat and Onion Couch elongated considerably and eventually Onion Couch emerged above the crop canopy. The tillers of Onion Couch in wheat were taller than the tillers of Onion Couch in oat during the earlier part of the growing season (March to the end of May), but tillers of Onion Couch in oat were much taller than the tillers of Onion Couch in wheat towards the end of the growing period. In addition, the wheat plants appeared to tiller early and undergo earlier thinning than the oat plants (Fig. 4.3.11).

4.3.4 Discussion

Although there was considerable variation between corresponding harvests (based on means of five replicates) from the single ramets and aggregates, due doubtless to field variation and the state of different aggregates, it was still possible to follow the general trends in growth and development from vegetative propagules of five sizes in a crop situation. In addition, apart from differences in crop types there were differences in soil type, cultural practices and clone variation, and one would necessarily expect different effects on Onion Couch in the two situations. However, the results clearly showed that the overriding factor responsible for these differences seems to be the crop type and probably also field management.

The observations made over two years in the two field situation show that very little regrowth of Onion Couch takes place after crop

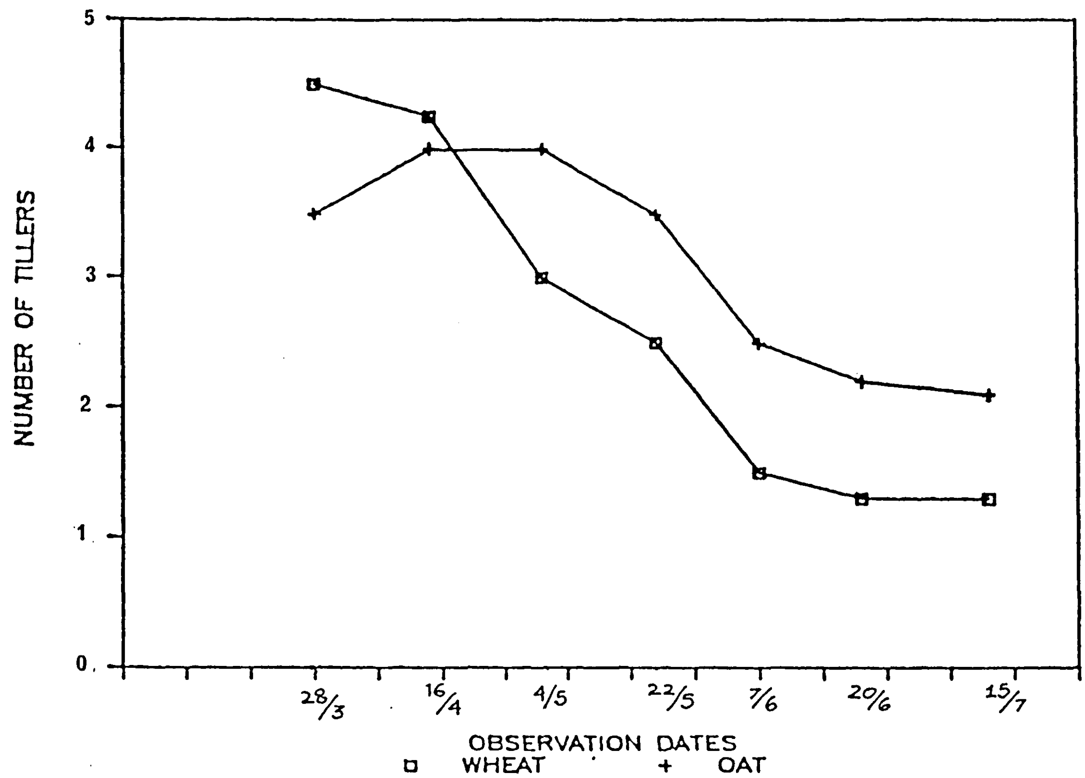


Fig. 4.3.11 Trends in tillering and thinning in wheat and oat.

harvest (August). This suggests that the ramets of Onion Couch undergo some sort of dormant phase before autumn regrowth resumes. Tillers formed in autumn, did increase in number slowly through the autumn but they started their main active growth in the following spring (depending on the duration of winter). Rapid tillering sets in in the spring (March or April) and the newly formed aerial shoots begin active growth. New bulbs are then initiated as superimposed swollen internodes at shoot bases in rapid succession: about two to four bulbs per shoot during April and May. Stem elongation coincides with thinning of aerial shoots (June), the surviving aerial shoots produce inflorescences during July and the remainder thin out gradually, though not without some contribution (of swollen basal internodes) to the resultant larger aggregate.

The comparison of regrowth of the single ramets harvested from the three locations clearly indicates that the regrowth in the wheat field was greatly suppressed. The regrowth from single ramets in the oat field resembled to a greater extent the regrowth from single ramets in a crop free control. These observations show that, as earlier suggested (Chaps.3.5, 3.6 and 3.7), wheat is an aggressive competitor in mixtures with Onion Couch when competing for the same space and the component of Onion Couch which wheat suppresses most is the basal bulb (number and dry weight) rather than the aerial tillers. In the oat field, Onion Couch takes advantage of the shorter tillers and more open canopy of the crop at the start of the growing season and completes its bulb formation stage early. In the oat field, competition comes at a later stage (stem elongation phase) of development of Onion Couch which resulted in very tall and slender tillers of Onion Couch with a weak infloresecence. Onion

Couch growing in the oat field underwent slight suppression compared to isolated plants growing in a crop free environment which produced the greatest amount of regrowth during a growing season.

The greater height (Plate 10) of tillers regenerating from aggregates (Fig.4.3.9) in the oat field (on chalk loam) compared to the wheat field (on clay-with-flint) in October, seemed most probably due to differences in soil type, though it may have been due to differences in previous cultivation practices or cropping and harvest dates (Ayres,1985).

It is clear from the results that the greater the numbers of bulbs or ramets in the aggregate the greater is the number of tillers regenerating from them in spring. In addition, the greater amount of regrowth from the aggregates in the wheat field (having more ramets per aggregate) compared to the oat field indicates that correlative dominance among ramets in the aggregates of Onion Couch is less pronounced compared to buds on intact rhizomes of E. repens (Chancellor, 1974). It is also clear from the results that an increase in number of ramets per aggregate resulted in increase in mortality of tillers developing from them. This self thinning then further affects the number and weight of the resulting ramets in the newly formed aggregates, and the relationship between smaller and larger aggregates in tiller and bulb production becomes non-linear. It is clear from the results that a greater increase in dry weight in both situations took place after the crop enters the grain filling phase. This stage is slightly delayed in Onion Couch growing in the wheat field (July) compared to the oat field (June). In addition, Onion Couch in both crop situations senesces (slightly

Plate 10 Regeneration from the aggregates of Onion Couch collected from the wheat field (left), and the oat field (right) in October.

earlier in the oat field) before the crop harvest (Plate 11). The period of maximum increase in dry weight is very similar to the inherent peak observed in the monoculture (Chap.3.5). This shows that, in spite of the crop competition the overall trend of dry weight production remains nearly the same.

Regeneration from all the four size categories of aggregates seemed to be affected by wheat and oat and the main difference seems to be in the allocation of dry matter to the aerial tillers or basal bulbs. The greater competitiveness of wheat seems to be due to greater height in the early stages of growth, and more intensive tillering, which provided a closed canopy for the developing Onion Couch tillers right from the start of the growing season till the end of May. This period of suppression by wheat coincides with the bulb formation phase of Onion Couch. Oat tillers, on the other hand, start elongating towards the end of May and competitiveness is felt by Onion Couch at a later stage of development (stem elongation). Oat plants provided poor competition in the early stages of growth, as a result of which the growth of Onion Couch from aggregates of all sizes resembled in all respects the development from single ramets in a crop free control.

It seems possible that light is the most important factor which controls the extent of bulb formation at the shoot bases. Uninterupted light received by aerial tillers of Onion Couch in the oat field early in the growing season appeared to have a promoting effect in completing its inherent bulb formation phase. The closed canopy provided by the taller tillers of wheat intercepted most of the light and forced the shoots of Onion Couch to cut short the bulb

Plate 11 A close view of Onion Couch infestation in a wheat field before crop harvest.

formation phase by investing more in aerial tillers in order to compete and coexist with the taller tillers of wheat.

It seems that the explanation of greater and more prolonged tillering observed in Onion Couch aggregates in the wheat field, apart from having more ramets, also lies in the earlier interception of light by the crop. It seems that the greater tillering observed in aggregates in the wheat field was due to a compensatory response of weak shoots (shoots with one or no new bulb at the base) which failed to assume dominance earlier in the growing period. Aggregates present in the oat field, on the other hand, developed fewer and stronger shoots (shoots with two to three bulbs at the bases), which assumed dominance early in the growing sesason. It can be concluded that the earlier the crop closes canopy the more suppression it will exert on the bulb formation stage of Onion Couch and hence the future reproductive potential.

4.4 Yield loss of crops and economic importance of Onion Couch in natural infestations.

4.4.1 Introduction

It was considered more realistic to assess the yield loss of crops and performance of Onion Couch in natural infestations. The results from Ayre's (1985) experiments on weed control (cultural and chemical) also suggest that the control methods which were found to be very effective in artificially planted plots were less effective in a natural infestation. In order to reveal effects of biotic or physical factors which are otherwise disguised by simply considering artificially planted plots (where Onion Couch is planted as single ramets), an atempt was made here to estimate the crop damage and Onion Couch growth (at the time of harvest) in two natural infestations. It was hoped that a comparison of results from natural infestations, with artificially planted plots (with wheat) and monocultures of Onion Couch would shed some light on the economic importance associated with increasing number of ramets in aggregates and provide a better understanding of cost effective use of control procedures.

4.4.2 Methods

The two naturally infested fields described in Chap. 4.3 were used to conduct the yield loss observation nearing crop harvest. $0.25m^2$ plots were harvested in the two fields. The harvest in the wheat field was conducted on 14 and 15.7.85. 27 plots were harvested; four of them were Onion Couch free and the rest were selected visually to obtain a range of weed densities on the basis of heads (or tillers) emerging above the crop canopy. In the oat field, the harvest was conducted on 16.7.85. 12 plots were harvested, out of which four were Onion Couch free. In the oat field, selection of plots was made difficult as the crop had lodged haphazardly. In both fields, plots were selected close to the crop spraying 'tram lines' to avoid any damage due to trampling. At the time of harvest, whole Onion Couch plants developing from agregates were dug up carefully to remove the newly formed aggregates and old aggregates (in partially decayed form) if possible from which they had developed. The crop culms were then cut at the soil surface. The material harvested from the fields was brought in bags to Silwood Park and the following measurements were made:

For Onion Couch:

1. Numbers of tillers.

2. Numbers of newly formed bulbs.

3. Number of bulbs per ramet.

4. Number of bulbs in the old aggregate (previous season)

5. Dry weights of tillers and bulbs (after washing and oven drying for 48 hours at 100°C.

6. Area of the newly formed aggregates.

For crops:

1. Number of culms.

2. Dry weight of the whole shoots (tiller plus ears).

The model of crop yield loss described in Chap. 3.7 was fitted using program RECHYP1 to the raw data collected from the two fields. The fitted yield loss so obtained was used to draw a comparison of crop yield loss between a natural infestation (where the ramets occur largely as aggregates) and artificially planted plots (which in effect simulated an intense cultivation regime where aggregates are fragmented into single ramets). The raw data were based on the Onion Couch population expressed as density of tillers and the crop as percentage reduction from weed free control. Furthermore, the degree of suppression of Onion Couch in the crop situation was considered by comparing the yield of Onion Couch (with the same number of bulbs per plot) in the crop situation, and in monocultures (Chap.3.5 and 3.7).

