TO TIMOTHY MATHENGE MANYEKI.

PHOTOSYNTHESIS AND PHOTOASSIMILATE PARTITIONING IN DETERMINATE AND INDETERMINATE *VICIA FABA* L.

by

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ABSTRACT

This study was conducted with the aim of appraising the relative performance of two recently bred determinate genotypes of *Vicia faba*, 645 and 642, and the well established indeterminate cultivar, Maris Bead (644). The physiological aspects studied included stomatal measurements, leaf area development, leaf chlorophyll content, leaf mesophyll anatomy, CO_2 assimilation, yield and yield components and assimilate partitioning at various developmental stages.

Leaves were found to be amphistomatous with more stomata on the abaxial surface. Stomatal densities for types 642 and 644 were similar while type 645 had fewer but larger stomata with longer and wider apertures. At maturity, the indeterminate type had a larger plant leaf area but the determinate genotypes showed a more rapid expansion of leaf area. Leaf chlorophyll content and chlorophyll a:b ratios were not significantly different. The indeterminate type senesced earlier and exhibited a faster rate of chlorophyll degradation.

The indeterminate type had more palisade mesophyll cells and the determinate type, 645, more spongy mesophyll cells while type 642 had fewer of both of these cell types. There was some indication that leaves of the determinate plants were thicker.

The pattern of CO_2 uptake was the same for the two growth habits. Higher photosynthetic rates were associated with higher

rates of stomatal conductance and transpiration. The indeterminate plants gave higher values for the measured yield components, although these differences were not significant. A proliferation of infertile branches contributed to the lower observed yields of the determinate plants.

At vegetative and flowering stages, most of the ^{14}C-photoassimilates were exported to the roots, stem and shoot apex, while pods received over 50% of the translocated assimilates at the pod filling stage. Actively growing organs had more specific activity per unit of dry matter. The activity in the fed leaf was higher than in the other organs after six hours.

It was concluded that the relative advantages of the determinate growth habit over the indeterminate one are outweighed by its lower yields, attributed to its inherent tendency to have fewer podding nodes coupled with more and almost infertile asynchronous branches. To enhance the advantages of the determinate growth habit, it is suggested that an intermediate type with more podding nodes on both the main stem and branches would be a worthwhile compromise in the future development of this crop. Also, more detailed studies should be conducted in the areas of anatomy of flowering and vascular development in flower racemes, C:N relationships and the efficiency of leaf area utilisation in the growing season.

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SECTION 1 : GENERAL INTRODUCTION

Most cultivars of *Vicia faba* L. grown today are indeterminate, are tall and therefore prone to lodging, have a long life cycle and show low harvest indices (Thompson, 1983). The recently bred determinate growth habit, which is still under improvement programmes, has been welcomed as a likely replacement of the indeterminate conventional types. This will only be feasible if these new types exhibit better efficiency in the utilisation of growth resources and also produce similar or higher yields than the conventional indeterminate types. The need to evaluate the determinate growth habit against the indeterminate types constitutes the main objective of this programme. The main emphasis here has been put on examining the two growth habits with respect to CO_2 uptake and photoassimilate partitioning. The determinate growth habit is shorter in height, develops more branches per plant and the apical meristem of the shoot becomes reproductive at the flowering stage. The potential of this new crop justifies these basic physiological comparative studies to evaluate its relative merits and demerits.

The study reported in this work has been undertaken at Wye College with two determinate improved X-ray mutants (Ti-series) and one determinate type. The two determinate types are coded 642 (Ticol) and 645 (Tinova). The former, 642, emanated from a Swedish cultivar, Primus, as described by Sjodin (1971) and has been a subject of selective breeding at Wye College for over a decade, and

the latter, 645, originated from Germany and described by Steukhardt. The indeterminate type, 644, is the well-established cultivar, Maris Bead.