4.4.3 Results

The dry weight of the whole shoots (Onion Couch free plots) of wheat and oat in the naturally infested fields, and wheat in artificially planted plots was: 496g, 422g, and 436g m^{-2} respectively, and number of fertile culms was: 168, 276 and 160 m^{-2} respectively. Table 4.3 shows that Onion Couch yield growing in the three situations is greatly suppressed when compared to its yield in monocultures. Table 4.3 also shows that Onion Couch in natural infestations reduced crop yield quantitatively more than Onion Couch at corresponding tiller density in artificially planted plots, moreover, it is shown in Fig. 4.4.1 that the reduction in number of fertile culms of wheat was much greater in the natural infestation than in artificially planted plots. The number of culms of oat were more drastically reduced than wheat with increase in the size of the aggregates. This probably reflects the tillering pattern of the two crops: oat seed produced two mature tillers compared to 1.25 of wheat (Fig. 4.3.10). In addition, Onion Couch in artificially planted plots (with single ramets) produced a greater number of tillers per plot compared to Onion Couch developing from the large aggregates with similar number of bulbs per plot. Table 4.3 also shows that the area occupied by the aggregates increased with increase in the number of bulbs or ramets in the aggregate. Figs. 4.4.2 shows that there are differences in the fitted crop yield loss and the values of A and I are much greater in natural infestations than artificially planted plots.

In the natural infestations, the values of A and I are higher in oat than in wheat. In addition, Onion Couch in the oat field allocated approximately equal amounts of dry weight to the bulbs and aerial tillers and produced a greater proportion of three bulb ramets and hence a greater number of bulbs. Onion Couch in the wheat field, on

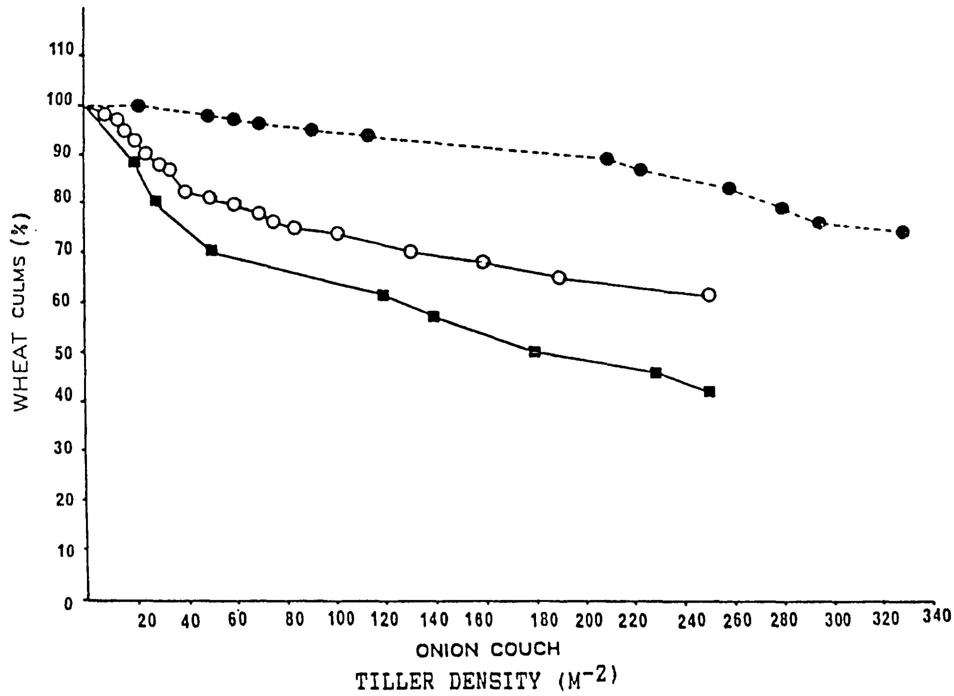


Fig. 4.4.1 Percentage reduction in number of crop culms in natural infestation in competition with oat (○), wheat (■) and in artificially planted plots with wheat (●).

NUMBER OF BULBS IN RAMETS AND AGGREGATES	AREA OF AGGREGATES (CM)	SITUATION	AERIAL TILLERS DRY WT. (g)	BASAL BULBS DRY WT. (g)	PROPORTION OF BASAL BULBS TO WHOLE SHOOT	RATIO OF TWO TO THREE BULB RAMETS	NUMBER OF TILLERS	NUMBER OF BULBS	% CROP YIELD LOST (FITTED)	CULMS LOST (%)
3		1	6.7	4.0	0.35	5	6	12	2	2
		2	6.2	6.9	0.47	0.29	9	30	3	3
		3	-	-	-	-	-	-	-	-
		4	9.0	7.10	0.45	0.44	11	35	-	-
10	5	1	22.5	10.5	0.27	5.6	18	45	4	6
		2	17.9	16.8	0.48	0.29	20	89	6	7
		3	20.0	12.0	0.36	1.6	24	62	4	0
		4	-	-	-	-	-	-	-	-
20	9	1	40.0	16.3	0.29	2.1	31	90	8	10
		2	24.8	21.2	0.46	0.30	27	125	12	22
		3	50.0	0.37	0.37	1.16	52	160	8	1
		4	78.7	72.9	0.48	0.32	76	290	-	-
45	18	1	68.2	30.7	0.31	3.1	50	163	16	17
		2	48.9	42.6	0.44	0.15	48	206	20	31
		3	62.0	44.0	0.40	1.26	68	246	11	3
		4	-	-	-	-	-	-	-	-
70	32	1	70.0	38.5	0.35	3.0	75	186	22	22
		2	58.2	50.5	0.46	0.77	70	295	30	35
		3	78.0	50.0	0.39	1.20	92	322	14	6
		4	-	-	-	-	-	-	-	-
250	50	1	112.0	48.9	0.30	1.50	125	460	34	30
		2	76.5	80.5	0.51	0.51	120	550	42	43
		3	180.0	120.0	0.40	0.88	225	810	24	12
		4	594.6	410.0	0.42	0.30	550	1898	-	-

TABLE 4.3 Comparison of growth characteristics of various attributes of Onion Couch developing in natural infestations: wheat (1), oat (2), and artificially planted plots: with wheat (3) and monoculture (4) at various densities and aggregate sizes, before the crop harvest (July) and their effect on crop yield loss.

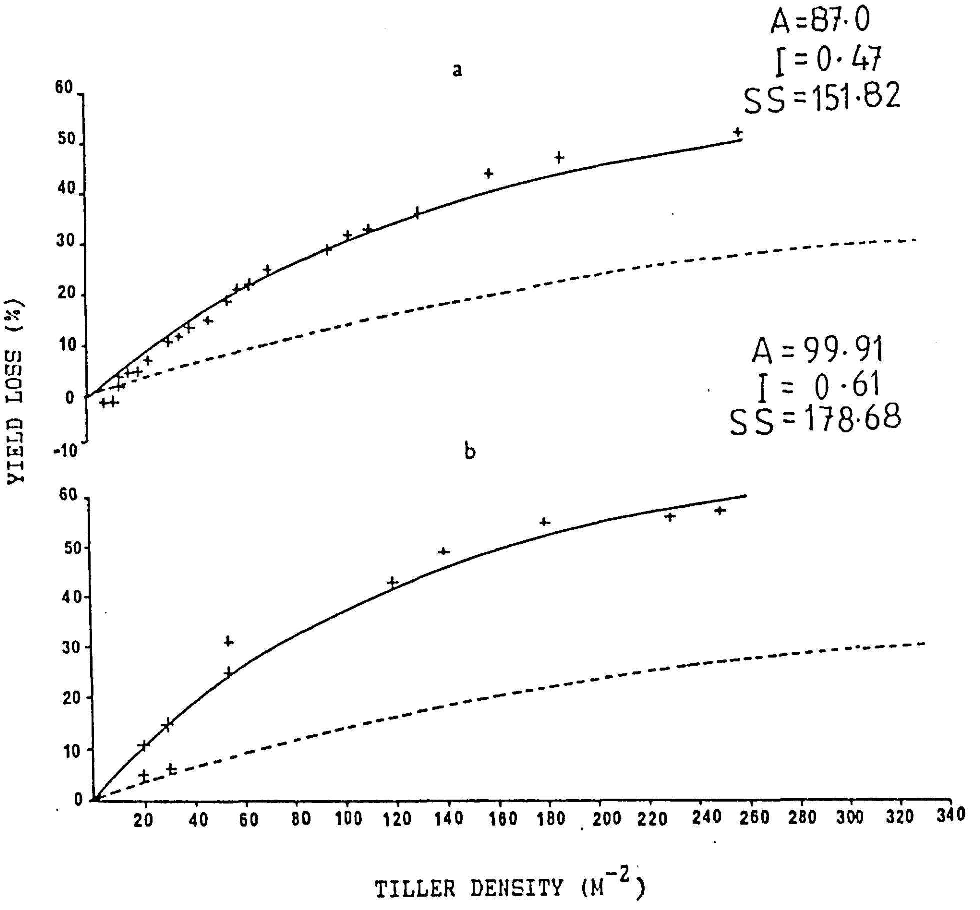


Fig. 4.4.2 RECHYP1 applied to crop yield loss (%) and Onion Couch tiller density in a wheat field (a) and oat field (b). Fitted curves for natural infestation are shown in solid lines, and artificially planted plots in broken lines. Actual data points are represented by symbols

the other hand, allocated less dry weight to the basal bulbs, and produced a greater proportion of two bulb ramets and hence fewer bulbs (Table 4.3). It is also clear from Table 4.3 that Onion Couch in the oat field resembled, in its growth attributes, the Onion Couch in the weed free control, whereas, greater resemblance is observed in growth attributes of Onion Couch in wheat, both in natural and artificially planted plots.

4.4.4 Discussion

Differences in the performance of Onion Couch at the time of harvest in the three crop situations and monoculture allowed a comparative account of its growth and development in different situations. The values of A and I were also found to be much higher in the natural infestations where vegetative propagules of Onion Couch exist in the form of aggregates, compared to artificially planted plots where they were planted as single ramets. The results of this study also indicated that, along with yield reduction of the crop, the development of an aggregate also adversely affects some aspects of growth and development of Onion Couch. The reduction in number of tillers, new bulbs, whole shoot dry weight per aggregate compared to plots with corresponding numbers of bulbs planted as single ramets, could be explained as partly due to correlative dominance but mainly due to density dependent mortality in the closely packed ramets in the aggregates. The predicted values of crop loss, which were much higher in both the farm situations compared to artificially planted plots, suggest that greater yield loss at lower Onion Couch tiller densities in farm situations seems to be associated with the increase in the size of the aggregate beyond a certain limit. It can be assumed that the larger aggregates (Plate 10) which are more common in the farm compared to the single chain ramets used in artificially planted plots (simulating an ideal intense cultivation regime), could be responsible for this sharper decline in the yield of the crop. It is apparent from the results that, with increase in the size of the aggregate, there is a corresponding decline in the crop yield and the number of culms, moreover, the larger aggregate sizes seem to cause greater loss to the crop irrespective of the sowing density. Although large agregates produced fewer tillers and bulbs compared to similar number of bulbs planted as single ramets per plot (due to correlative dominance and density dependent mortality), they could intensify crop yield loss by physically obstructing the growth of the seeds which lodge on and around these aggregates, hence affecting the establishment of the crop seeds. This is also evident from the greatly reduced number of fertile crop culms from such sites at the time of harvest. The lower competitive ability of Onion Couch in artificially planted ramets compared to natural infestations also points out the importance of intensity of cultivation practices. Under a cultivation regime, larger aggregates are liable to be broken into smaller chains, which in turn would suffer more suppression (in terms of competition and space occupation) by an early tillering crop and would not interfere greatly during the establishment phase of the crop by physically occupying space.

Differences in the various aspects of regrowth of Onion Couch from aggregates collected from wheat and oat fields, and their similarities in trends of growth and development to artificially planted plots and monocultures of Onion Couch respectively, can be explained as due to differences in the earlier interception of light by the crop which they are developing in. Wheat tillered profusely, grew vigorously, and in a well managed field formed a dense canopy very early in the growing season. Oat on the other hand due to slow growth hardly offered any competition at this stage (see Chap 4.3).

The results also agree with an earlier investigation carried out on this subject (Cussans, 1968; Permin, 1985). However, Permin (1985) described oat as a better competitor against Elymus repens then spring wheat and barley. The explanation of this finding probably lies in the differences in the trends of dry matter increase in Onion Couch and E. repens. The greatest increase in dry weight in Onion Couch takes place during the grain filling phase of the crop, whereas in E. repens it takes place very late in the crop ripening or senesceing phase (July and August) as reported by Cussans (1968). Compared to wheat, oat starts shoot elongation rather late (Ammon,1985) and grows taller than wheat and thus offers greater competitiveness during the period of maximum growth of E. repens. This period of E. repens maximum growth corresponds to the time when most Onion Couch tillers senesce.

4.5 Conclusions

The results described and discussed in this and earlier chapters have given a fair idea of the regeneration capacity, and factors governing the regrowth of the vegetative propagules of Onion Couch and the manner in which they affect crop yield.

Unlike other important perennial weeds of arable land, e.g Elymus repens and Cyperus rotundus, where vegetative dispersal can take place by natural spread and separation (and which becomes much more efficient under cultivation practice), it has been observed that the vegetative propagules of Onion Couch largely occur in the form of aggregates of ramets. The explanation for this higher frequency of aggregate compared to single ramets seems to be due to the poor ability to spread by vegetative means; in spite of the rotting of the parent aggregate, the newly formed ramets remain together (connected or unconnected) as one mass and do not disperse vegetatively without soil cultivation or other mechanical disturbance. The poor ablity of vegetative propagules of Onion Couch to spread naturally seems to lie in the fact that they are modified from the perennating organ (which can perhaps be regarded in Onion Couch in arable situations as a relict character) of the Tall Oat-grass.

The presence of a larger number of vegetative propagules of Onion Couch occurring as aggregates rather than single ramets in a crop situation increases its economic significance in many ways:

1) Increase in the size of the aggregate allows them to physically dominate a greater effective area and affect crop yield by interfering with the establishment of the crop seed. It is evident from the results that single ramets of Onion Couch at a very high tiller density (330 tillers) and planting density (405 bulbs or 134 ramets) m^{-2} cause 31% yield loss of the crop, whereas an aggregate having much less number of bulbs (150) and tillers (100) m^{-2} can cause an equal amount of yield loss. The yield loss in the case of single ramets seems to be due to competition for space (light and

nutrient), and as the crop is proven to be a far better competitor against Onion Couch (Chaps. 3.6 and 3.7), its yield is not drastically reduced by the growth from single ramets even at a very high planting density. On the other hand in the case of larger aggregates yield loss seems to be more due to physical loss of space which otherwise would have been available for crop seed establishment and growth.

2) Increase in the size of the aggregate also makes them more resistant to cultural control measures. It has been observed (Chap.4.2.) that single ramets were less resistant to burial compared to aggregates, which showed less mortality and more vigorous regrowth from greater burial depth, probably due to the greater amount of reserves in the aggregates (Plate 12). It is propable that the greater effectiveness of Onion Couch control observed by Ayres (1977, 1985) in artificially established Onion Couch compared to natural infestation could have been the result of the presence of much larger aggregates in the field which might have recovered from even greater burial depths.

3) Increase in the number of ramets in the aggregates confers no advantage to Onion Couch as far as the amount of regrowth and resulting new ramets are concerned; the larger the number of bulbs in the aggregate, the more its growth will be reduced by correlative dominance and density dependent mortality (Chap.4.3). The smaller amount of regrowth from larger aggregates could result in poor control of Onion Couch in post-harvest control by herbicides. In addition, senescence of most of the Onion Couch tillers at the time of harvest makes the pre-harvest application of herbicides less

Plate 12 Regeneration from aggregates buried at 6cm in an arable field.

effective. The results suggests that Ayres (1985) was right in assuming that decrease in the efficiency of chemical control in natural infestations compared to artificially planted plots could have been the result of the presence of a greater frequency of aggregates. Birnie's (1983) work on pre-harvest application of glyphosate used for Onion Couch control also suggests that in the plots with fewer bulbs m^{-2} the pre-harvest treatment is far more effective than in plots with a larger number of bulbs m^{-2} (the larger numbers of bulbs probably reflecting larger size or frequency of aggregate).

4) The regrowth from aggregates and single ramets was found to be equally suppressed by an aggressive crop (early tillering, tall and dense) which, by causing greater light interception, reduces and delays the bulb formation stage of Onion Couch compared to aggregates developing in a later growing or less intensively sown crop.

The observations suggest that tiller number is not an absolute measure of level of Onion Couch infestation, or a good criterion in judging damage to a crop. Field observations also suggest that, apart from the competitive power of Onion Couch, there are other aspects of its growth, e.g. aggregate forming ability of vegetative propagules, which needs equal consideration when planning its control. This is because the aggregates of Onion Couch not only cause crop reduction (by interfering with seedbed establishment) before the commencment of crop-weed competition, but also can make the control measures less effective.

CHAPTER 5

A PRELIMINARY APPROACH TOWARDS THE DEVELOPMENT OF A MODEL OF ONION COUCH UNDER DIFFERENT CULTIVATION MANAGEMENT SYSTEMS.

5.1 Introduction

The crop-Onion Couch growth model presented here could be defined as a simplified structured representation of the physical and biological mechanism underlying the growth of crop and Onion Couch in an arable system. The choice of using a structured model was mainly because of its simple and explicit way of explaining and incorporating the phases of life cycle of a crop and associated weed in an arable system (e.g, Fawcett, 1983). The assumptions made for this simulation model are mostly based on experiments and observations conducted under controlled conditions and field situations (Chaps. 3 and 4). The proposed structured simulation model presented here, could be regarded as an outline to the research into the behaviour of vegetative propagules of Onion Couch in an arable system. It was also hoped that the model would offer some explanation as to why some aspects of the agro-ecology of Onion Couch are more important in economic terms (crop yield loss and control) than others and thus would provide bases for more experimental work on the processes which are apparently important but not yet sufficiently understood when planning the control of Onion Couch.

Trends of increasing Onion Couch infestations over recent years have been blamed on minimum tillage systems and increased areas of autumn sown cereals (Chap. 2). This shift in agricultural practice has been regarded by Halley, (1984) as due to the fact that winter sown cereals give greater yields than spring sown cereals and that minimum tillage has proved to be more economic than traditional cultivation practices. Experiments described in the earlier chapters of this thesis also indicated that the autumn sown cereals seemed to be more suitable for the growth and development of Onion Couch as they allow it to complete its bulb formation stage early (spring) during the growth cycle of the crop, without any intervention (mechanical disturbance). Additionally, reduced cultivation results in a greater frequency of large aggregates compared to single ramets or small aggregates in the autumn-sown fields. The large aggregates are more resistant to control measures and also result in poor establishment of the crop. Keeping these factors in mind it was decided to simulate Onion Couch development in winter wheat, on a chalk loam soil. Two fragment classes, that is, single ramets, representing intensive cultivation, and aggregates representing a minimum cultivation system, were selected for modelling.

5.1.1 Design of the model

Principle and processes

This section deals with the modelling of particular phases in the life cycle of Onion Couch in a winter cereal crop by describing the principles and processes which operate and the way in which they are simulated. Fig. 5.1 shows the stages in the growth cycle of a crop and accompanied Onion Couch and the path taken by the single ramets and aggregates during a single year.

Shoot regeneration

The starting point of the model is taken as the end of March when the autumn sown crops have completed there tillering phase after the winter pause. The ramets and aggregates of Onion Couch which are present at the surface or buried within the soil (depending on the cultivation regime) have also completed their tillering phase. Shoot regeneration from single ramets and aggregates is very different. The following four factors affect regeneration of shoots from single ramets and aggregates:

1). Fragmentation into single ramets decreases density dependent mortality, which is more pronounced in aggregates.
2). Fragmentation into single ramets releases the ramets from correlative dominance, which is more obvious in aggregates.
3). Fragmentation into single ramets makes them more susceptible to burial than aggregates which can support shoot regeneration from greater burial depth.
4). Fragmentation into single ramets makes them more susceptible to mechanical damage compared to aggregates.

Data relating to the emergence of shoots from single ramets and aggregates, exposed on the surface and buried at a range of depths in the soil were obtained from experiments described in the Chaps. 3.8 and 4.2, and they showed quite a good agreement despite differences in soil type and experimental designs. the values for these used in the model are given in Table 5.2. The estimate of number of shoots produced from large aggregates when buried at different depths was partly based on field observations (Plate 13) and partly on experiments with small aggregates, buried at similar

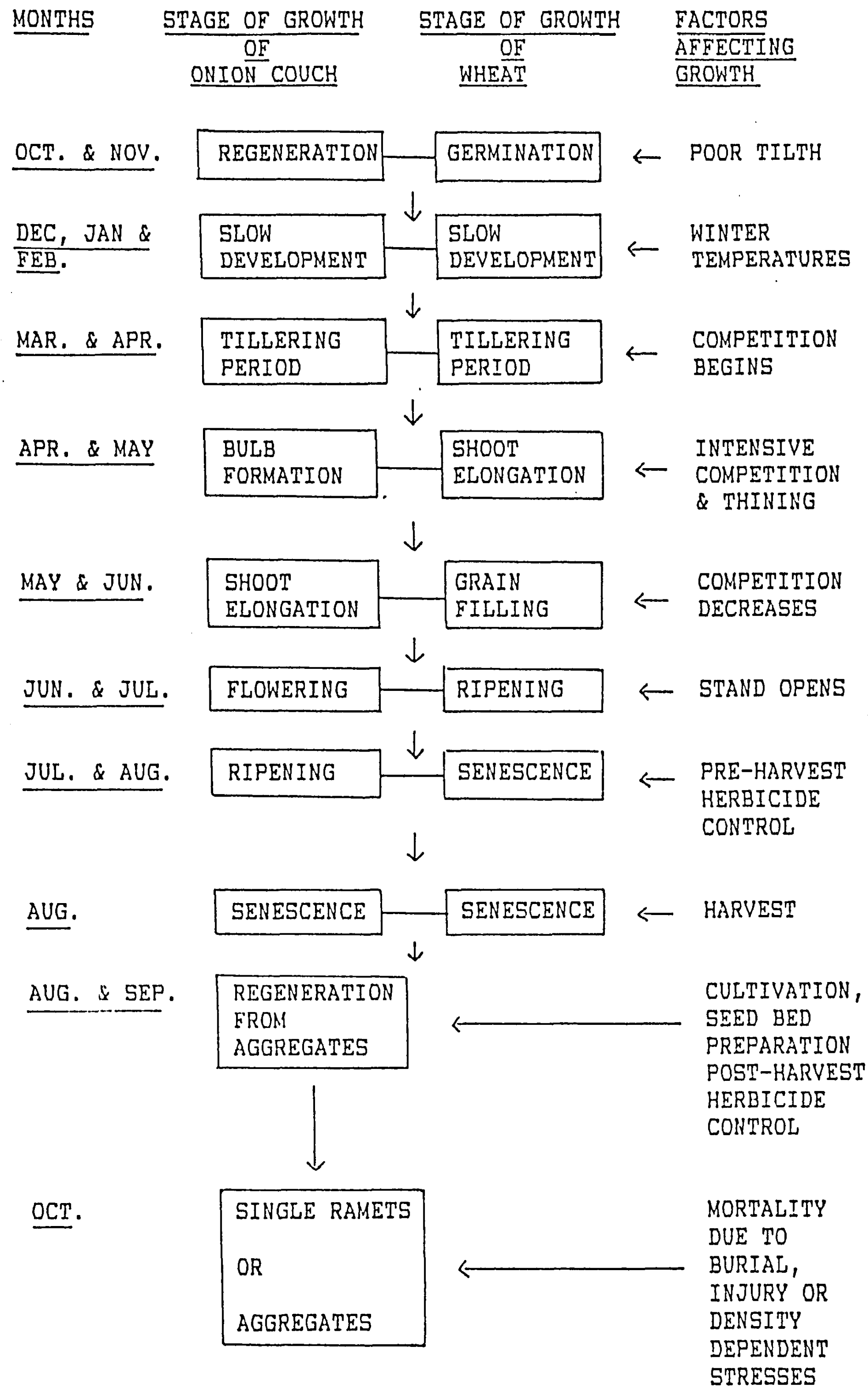


Figure 5.1 Life cycle of single ramets and aggregates of Onion Couch in winter wheat.