The main thrust of this study was directed towards an investigation of several factors which influence the uptake and assimilation of CO_2 in photosynthesis, and the fate of the assimilated carbon in various plant organs. Thus, the following measurements were undertaken: stomatal frequency and aperture, chlorophyll content, plant leaf area, plant yield, photosynthetic rates, leaf anatomy with respect to photosynthetic tissue and ^{14}C-photoassimilate partitioning.

Chapman and Peat (1978) have described several advantages of the determinate habit over the indeterminate types. These include: a shorter plant less prone to lodging; a shorter life cycle and early pod set, which results in aphid avoidance, i.e. there is the absence of a growing shoot apex during the period of highest potential aphid infestation; and a harvest index which is higher than that of the indeterminate plant. Baker, Chapman, Standish and Bailey (1984) observed that although there are not major differences in the two types of growth habit in terms of photosynthetic potential, the leaves of determinate plants have a delayed senescence and remain photosynthetically active for a longer period of time. On $^{14}CO_2$ feeding, they observed that the genetic removal of the indeterminate stem growth alters the number of competing sinks but does not increase the percentage of assimilates moving to developing pods.

Although some studies have been undertaken concerning assimilate partitioning in *Vicia faba*, see for instance Crompton, Lloyd-Jones and Hill-Cottingham (1981), only limited information exists concerning determinate material (Austin, Morgan and Ford, 1981; Baker, Chapman, Standish and Bailey, 1983). Information from these studies show that the inherent advantage of the terminal inflorescence may be diluted when tillers and axillary branches, which develop asynchronously with the main shoot, remain infertile. These branches therefore compete for assimilates as an alternative sink, just as the continued growth of the apex in the indeterminate habit. Austin, Morgan and Ford (1981) in a field study of a determinate (Topless) and an indeterminate type (Maris Bead) observed that, initially, the determinate type grew more rapidly than the indeterminate habit, but that there was little difference between the two genotypes in total dry matter yield at maturity. Yield of the determinate type was 89% of that of Maris Bead in irrigated and non-irrigated plots. Measurements also showed that determinate plants were shorter at maturity and produced many infertile tillers and axillary branches. The pattern of photosynthesis and translocation by both types was similar before flowering. At pod growth, the leaves were the major source of assimilates; the larger, upper leaves contributing more assimilates in the determinate type while more leaves in the indeterminate type contributed assimilates with no single source showing dominance.

This study aims at taking this ongoing investigation a step further by examining the factors stated above at a more detailed level and to demonstrate whether differences do occur in the two

growth habits with respect to the efficiency with which they assimilate CO_2 and the subsequent partitioning of carbon fixed into various sinks, and especially the percentage partitioned into the reproductive organs. In other words, how do the two growth habits compare in their relative efficiency to produce yield under similar environmental conditions? To a large extent, the study seeks to answer this basic question.

SECTION 2 LITERATURE REVIEW

2.1 : Plant Photosynthesis and productivity

Photosynthesis has been defined by Lawlor (1987) as the process by which living organisms, mainly plants, convert the energy of light into the chemical energy of organic molecules. It is through photosynthesis by autotrophs that energy is directly or indirectly provided for the whole living world.

Among other aspects of metabolism, photosynthesis shows the most prominent variation under the dictates of the immediate environment (Talling, 1961; Bjorkman, 1975, 1981). This sensitivity, and the dominance of the process in the synthetic economy of nature, has stimulated its study under more or less field conditions (Monteith, 1964, 1965; Black, 1973; Nasyrov, 1978; Parkinson, 1980, 1981). The photosynthetic rates in any vegetation cover are controlled by a considerable number of internal and external factors and by the interactions between them (Thomas, 1955; Monteith, 1965; Salisbury and Ross, 1978; Beadle *et al*., 1985).

Light as an energy source can be regarded as the 'master' factor. It shows more remarkable variation than any other environmental factor. Its behaviour can be interpreted in relation to the rate intensity characteristic of photosynthesis, its modification in response to other factors and its expression and variation in time and space of photosynthetic rates under natural conditions (Monteith, 1965; Wareing and Khalifa, 1968; Sale, 1977;

Fasheun and Dennett, 1982). This characteristic also expresses two limiting universal factors of the efficiency of energy utilisation; the maximum quantum yield at low intensities and light saturation at high intensities.