Plate 13 Regeneration from aggregates exposed on the soil surface (left) buried at a depth of 1cm (middle) and 3cm (right) in an arable field.

depth, in order to simulate number of shoots regenerated from those depths (Table 5.1).

Apart from burial, the potential of ramets to regenerate shoots could be decreased by other factors mentioned in the previous paragraphs. Such decreases were either inbuilt as shown in Table 5.1 (mortality due to burial and density dependent factors) or represented as shown in Table 5.2 (mortality due to mechanical injury), as factors of unity or less, being fixed for a particular cultural treatment. These values are used as inputs for various treatments. The result was a matrix which is referred to as the shoot regeneration matrix (Table 5.2). In addition, single ramets seem to cause less interference with the crop seed establishment than aggregates. It has been demonstrated (Chaps. 3.7 and 4.4) that crop culm losses and crop yield losses in naturally infested plots with large aggregates were much greater than in plots with small aggregates, single ramets, or artificially established populations (single ramets) of Onion Couch. It has been observed that crop yield is less sensitive to Onion Couch tiller density and more sensitive to the presence of large aggregates (Plate 10) which create poor tilth and hence poor establishment of the crop (another aspect of space lost by the crop). Representation of this observation was expressed in the input values by adjusting crop seed rate.

Shoot emergence of both crop and Onion Couch is completed at the start of the model. Two classes of fragments, i.e, single ramet and aggregate were used at four burial depths. Single ramets and aggregates are not handled simultaneously in one run of the program due to differences in their behaviour in arable systems.

Depth of Burial(cm)	Single ramets	Aggregate of 2 ramets	Aggregate of 3 ramets	Aggregate of 15 ramets
0.0	5	12	10	25
1.0-3.0	12	21	25	75
6.0-9.0	2	12	18	50
> 15.0	0.75	6	9	20

Table 5.1 Number of tillers produced by vegetative propagules buried at different depth in the soil.

Parameters	Standard value
1. Time span of runs	5 years
2. Initial population of ramets of Onion Couch	15 ramets m^{-2}
3. State of ramets	a) single ramets b) aggregates
4. Crop seed rate	a) $250m^{-2}$ b) 400 m^{-2}
5. Crop seed lost due to poor tilth	a) one aggregate = 10% b) two = 17% c) three = 35% d) four = 50%
6. Mortality due to intensive fragmentation	0.25
7. Time available for plant growth before harvest	18 week
8. Frequency of soil tillage	every year

9. Shoot regeneration matrix:

Burial depth cm	regeneration from single ramet	survival after fragmentation	number of shoots from 15 ramets	regeneration from aggregates
0.0	5	0.75	15 = 56	25
1.0-3.0	12	0.75	15 = 135	75
6.0-9.0	2	0.75	15 = 22	50
15.0	0.8	0.75	15 = 9	20

Table 5.2 Standard values of all parameters used in the model

Plant growth and competition

Onion Couch makes most of its growth during the active growth period of the crop and senesces before the crop harvest. Experiments (Chap. 3.6) also suggest that Onion Couch and crop compete for the same biological space (in terms of de Wit, 1960). It was also observed that the dominant influence restricting weed proliferation and bulb production is competition with the developing crop (Chaps. 3.7, 4.3 and 4.4). In perennial grass weeds, orthotropic tillers (aerial tillers) are regarded (Fawcett, 1983) as units supporting the growth of vegetative propagules, so it was decided to use aerial tillers as a measure of space occupation, in terms of density m^{-2}.

The results of the experiment with wheat (Chap. 3.5) have shown that each m^2 provides enough space for 500-600 tillers of wheat (Fig. 3.5) which is also in agreement with Fawcett's (1983) results on similer soils. The equivalent measure for Onion Couch was found to be 950 tillers m^{-2}. This measure also included the plastic responses to density dependent stress; in Onion Couch, after an initial rise of tiller number to 1400 m^{-2}, there follows a gradual decline due to self thinning resulting in 950 tillers m^{-2} (June). This decline continues until sencescence (Figs. 3.5.1 to 3.5.8). Although all tillers do not survive until the harvest of the crop they do manage to contribute towards the ramet bank. Therefore, 950 tillers m^{-2} assumes that all the tillers surviving the early self thinning, produce potentially viable ramets.

β values (de Wit, 1960), which are widely used for assessing the competitive status of competing plants (Spitters and Van den Bergh, 1982; Fawcett, 1983), were used here to determine the status of individual tillers (in terms of space occupation) in the stand during the growth cycle. The experiment in Chapter 3.5 demonstrated the trends of space occupation by the tillers of wheat and Onion Couch (Figs.3.5.1 and 3.5.2). The results clearly bring out the differences between the occupation of space by the tillers of wheat and Onion Couch and are in agreement with the competitive status of wheat and Onion Couch, determined by other experimental designs (Chaps. 3.6 and 3.7).

5.1.2 Structure of the proposed model based on principles described above

1. Growth and competition is simulated within an area of a 1 m^2 located in the centre of the field sown evenly with a crop. Within this area, the Onion Couch population is also evenly distributed. The area of 1 m^2 is represented as 600 unit sites, each corresponding to the area occupied by a single wheat tiller or 600/950=0.63 (parameter RS) Onion Couch tillers.

2. The step length of the model is one week. The growing season is assumed to begin when the tillering phase is completed by the end of March or begining of April and to end at crop harvest, allowing a period of 18 weeks.

3. Growth and occupation of space are simulated on the basis of single tillers. Each seed and single ramet produce 3 and 11 tillers respectively. All tillers are assumed to emerge at the begining of the first step. Multiplication of the number of tillers per seed or ramet by the respective total number of seeds or ramets in the whole 1 m^2 then gives the equivalent measure for the whole 1 m^2 (Table 5.2).

4. The growth of Onion Couch tillers is simulated in terms of their

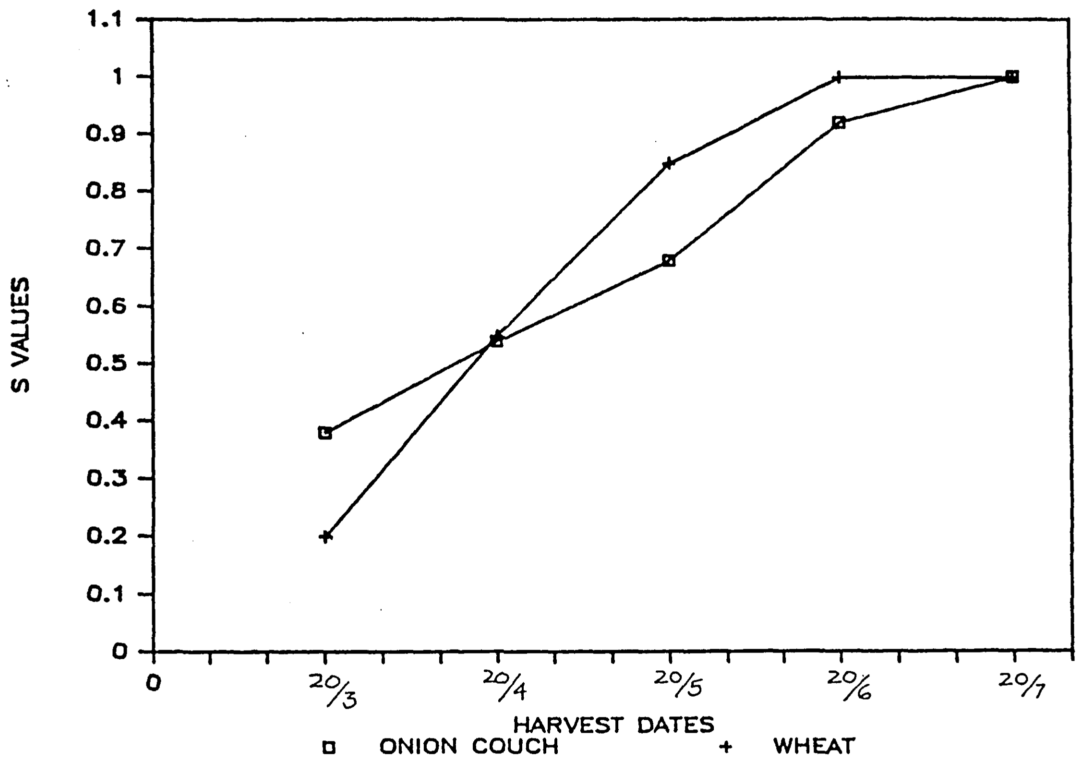


Fig. 5.2 S values derived from β values, showing trends in space occupation by tillers of wheat (+) and Onion Couch (▫).

occupation of space. The β values are transformed on a scale from 0 to 1 and represent the fraction of a unit site which each tiller of wheat or Onion Couch is occupying (Fig. 5.2). This measure is termed S and like β, is described as a function of time. The evidence of this relationship comes from the experiment described in Chapter 3.5. which clearly shows that the rate of growth and space occupation by the wheat and Onion Couch declined continuosly, thereby producing a convex curve.

5. Each tiller surviving the initial self thinning is capable of producing a single ramet. It has been observed that, in circumstances where the competition is from an aggressive crop, ramet formation of Onion Couch suffers most (Chaps. 4.3 and 4.4). A systematic representation of this observation which reflects a mortality, where some tillers die without leaving a ramet (Chap.3.5), is expressed by linking the higher seeding rate with a condition where 20% of tillers fail to leave a ramet.

6. The total amount of space occupied by the wheat and Onion Couch stand is assessed each week by summing the S values of all the tillers present with appropriate weighting for those of Onion Couch. As long as this total is less than 600 growth continues.

7. When all the available space has been occupied the stand is said to have closed and thinning begins. This is simulated as an instantaneous event, although in reality it can take place in several weeks especially in the case of Onion Couch. A flow diagram of the structure of the model and the systematic representation of the events described in the above paragraphs are shown in Fig. 5.3.

Crop ripening and senescence

After the thinning phase of wheat, followed by Onion Couch, the

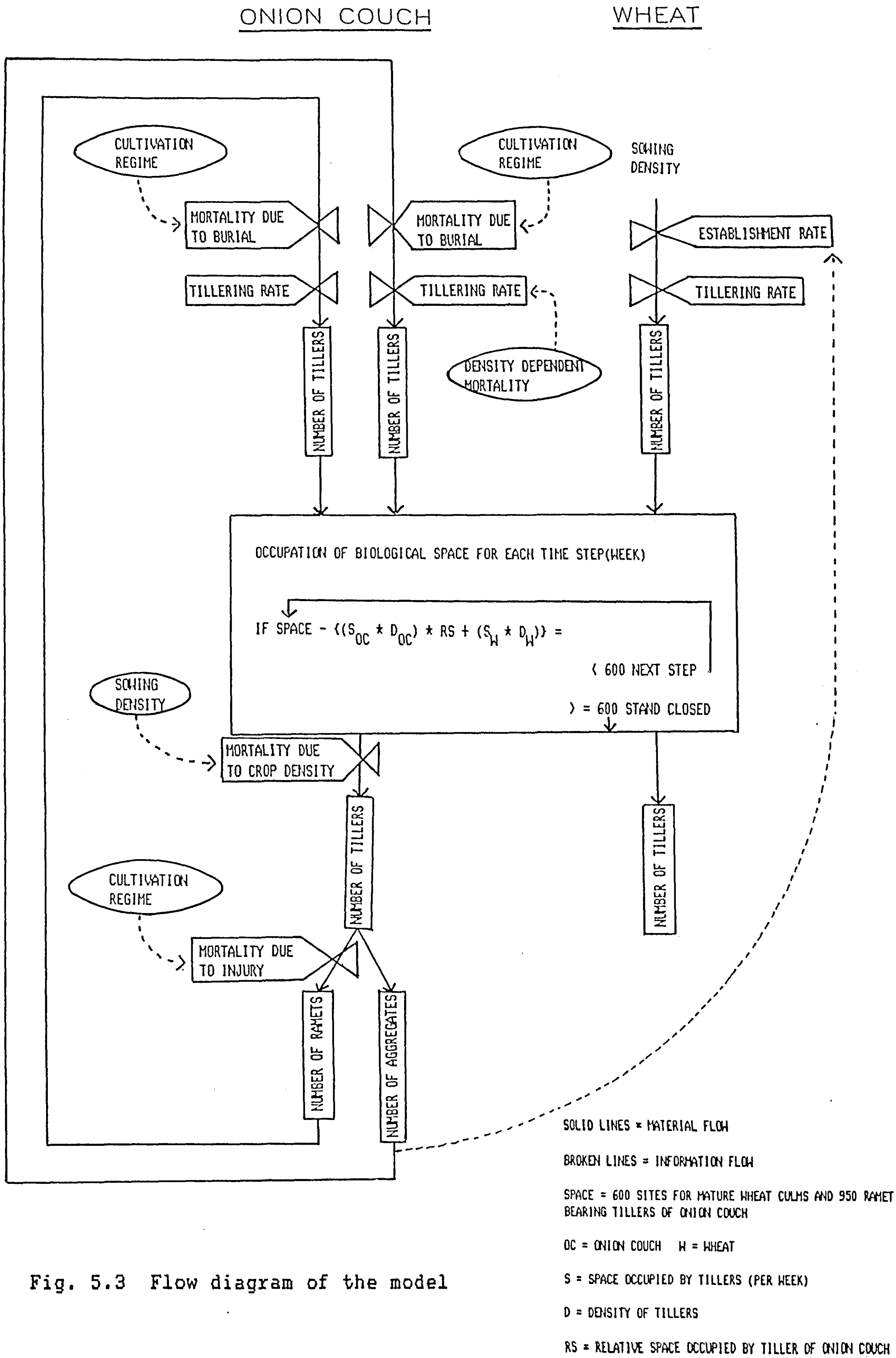


Fig. 5.3 Flow diagram of the model

stand remains closed, crop and Onion Couch continue to develop until the ripening phase is completed and the seed is set. The crop, followed by Onion Couch, then approaches senescence. The space occupied by the crop and Onion Couch then starts to open as the canopy degenerates but no active growth is observed from the newly formed aggregates of Onion Couch. At the end of this period, either the crop is harvested with the result that the aggregates remain dormant and do not produce regrowth until the end of the summer, or herbicides are applied which, if the tillers of Onion Couch are still green (in wetter years it retains some green tissue) could kill the newly formed ramets and can considerably reduce the level of infestation.

Post-harvest growth and control

Regeneration of tillers from newly formed aggregates can commence after the harvest, depending upon the weather conditions and cultivation practices. This regeneration of shoots from the newly formed aggregates continues until the onset of winter but no (or very little) bulb formation is observed at this stage. This is a stage when the farmer could adopt some control measures in the form of soil tillage, herbicides or both.

Soil tillage is the final stage of this model. Where tillage is intensive the aggregates in the model are fragmented into single ramets, otherwise they remain as aggregates. When ploughing is simulated, the single ramets and aggregates are distributed evenly over a range of four depths. Two forms of vegetative propagules i.e. single ramets and aggregate provides the input for the simulation of shoot emergence. The frame work of representation of these data in the model is already described. The aim of the tillage routine is to reallocate the ramet or aggregate population to the next crop growth cycle. Simulation of the burial effects on the two tillage regimes is accomplished by varying the inputs: the number of shoots capable of emerging from a particular range of depths from single ramets and aggregates. The second dimension of space occupation (physical interference with crop seed establishment) inherent to the aggregate situation is included as a function which relates the number of resulting aggregates at the end of the year to the crop seed rate at the start of the new year.

A listing of Pascal programs of the model (for both situations, i.e. single ramets and aggregates) appears in Appendix 1 and 2.

5.1.3 Results and Discussion

The results of the runs based on shoot regeneration from ramets and aggregates buried in the top 3cm of the soil at the end of the first year, were in good agreement with the experimental work and field observations (Chaps. 3 and 4).

The results give an assessment of the effectiveness of the two tillage practices and the behaviour of the resulting sizes of the vegetative propagules on the control of Onion Couch infestation in the context of the size of infestation. The standard values shown in Table 5.2 were used on the whole for the two situation, i.e, single ramets and aggregates, to represent the two cultivation regimes. 15 ramets m^{-2} represent medium infestation. The series of computer simulation runs explored the sensitivity of the output of the two situations simulated to variations in the values of parameters, over a five year period without a break. Figs. 5.4 and 5.5 demonstrate the sensitivity of the model in the two situations to variation in the crop seed rate and regeneration from various depths.

The top 3cm of the soil seems to be an ideal position for the ramets to produce maximum growth in both situations. Crop seed rate seemed to have some effect in the first two years but without any other control measures the prolific production of ramets would soon result in severe crop loss. Single ramets seemed to be producing tillers, and hence new ramets, at a faster rate than the aggregates.

The runs representing regeneration from a burial depth of 6-9cm had a marked effect on the output of the situation representing intensive tillage. Such cultivation measures, if practiced for a longer duration would result in the eradication of single ramets. This run had a less marked effect on the output of the situation representing minimum cultivation, but seems to be quite effective if the crop seed rate is high.

The runs based on shoot regeneration from a burial depth of 15cm had a much more marked effect on the output of both situations than the runs from any other burial depths. It would result in complete eradication of single ramets, and aggregates would also be effectively controlled.

The runs representing regeneration of shoots from ramets and aggregates brought to the surface (hence subjected to atmospheric temperature and humidity fluctuations) had a much more marked efffect on the output of the situation representing minimum tillage

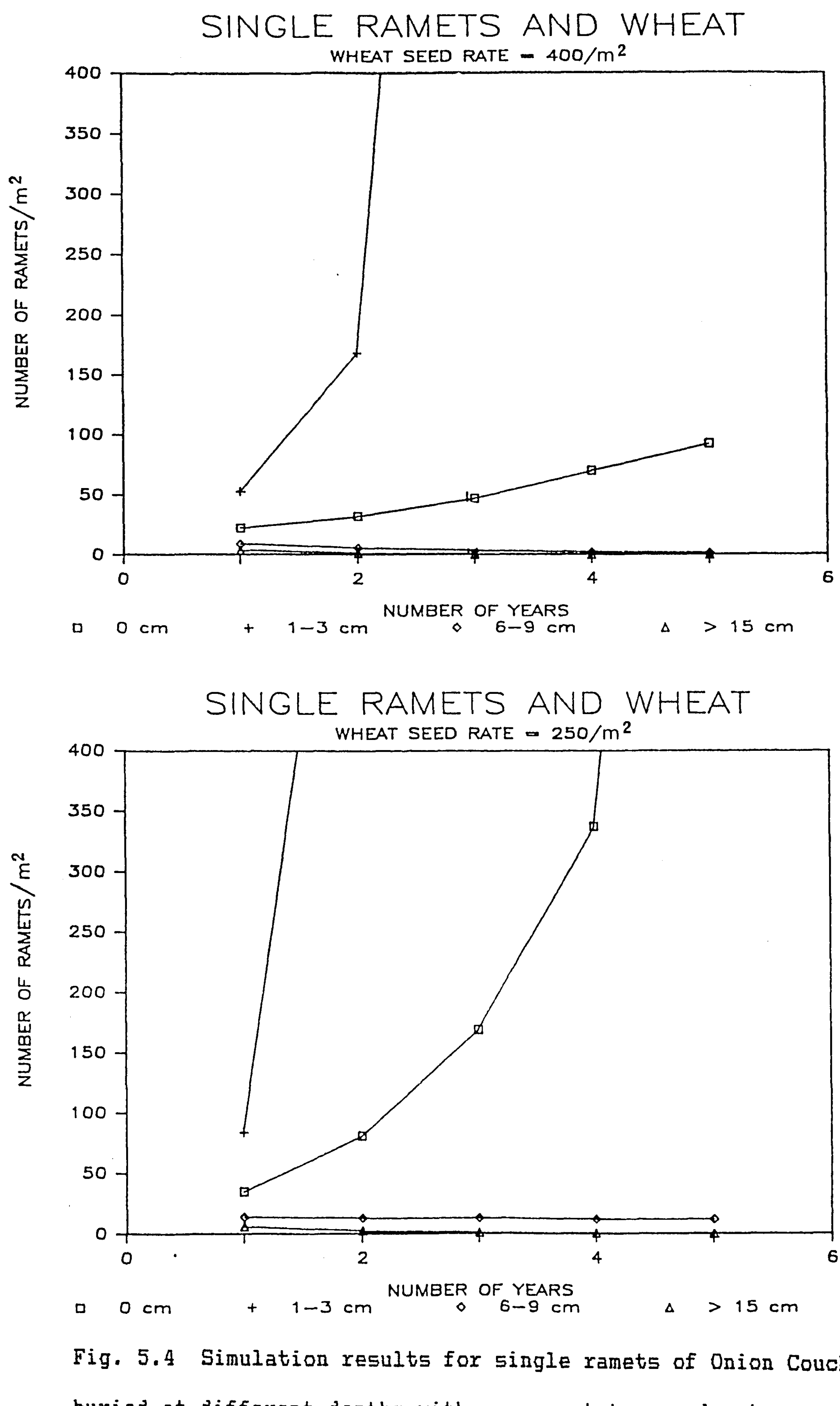
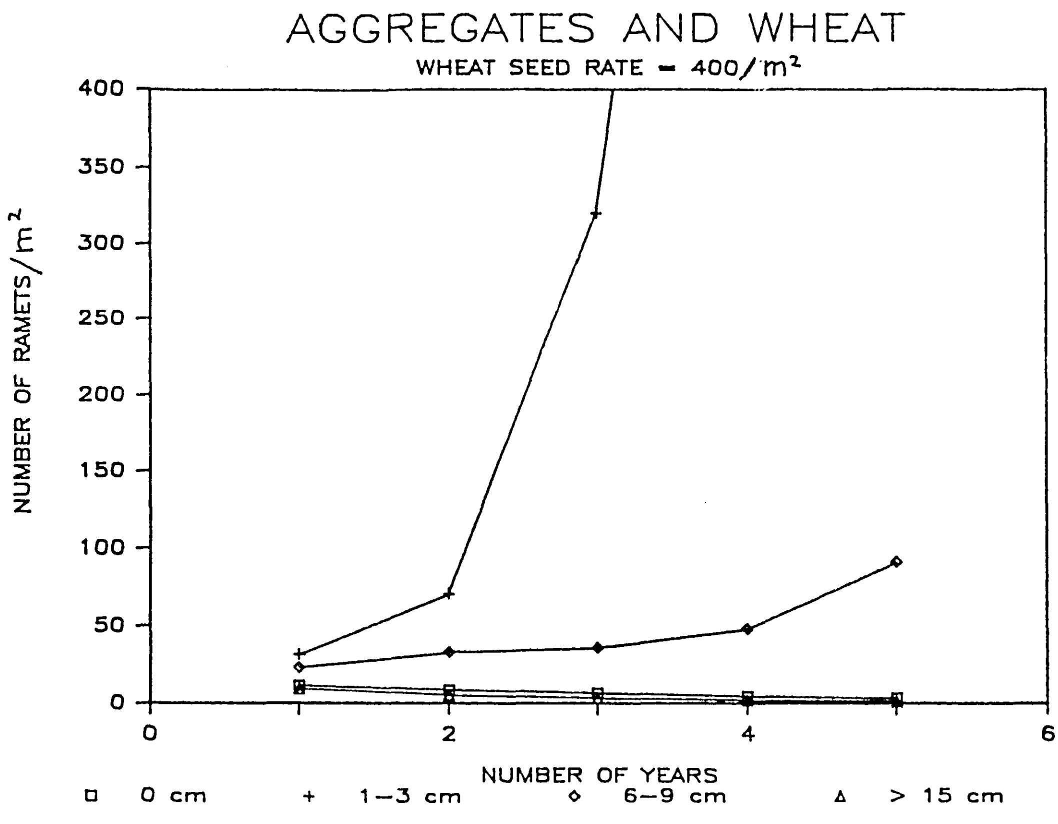