Increase in the yield of crop plants may be realized from several areas; such as better adaptation to environmental conditions, greater resistance to pests and diseases, improved agronomic practices, increased genetic yield potential and interactions between these (Gifford and Evans, 1981; Gifford, Thorne, Hitz and Giaquinta, 1984). To comprehend the development of yield, we need to treat photosynthesis, translocation, growth and storage as an integrated whole. So far, increase in yield potential has been achieved by direct ability to yield organs of interest under progressively improved systems of agronomic inputs (Evans, 1976). Donald (1962) has also pointed out that in the absence of a genetic increase in the photosynthetic process itself, improvements in yield potential have been derived largely from increases in the proportion of accumulated dry weight in harvestable organs. Both the size and the number of these organs have been increased as have the rate and the duration of their growth in many species. Increases in duration have been associated with greater longevity of leaves or with the storage phase making up a larger proportion of the crop life cycle. As a result, yields of modern wheat and soybean cultivars are nearly 40% greater than those of earlier cultivars (Frey, 1981) those of corn hybrids have increased 50% (Duvick, 1977) and peanuts by nearly 100% (Duncan, McCloud, McGraw and Boote, 1978).

The rate of photosynthesis and dry matter production varies with habits and the prevailing environmental factors. The photosynthetic rate of a whole leaf as canopy also differs greatly between species of plants with habitat, and depends on the rate of synthesis of ATP and NADPH (Atkins, 1969; Dornhoff and Shibbles, 1970, 1976), the rate of synthesis of ribulose biphosphate carboxylase which is in turn controlled by the photosynthetic carbon reduction cycle (Baker and Bradbury, 1981), the rate of carboxylation of RUBP which is a function of the activity of RUBP carboxylase enzyme (Berry and Bjorkman, 1980) and the ratio of RUBP oxygenase to carboxylase activity (Bjorkman, 1981).

Light penetration of canopies is depleted exponentially by successive leaf layers, approximately obeying the Bouger-Lambert Law (Mousi and Saeki, 1953 as quoted by Etherington, 1982). Thus:

$$R_i = R_o e^{-K_{ext} L}$$

where R_i and R_o are the irradiance within and above the canopy in Wm^{-2} respectively; L, leaf area index; K_{ext}, extinction coefficient and e, the base of the natural logarithm (2.718). If the uppermost layer of leaf canopy is just at light saturation, and if photosynthesis is linearly related to light intensity, the model would predict a progressive exponential reduction in photosynthetic rate of each sequential leaf layer. With sufficient canopy depth, the lowest layers will be below the light compensation point and represent a respiratory drain on canopy net photosynthesis (Monteith, 1964).

Differences in photosynthetic rates have been observed between sun and shade leaves with sun leaves showing higher rates (Bjorkman, 1975; Boardman, 1977). The differences in photosynthetic rates of sun and shade leaves may arise from either differences in the morphology and anatomy or the biochemistry of photosynthesis and respiration (Duncan, 1971; Esau, 1977).

Differences from year to year in the rate of development of leaf area can influence final crop yields and in particular, larger yields may be obtained if optimal leaf area index (L) is attained earlier in the season (Watson, 1952; Monteith, 1965; Johnson *et al*. 1969; Porter and Jones, 1977; Schoper *et al*., 1982). Leaf area of a crop depends on numbers and sizes of leaves, both of which are influenced by the effects of the environment, particularly on leaf initiation and expansion. Such factors as air and soil temperatures, light level and wind speed have been found to directly or indirectly influence leaf expansion (Wilson, 1966; Bull, 1969; Dennet *et al*., 1980). In *Vicia faba* plants, the relative rates of increase in leaf area per plant was found to fluctuate greatly during the early growth of plants, which was closely related to daily maximum temperatures (Bull, 1968; Auld *et al*., 1978). After podding, the relative rate of leaf area increase in determinate field bean, Maris Bead, was less influenced by environmental factors. The general decline of this rate was attributable to competition for light between plants and the diversion of assimilates and other materials to the growing pods (Bull, 1968; Flinn, 1974).

In kale and sugarbeet plants, the net assimilate rate (NAR)

was found to decrease with (L) in the range 1-5, while that of sugarbeet was less affected (Watson, 1958). Increasing LAI raises dry matter production, but this relationship does not hold indefinitely because of increased mutual shading of leaves so that mean photosynthetic rate per unit leaf area decreases (Watson, 1952; Yoshida, 1972).

2.2 CO_2 uptake and transpiration

Since most of dry weight of plants consists of carbon compounds, the increase in harvested yield is intimately linked to changes in the photosynthetic fixation of carbon dioxide per unit of land area and the subsequent partitioning of the photoassimilates between various organs (Gifford, Thorne, Hitz and Boote, 1984). The growth and dry matter accumulation of crops is usually determined by dry weight change determined by destructive harvesting. This technique is useful for assessing long-term changes but is unsuitable when the objective is to determine dry matter gain on a short term basis, i.e. minutes, hours or days. CO_2 uptake mesurements in intact plants provide an alternative and direct method of measuring productivity. It's advantages are that it is instantaneous, non-destructive, allows separate investigation of individual leaves and allows separation of photosynthetic gain from respiratory losses (Parkinson, 1980, 1981). Long and Ireland (1985) have outlined the methods of determining photosynthetic CO_2 uptake from intact plant tissues. This involves passing air of known concentration at a constant rate through a cuvette enclosing a leaf segment or whole leaf. Cuvettes have been designed to produce minimum alteration of

natural microclimate either in the field or laboratory studies (Fanjul, Jones and Treharne, 1980; Von Caemmerer and Farquhar, 1981).

The net flux of CO_2 (A) and the efflux of water vapour (E) for an enclosed leaf in a cuvette is determined from the change in the mole fractions of the CO_2 ($\triangle c$) and water vapour ($\triangle \chi$) between the inlet and the outlet of the cuvette and by correcting for the dilution of CO_2 by the current increase in water vapour content resulting from leaf transpiration (Von Caemmerer and Farquhar, 1981; Leuning, 1983). Thus:

$$E = (f/s)\ [(\chi o - \chi i)/(1-\chi o)] \quad \text{mMol } m^{-2} s^{-1} \text{ of water vapour}$$

$$A = -(f/s)\ \{[(1-\chi i)/(1-\chi o] \cdot co-ci\}\ ci \quad \mu\text{Mol } m^{-2}\ s^{-1} \text{ of } CO_2$$

where Ci and Co are the mole fractions of CO_2 in air at the cuvette inlet and outlet, respectively. χi and χo are the mole fractions of water vapour in air at the cuvette inlet and outlet, respectively. f is the mole flow of air in mol s^{-1} and s is the leaf area in m^2.

The photosynthetic plant faces the dilemma of CO_2 gain and water loss (Raschke, 1975, 1976; Cowan, 1977; Farquhar, 1980; Farquhar and Sharkey, 1982). Furthermore, once CO_2 has entered the autotrophic metabolic pathway, there is a problem in that the same proportion of assimilated CO_2 is immediately required to fuel the respiratory needs of maintenance, growth and production. Transpiration is the inevitable consequence of the fact that a plant must expose a large area of moist cell walls to the air in order to

facilitate the absorption of CO_2 by the leaves (Meidner and Mansfield, 1968; Cowan and Troughton, 1971; Raschke, 1976). This dilemma is further compounded by the fact that the plant must get CO_2 from the atmosphere in which its concentration is very low (0.03 percent by volume) and at the same time retain water for normal metabolic processes (Salisbury and Ross, 1978). The normal atmospheric CO_2 concentration of 340 ppm limits assimilation in C_3 species more than in C_4 species under saturating light levels (Akita and Moss, 1973; Biscoe, 1977; Sale, 1977). Despite this fact CO_2 might not be considered as a variable, since the relative magnitude of normal change is small when compared with other factors such as light, temperature and ambient humidity. With a dense stand or canopy of plants, the CO_2 concentration on a still day when photosynthesis is maximal, may drop to 250 ppm and rise to values near 400 ppm in the early morning during climatic inversions (Monteith, 1964).