Fig. 5.4 Simulation results for single ramets of Onion Couch buried at different depths with a crop at two seed rate.



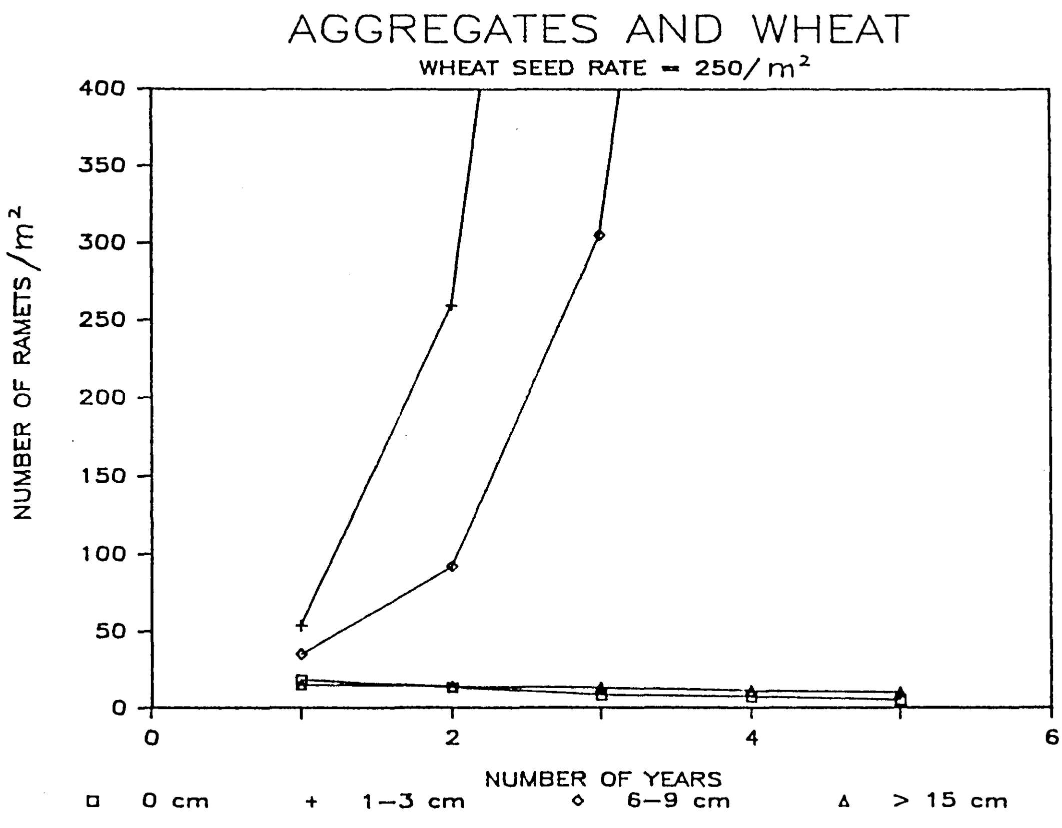


Fig. 5.5 Simulation results for aggregates of Onion Couch buried at different depths with a crop at two seed rate.

compared to intensive cultivation.

It seems that burial or exposure of the ramets and high seed rate of the crop can bring about a decrease in the crop yield loss (expressed as culms lost). The reason for this decrease in the crop yield loss is due to the fact that: Firstly, the crop shoots occupy space earlier than the tillers of Onion Couch, therefore, the greater the crop seed rate, the earlier the stand as a whole approaches the closed state. Secondly, the closed state of the stand would be largely determind by the crop, especially when the ramets or aggregates of Onion Couch are subjected to an unfavourable environment. This would in turn adversely affect the shoot regeneration capability from the ramets or aggregates of Onion Couch, and hence its future infestations. In addition, depth of burial seems to be more effective in reducing regeneration from situations representing intensive cultivation compared to minimum tillage, whereas, exposure seems to be more effective in reducing regeneration from situations representing minimum tillage compared to intensive cultivation. It must be realized, however, that in practice, complete burial or exposure of all propagules is unlikely.

5.2 Conclusion

Since the values used in the model are based on experiments, observations and approximations, the outputs can be viewed as giving what should be a reasonable estimate of the two tillage systems in reaction to agricultural practices over a span of five years.

A general conclusion can be drawn regarding the sensitivity of the model output to input values of the parameter in the two tillage systems. The results suggest that fragmentation and deep cultivation followed by planting an early tillering crop would result in rapid control of Onion Couch, whereas in the absence of such a cultivation regime the resulting aggregates will not be easily controlled. A comparison of the simulation output of the two situations representing an ideal intensive cultivation (into single ramets), and minimum cultivation (represented by aggregates), seems to reflect to some extent the variable responses to cultural and chemical control so often reported (Chap. 2) in natural infestations.

A more unified model based on a range of sizes of propagules and range of burial depths resulting from a range of cultivation options, backed up with more detailed experimental work in the field situation could be used as an advisory aid to explain the control of Onion Couch, demonstrating the response of resulting propagules to different farming practices, or the chemical control needed to control it in a particular management system.

CHAPTER 6

GENERAL DISCUSSION

This chapter is divided into two main sections. Section 6.1 deals with the present threat of expansion of *Arrhenatherum*, and the evaluation of the status of Onion Couch as a weed of arable land is reviewed in the light of this work. Section 6.2 is based on some recommendations derived from experiments, observations and the results of the simulations, and their implications for the control of Onion Couch.

6.1 The ecological status of *Arrhenatherum*

In Britain, the system of agriculture, both arable and grassland, has considerably changed over the years. The present state of arable and grassland management is based on intensification of production, as a result of which cultural farming practices are replaced by continuous cereals, winter sown cereals, minimum tillage, chemical control and regular fertilisation. This trend of intensive farming is regarded (Cussans, 1976) to have reached one extreme of the agricultural scene.

This changed pattern of farming has conferred considerable advantage on the spread of *Arrhenatherum*. On account of its preference for fertile undisturbed sites, the Tall Oat-grass variety has assumed dominance in the vicinity of farmlands (see chap. 2). The Onion Couch variety has very limited colonizing potential but is better able to withstand disturbance and is restricted in distribution to the arable fields. The cosmopolitan distribution of Tall Oat-grass and restricted distribution of Onion Couch suggests that there is very little possibility that Tall Oat-grass would act as a seed bank for the Onion Couch variety. It is possible, however, that increasing abundance of Tall Oat-grass in the farmland vicinities, especially where Onion Couch is prevalent, might lead to more frequent cross pollination between the two varieties and an increase in the frequency of seeds giving rise to a range of intermediate forms. These, by further interbreeding might produce the Onion Couch variety, (the formation of which is the result of an additive genetic effect on the polygenic character, bulbosity). Since there is a better chance of seedling establishment in the headlands than in the fields, possibility exists that under such circumstances Tall Oat-grass might make some contribution towards the future ingress of Onion Couch in arable fields from the field margins and headlands by vegetative propagules.

Onion Couch has a long history of association with arable agricultural systems and it is possible that it may have evolved weedy attributes which have optimised its survival within the system. In addition, it regenerates vegetatively, which is a common feature of some of the world's worst weeds. In spite of possessing these features, the very localised occurrence of Onion Couch, preferring arable fields with lighter soils, gives it a very low national status as a weed of arable lands compared to the other more widespread weeds. It is therefore considered relevant at this stage to evaluate the weedy attributes of Onion Couch, in the light of the present work, by comparing them with the much studied perennial grass weed Elymus repens (L.) Gould, which still remains one of the most troublesome grass weeds in temperate agriculture. It is hoped that such a comparison will highlight their respective successes in arable systems and at the same time assess and predict the economic importance of Onion Couch under a changing system of agriculture.

The success of the two weeds in arable systems is compared and evaluated in the context of the following weedy attributes:

6.1.1 Method of dispersal or propagation

Weeds possessing a combination of vegetative regeneration and sexual reproduction are regarded (Hakansson, 1982) as better adapted and could increase weed problems of the future, because the potential for rapid adaptation is greater in plants possessing both method of reproduction.

a) Sexual reproduction

Absence of dormancy in the seeds of both grasses is a serious handicap to the efficiency of sexual regeneration because the seedlings of both species are easily killed by soil cultivation. *E. repens* has a greater chance of establishing from seeds than Onion Couch because the seedlings of *E. repens* do show regenerative ability when they develop a rhizome of a few centimetre (cm). This rhizome then behaves essentially like a fully developed rhizome in terms of regeneration (Hakansson, 1982). Onion Couch, on the other hand has much less chance of establishing from seed because all the seeds of Onion Couch do not produce the Onion Couch variety, and the rudimentary bulbs produced by the seedlings are not strong enough to act as vegetative propagules.

b) Vegetative reproduction

In both grasses, the following factors associated with vegetative propagation are considered to be the main weedy attributes because they are capable of surviving unfavourable periods and thrive well under disturbance which is an integral part of the arable system:

Vegetative spread: This seems to be more efficient in E. repens. This is because the vegetative propagules are the buds on the rhizome. The horizontal growth form of the rhizome which branches and penetrates the soil in different layers, covers a large area (Fig. 6.1). On the basis of this slender, extensive and shallow system of rhizomes, the dispersal of vegetative propagules is very efficient because separation on the death of connecting tissues and fragmentation of such rhizome systems results in wider dispersal and the colonization of new locations. In contrast, although the individual bulbs in the single ramets of Onion Couch are capable to some extent of acting as vegetative propagules, morphologically they are part of a single stem base and fragmentation into separate bulbs causes damage (Fig. 6.1) and considerable loss of viability. Fragmentation in Onion Couch usually occurs at an innately brittle point (the caudex) and results in single ramets consisting of single stem bases, often with three bulbs or small aggregates of these stem bases. In addition, the vegetative propagules of Onion Couch are present in the top 3 cm of the soil and are usually confined to the place from where they have emerged and do not fragment or disperse without mechanical disturbance, in the absence or ineffectiveness of which they form massive aggregates.

Resistance to drought: The penetration of rhizomes into deeper soil layers gives the vegetative propagules of E. repens greater protection from drought and frost compared to the vegetative propagules of Onion Couch, which are partially exposed and are more susceptible to drought and frost damage. It is suggested (Chap. 4.2) that restriction of Onion Couch to loamy soils and complete absence from heavy clays and sand, could be due to the moist and protective environment provided by the texture of the former soils to the partially buried vegetative propagules of Onion Couch.

Longevity of the vegetative propagule: The rhizome system in E.repens may have old (the previous year's) and young rhizome, and buds on both are capable of developing new shoots. They are known (Leakey, 1984) to remain viable for 2-3 years. In Onion Couch, however, all the vegetative propagules are of one age, as the previous years propagules usually degenerate at the end of the growing season after producing new vegetative propagules. This could be due to a large amount of reserves in the bulbs which, under a moist warm environment, are attacked by pathogens.

Capacity for regeneration after fragmentation: In E. repens, intensive cultivation could result in rhizome fragmentation into several single-bud fragments, each of which becomes activated and develops into a new shoot in the absence of correlative dominance. Under reduced cultivation and fragmentation, several buds on the rhizome system remain dormant due to correlative dominance (Hakansson, 1982). In Onion Couch, intensive cultivation results in single ramets each consisting of a few bulbs which shows correlative dominance, the distal buds in the bulb chain suppressing the shoot growth of the remaining buds at the nodes. Under a reduced cultivation system, ramets tend to exist as aggregates, and single ramets in the aggregates do not suffer from much correlative dominance; most of them produce shoots, but density dependent mortality causes intensive thining. Small rhizome fragments of E. repens possess greater ability to tiller compared to the single ramet of Onion Couch; a 4cm fragment of E. repens rhizome can produce 60 aerial shoots (Hakanson, 1976) compared to 12 aerial shoots from single a ramet of Onion Couch.

Resistance to fragmentation and burial: The vegetative propagules of both perennials are in the upper layers of the soil as a result of which rhizomes and aggregates of E. repens and Onion Couch, respectively, are susceptible to fragmentation. More efficient fragmentation is achievable, even by shallow tillage, in E. repens and if it is followed by ploughing the burial of the small fragments of E. repens could give good control. On the other hand, aggregates of Onion Couch are more resistant to fragmentation; and the resulting single ramets or smaller aggregates are more resistant to control by burial because these propagules contain more food reserves compared to E. repens and produce more vigorous shoots, even when buried to a considerable depth. A burial depth of 10cm to 15cm, seemed more effective (in terms of lessening tiller emegence) for rhizome fragments of 4, 8 and 16cm length (Hakansson, 1976) compared to single ramets and aggregates of Onion Couch at similar depths.

6.1.2 Growth pattern

The growth pattern of E. repens is typical of many perennial grasses: aerial shoots developed in spring die in autumn or early winter. Shoots developed later in the growing season may, however, survive winter to a greater or lesser extent. In an arable situation primary aerial shoots of _E. repens_ begin to grow tillers and new rhizome in spring. Subsequent undisturbed growth means a gradual dry matter increase (in the form of new shoot production and rhizome growth) which continues until late autumn (Fig. 6.1). This autumn period before and after harvest (in an annual crop) is important for the growth and development of _E. repens_. Onion Couch, on the other hand, resembles an annual plants in its growth pattern: The tillering phase is completed in the spring, followed by bulb formation. No new tillers and bulbs are formed in the subsequent period (Fig. 6.1). Increase in dry matter takes place during the rest of the growth cycle (in the form of increase in dry weight of tillers and bulbs). Tillers senesce by the end of summer. The new vegetative propagules regenerate during autumn but new bulb formation takes place during spring.

6.1.3 Competitiveness with a crop

E. repens, on the basis of possessing a very efficient rhizomes system which, due to its intensive growth and lateral spread, enhances exploitation of soils by competing, even at a considerable distance from the aerial shoot, with the neighbouring crop plants for water and nutrients. In addition, due to its perennial growth habit, _E. repens_ competes and further increases the effectiveness of competition for light, water and mineral nutrients by providing a high plant density throughout the growth cycle of a crop. Moreover, the continuous growth habit of _E. repens_ may prolong the ripening process in an annual crop by the presence of green transpiring tissue during crop senescence (Fawcett, 1983). The growth pattern

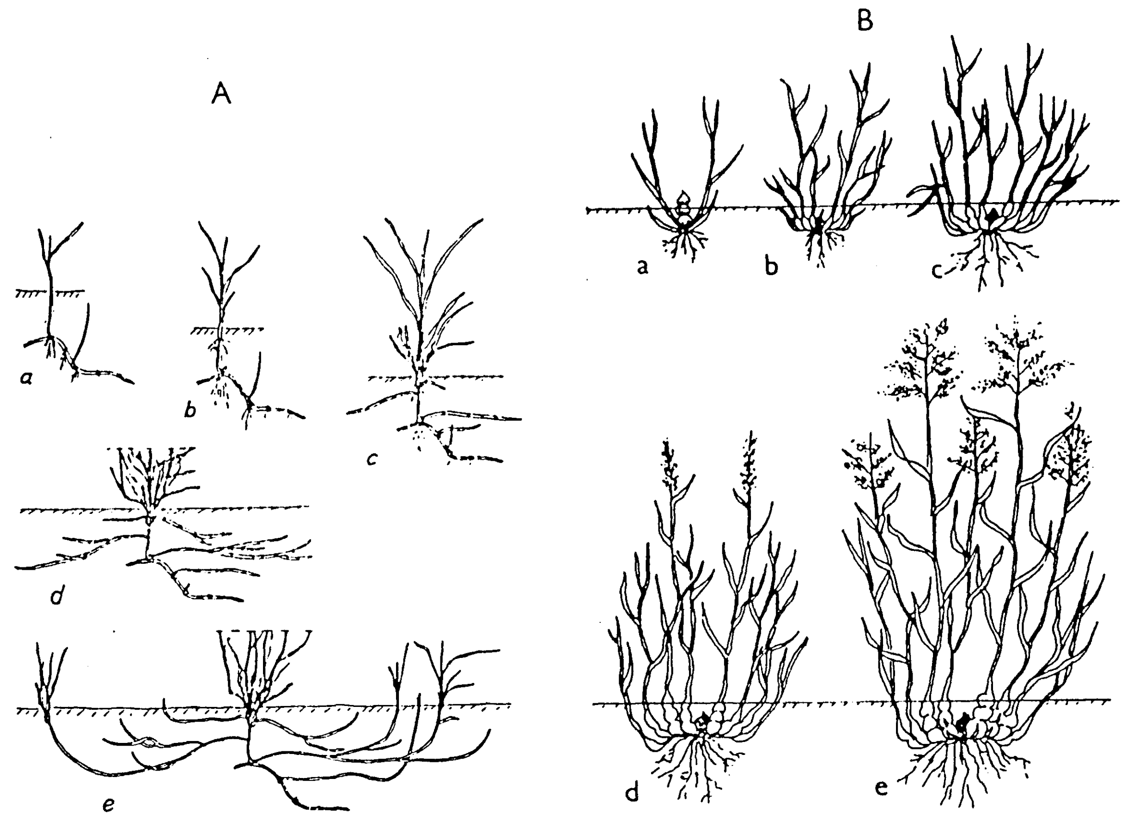


Fig. 6.1 Stages of growth and developement of E. repens (A)(after Hakansson, 1982) and Onion Couch (B). a. Early spring; commencement of active growth (regeneration phase). b. Spring; intensive tillering from the vegetative propagules and bulb initiation phase of Onion Couch, and emergence of aerial tillers and initiation of new rhizome from vegetative propagules of Elymus repens. c and d. Late spring and early summer; completion of bulb formation stage and begining of stem elongation phase in Onion Couch, and emergence of new tillers and rhizomes in Elymus repens. e. Late summer and autumn; ripening and senesceing phase of Onion Couch, with no new regrowth from the newly formed aggregate, and developement of new aerial shoots from newely formed rhizomes of Elymus repens at some distance away from the older shoots.

and phenology of E. repens suggests the liklihood of a strong competitive interaction with an associated crop; commencing in early spring and extending until the crop harvest (in an annual crop). Onion Couch, on the otherhand, behaves more like an annual crop in its growth pattern and offers competitive interaction in the early phases of growth. Crops with strongly shading stands are of particular interest in the control of both weeds because shading in both species reduces the underground growth more than the aerial growth. An early tillering crop like wheat or barley, forming a closed canopy early in the season would be more deterimental to the growth of Onion Couch than the late tillering, tall statured crops (e.g. oat). An early tillering crop, by forming a dense canopy early in the growing season, affects the critical bulb formation stage of Onion Couch. In E. repens, on the other hand, a crop with comparatively slow tillering rate but which forms a tall stature, especially towards the end of the growth cycle, would be equally effective due to the presence of a tall shading stand throughout the later part of the growth cycle. In addition, spring sown cereals would suppress Onion Couch more than winter sown cereals because the spring cereal system interferes (by spring cultivation) with the bulb formation stage of Onion Couch, whereas in the winter cereal system this phase is completed without interference.

6.1.4 Response to control measures

Onion Couch seems to be more resistant than E. repens to both chemical and cultural control measures. This resistance to control measures is largely conferred on Onion Couch by the aggregates which result from reduced cultivation. These aggregates, due to scanty regrowth in the autumn of the large numbers of ramets (which may or may not be connected) make post-harvest chemical control rather ineffective. In addition, pre-harvest control would also be less effective in Onion Couch compared to E. repens because most of the tillers of Onion Couch senesce before the normal pre-harvest application dates of herbicides.

6.1.5. Other weedy attributes

The ability of Onion Couch to form aggregates and exist in arable fields as large clumps of connected ramets cemented by the soil can give a poor tilth to the soil during seed bed preparation and thus interfere with the seed planting operation. In addition, seeds dropped in or around such aggregates would not be able to establish and would not provide the desired population of vigorous healthy crop plants. The slender and branching rhizome system of E. repens does not form such an interfering structure in cultivated fields.

6.2 Management recommendations for Onion Couch

In present day agriculture, importance is attached to those methods of weed control which can be manipulated in a crop-weed relationship in such a way that weeds are reduced to a harmless level. Techniques commonly proposed to accomplish effective measures for the control of perennial weeds are viewed here in the light of the biology and agro-ecology of Onion Couch based on experiments, observations and results of simulations.

6.2.1 Mechanical and chemical control

The choice of whether control by tillage should be employed is often determined by the growth habit of a weed. The aggregate forming ability in Onion Couch, especially the aspect of space occupation and resulting poor tilth (due to the presence of these aggregates and the corresponding crop yield loss) makes tillage essential for the control of Onion Couch. Breaking these aggregates into single ramets stimulates regeneration of new shoots. This breakage into single ramets or small aggregates could in fact increase the spread of weed if the fragmentation into smaller units is not subsequently followed by other control measures, e.g:

a) Rotary cultivation using adequate tractor power has proved to be very effective in the control of rhizomatous grasses (Proctor, 1960), and can be effectively used to fragment the aggregates of Onion Couch into single ramets. This method of cultivation followed by subsequent burial by mouldboard plough would be very effective in the control of Onion Couch as most of the vegetative propagules would be buried and, since the previous years vegetative propagule usually decay, there would be no chance of regrowth from the older vegetative propagules thus brought to the surface by such a practice, in contrast to what has been observed in E. repens (Proctor, 1960).

b) Rotary cultivation would be more effective in spring, when the newly regenerated tillers of Onion Couch have completed tillering and started the bulb formation stage. Such cultivation practice repeated at fortnightly intervals would deplete the food reserves of the vegetative propagule by repeated defoliation and thus interfere with the bulb formation stage. This kind of cultivation regime would be very effective on fields where Onion Couch is a serious pest. Introducing such a cultivation regime, and by selecting a crop variety that can be planted late, thus allowing time for killing a number of weed flushes, could prove to be an effective way of controlling a severe Onion Couch infestation.

c) There has been a growing trend toward reduction in the amount of tillage, moreover in some fields the number of tillage operations is dictated by the physical condition of the soil. Disking (instead of tillage) a seedbed a couple of times at a fornightly interval prior to planting a spring sown cereal, could prove to be an effective measure for the control of Onion Couch which is known to be highly susceptible to clipping.

d) It is evident from the results of the simulations that if no further efforts are made to control Onion Couch after a single cultivation, the infestation will spread because of the increase in population of single ramets instead of aggregates. If the newly emerged shoots from single ramets are controlled shortly after emergence by herbicides (post-harvest) it would be far more effective than when herbicide is applied to the aggregates (which are more frequent in untilled fields). This indicates that a combination of chemical control with rotary cultivation in autumn would give a very effective control.

e) Aggregates of Onion Couch are contained in the upper 3cm of the soil and can be brought to the surface without much effort. On heavy soils, cultivation by spring tines, which are known (Halley, 1984) to be effective in bringing up trash and hard clods, could be employed to bring the aggregates to the soil surface. The aggregates then, because of their size and small surface area of contact with the soil, become very susceptible to desiccation and cold injury (Plate 13). This method would be less effective in soils where the soil was too loamy and well structured to dry out.

6.2.2 Utilisation of management and crop competition for Onion Couch control

The interaction between weed and the management environment of the associated crop is delicately balanced and a shift in the timing of events e.g, kind and type of crop, sowing density, fertilizer treatment and weed control measures, may have a great effect on the vigour of an associated weed. The experiments and observations suggests that Onion Couch is suppressed by an early tillering crop planted at high seed rate on soils of high fertility status. The results of the simulations also show (from the long range point of view) that in spite of this suppression by the winter sown cereals there is a trend towards increase in the infestations. This presumably is due to a greater suitability of the life cycle of Onion Couch to the winter sown cereals than the spring sown cereals. A rotation that utilises crops with subtle differences in growth cycle (e.g Spring sown cereals), and timings of associated cultural practices (spring cultivation) would more effectively control Onion Couch infestations.

Fallowing, which is regarded (Chap. 2) as one of the most uneconomical control measures, could prove to be an effective control, if properly planned, especially, in a field where there is a whole field infestation (compared to patchy distribution). Onion Couch is very sensitive to defoliation (Chap. 3), so program of a year or two of continuous close defoliation (tillage or grazing or both) will not only deplete the food reserves but also expose the subsurface parts to desiccation and frost damage.

6.3 Conclusions

The comparative account of the two weeds clearly indicates that E. repens possesses more efficient weedy attributes than Onion Couch. E. repens on the basis of possessing an efficient dispersal mechanism of vegetative propagules, decreases the effectiveness of control measures. Vegetative propagules of Onion Couch, on the other hand, tend to become spot-bound aggregates which are even more resistant to cultural and chemical control.

The recent spread of Onion Couch and the reported variable and unsatisfactory results of control measures seem to be the result of the recent shift in agricultural practices, especially towards a winter cereal system and minimum tillage.

Onion couch has acquired many attributes of survival in disturbed conditions but it still possesses some characteristics of the Tall Oat-grass from which it has orignated. Knowing the wealth of genetic variability which Arrhenatherum carries with it, I shall not be surprised if intensification of selection pressure imposed by the present day farming practices, might hasten the spread and evolution of more efficient weedy atributes in the Onion Couch variety.

CHAPTER 7

SUMMARY

The agro-ecology of the perennial grass A. elatius described in this thesis is based on the two distinct varieties of Arrhenatherum i.e. Onion Couch, which produces bulbous swollen internodes and is an arable weed of local importance, and Tall Oat-grass which is non-bulbous and more widely distributed, representative of Arrhenatheretum a mesotrophic grassland.

A number of comparative studies was made to study certain features of the biology and ecology of the two varieties of the perennial grass Arrhenatherum elatius in order to determine the factors responsible for the success of one of the varieties as an arable weed. These included: early growth and development, responses to cutting and density dependent stresses, and regenerative capacity of the perennating organs and propagation of the Onion Couch variety by seeds. In addition, the competitive status of the two varieties was examined by determining β curves (de Wit, 1960) and also using Replacement Series and Additive designs of competition experiments.

The results of these experiment clearly indicated that the two varieties exhibit significantly different patterns of growth and developments and different responses to density dependent stresses. Onion Couch developed few tillers and, as a result, few axillary buds during the early phase of growth and thus showed very slow rate of recovery under even a mild cutting regimes. Tall Oat-grass on the other hand developed many tillers and hence axillary buds during the

establishment phase which in turn helped it to survive a mild cutting regime. Onion Couch was high yielding and allocated equal proportions of its whole shoot biomass to the development of basal internodes and aerial tillers, this being reflected in its slow occupation of space, late tillering and delayed density dependent mortality. Tall Oat-grass allocated large reserves in producing vigorous aerial tillers which underwent rapid elongation, early density dependent mortality and space occupation. On the basis of these characteristics, Tall Oat-grass competed better with wheat and also suppressed Onion Couch when grown with it.

Although the Tall Oat-grass variety competed better with wheat, it is the Onion Couch variety which exists as a weed. It seems that pattern of growth in Onion Couch, where it invests large amount of reserves in the basal bulbs at the expense of slow development of aerial tillers, has resulted in these highly specialized perennating organs, which also act as vegetative propagules. It seems obvious that possession of such perennating organs is the main weedy attributes of Onion Couch; it enables the variety to regenerate under disturbed conditions (fragmentation and burial) associated with agricultural practices.

The results from comparative studies clearly indicate that the growth pattern and response to various stresses shown by the two varieties of <u>Arrhenatherum</u> reflect the adaptive strategies evolved by them under two different habitats, and are due to the genetic factors which determine the presence or absence of characteristic basal internodes.

Additional experimental work in the context of growth and development of Onion Couch, especially relating to its behaviour in natural infestations included: preference of soil types, status of the vegetative propagules, growth and development, and effect on crop yield. Experiments and observations clearly indicate that medium textured soils provide a more protective micro-environment for the ramets which are formed in the top 3cm of soils. The results from field observations also indicate that the poor ability of vegetative propagules to disperse naturally, and their existence as aggregates rather than single ramets, could increase the economic importance of this variety, because large aggregates can affect crop yield by interfering with the establishment of crop and are more resistant to control measures. The observations also confirm the results obtained from the artificially planted plots that wheat, which tillers early and forms a dense stand early in the growing season, is a much stronger competitor and suppresses the bulb formation stage of the accompanied Onion Couch.

The simulation runs of a crop - Onion Couch growth model, based on a simplified structured representation of the physical and biological mechanism in an arable system, were in agreement with the experimental work and field observations. A comparison of simulation outputs based on shoot regeneration from ramets and aggregates at different burial depths and two crop seed rate situations has also clearly reflected the variable responses to cultural and chemical control so often reported by farmers.

In a comparison with E. repens, another perennial grass weed of arable land, it was apparent that E. repens possesses a more effective means of vegetative propagation, a rhizome system which branches and penetrates the soils at different levels, compared to Onion Couch, where the vegetative propagules are modified stem bases which become spot-bound in the absence of disturbance. The large amount of resereves in the ramets and aggregates of Onion Couch, however, makes them less susceptible to burial and thus gives them an advantage over the slender rhizomes of E. repens. In addition, the perennial and continuous growth pattern of E. repens offers competition to the annual crop throughout its growth cycle, but at the same time makes the weed susceptible to pre-harvest chemical control. On the other hand, the growth pattern of Onion Couch is more akin to that of an annual crop, which makes pre-harvest control measures less effective.

From this study of the agro-ecology of A. elatius, one can speculate that the recent changes in the pattern of agricultural practices in this country, and the continuation and increasing popularity of minimum tillage and a winter cereal system, would result in the spread of Arrhenatherum generally and also a greater incidence and spread of Onion Couch, on suitable soils and an increase in the ineffectiveness of the control measures.

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Appendix 1

```
PROGRAM ARRHEN(INPUT/,OUTPUT,MODDATA);
CONST
     NT=18;
     NY=5;
     RS=0.63;
VAR
I,J: INTEGER;
   DW,TR,NR,DOC,STOT,SW,SOC:REAL;
   BWHEAT,BOC:ARRAY[1..NT] OF REAL;
   MODDATA:TEXT;
BEGIN
RESET(MODDATA);
 FOR I:=1 TO NT DO READ(MODDATA,BWHEAT[I]);
 FOR I:=1 TO NT DO READ(MODDATA,BOC[I]);
 WRITELN(' ENTER WHEAT AND ONION COUCH  TILLER DENSITY ');
 READLN;
 READ(DW,DOC);
WRITELN(' ENTER NUMBER OF TILLERS REGENERATED ');
READLN;
READ(TR);
FOR J:=1 TO NY DO
BEGIN
 I:=0;
 STOT:=0;
 WHILE (STOT<600.0) AND (I<NT) DO
  BEGIN
  I:=I+1;
  SW:=DW*BWHEAT[I];
  SOC:=DOC*BOC[I]*RS;
  STOT:=SW+SOC;
  WRITELN(SW:10:1, SOC:10:1, STOT:10:1);
  END;
DOC:=SOC/RS;
IF DW > 900 THEN NR :=DOC * 0.80 ELSE NR:= DOC;
WRITELN('WHEAT FINAL DENSITY= ',SW:10:1);
WRITELN(' NEW RAMET DENSITY= ',NR:10:1);
DOC:=NR*TR;
WRITELN;
WRITELN;
END;
END.
```

Appendix 2

```
PROGRAM ARRHEN(INPUT/,OUTPUT,MODDATA);
CONST
     NT=18;
     NY=5;
     RS=0.63;
VAR
I,J: INTEGER;
   DW,FR,FW,FC,TR,NR,DOC,STOT,SW,SOC:REAL;
   BWHEAT,BOC:ARRAY[1..NT] OF REAL;
   MODDATA:TEXT;
BEGIN
RESET(MODDATA);
 FOR I:=1 TO NT DO READ(MODDATA,BWHEAT[I]);
 FOR I:=1 TO NT DO READ(MODDATA,BOC[I]);
 WRITELN(' ENTER WHEAT AND ONION COUCH  TILLER DENSITY ');
 READLN;
 READ(DW,DOC);
 WRITELN(' ENTER NUMBER OF TILLERS REGENERATED ');
 READLN;
 READ(TR);
FOR J:=1 TO NY DO
BEGIN
 I:=0;
 STOT:=0;
 WHILE (STOT<600.0) AND (I<NT) DO
  BEGIN
  I:=I+1;
  SW:=DW*BWHEAT[I];
  SOC:=DOC*BOC[I]*RS;
  STOT:=SW+SOC;
  WRITELN(SW:10:1, SOC:10:1, STOT:10:1);
  END;
DOC:=SOC/RS;
IF DW > 900 THEN NR :=DOC * 0.80 ELSE NR:= DOC;
WRITELN('WHEAT FINAL DENSITY= ',SW:10:1);
WRITELN(' NEW RAMET DENSITY= ',NR:10:1);
FR:=NR/15;
DOC:=FR*TR;
FC:=FR*0.51;
IF FR> 1  THEN  DW:=DW/FC ELSE DW:=DW;
WRITELN;
WRITELN;
END;
END.
```