Plants fall into three categories in their mode of CO_2 fixation. These include the C_3 plants which fix CO_2 through the Calvin cycle; C_4 plants, e.g. many tropical grasses which fix CO_2 initially into C_4-carbon compounds; malate, oxaloacetate and aspartate in addition to CO_2 fixation by the Calvin cycle (Hatch and Slack, 1970; Bjorkman, 1975; Black, 1973). The third type is the Crassulacean acid metabolism (CAM) plants which include many succulent plants growing in arid environments. The latter fix CO_2 in the dark to oxaloacetic and malic acid and can be considered as temporal C_4 plants. For the same environmental conditions, the rate of photosynthetic CO_2 fixation by C_4 plants is higher than in C_3

plants (Singh, Ogren and Widholm, 1974; Boardman, 1977).

2.3 Stomata

Willmer (1983) has defined stomata as pores formed by a pair of specialized cells, the guard cells which are found on the surface of aerial parts of most higher plants and which can open and close to control gas exchange between the plant and the environment. They are entrance points of CO_2 into the leaf and exit of water vapour to the air, during the process of photosynthesis. Conventionally, a stoma is accepted to mean the pore and the surrounding pair of guard cells. The stomatal complex includes the guard cells and the neighbouring subsidiary cells (Meidner and Mansfield, 1968). Stomata are commonly associated with leaves but may also occur in the epidermis of herbaceous stems, petioles, fruits and in parts of angiosperm flowers (Meidner and Mansfield, 1968).

In leaves of most herbaceous plants, stomata are found on both the adaxial and abaxial surfaces but usually there are fewer stomata on the adaxial than on the abaxial surface (Meidner and Mansfield, 1968; Cole and Dobrenz, 1970; Heiche, 1971; Teare and Patterson, 1971; Carpenter and Smith, 1975; Ciha and Brun, 1975; Pallardy and Kozlowski, 1979). Such leaves are termed amphistomatous. In contrast, leaves with stomata on the abaxial surface only are termed hypostomatous leaves while those with stomata on the adaxial surface only are termed epistomatous leaves.

Usually, stomata are randomly scattered within the epidermis.

However, the pattern may differ between species. In most monocotyledons and gymnosperms stomata may be located in rows (Meidner and Mansfield, 1968). Environmental and genetic factors are involved in the morphogenesis of stomata. Water availability, light intensity, temperature and CO_2 concentration have been observed to affect stomatal frequency (Meidner and Mansfield, 1968; Knecht and Orton, 1970; Knecht and O'Leary, 1972; Aston, 1976). The number of stomata per unit area of leaf surface varies, not only between species, but also within any one species owing to the influences of environmental factors during growth (Aston, 1978). Stomatal frequencies are usually higher in plants grown in full sunlight than in plants grown in shade. Also, plants grown in dry soil and low humidity generally have higher stomatal frequencies than plants growing in wet soil and high humidity. Ciha and Brun (1975) working with soybean plants found that increasing temperature caused decreased stomatal frequency per unit leaf area in the abaxial leaf surface, while the frequency increased in both leaf surfaces with increased light intensity. Number of stomata per leaflet was not found to differ significantly but water stress resulted in greater stomatal numbers per leaflet.

In crop plants, stomatal frequency can differ greatly among different genotypes of the same species growing under identical conditions. Stomatal frequencies also vary within a plant, higher frequencies often being found in the leaves at the top of the canopy (Miskin and Rasmussin, 1970). Even within a leaf, the stomatal frequency may vary, e.g. in grasses the highest frequency occurs at the point of insertion of the leaf (Geok-Yong and Dunn, 1975).

Stomatal frequency may possibly influence the processes of photosynthesis and transpiration. A maize cultivar with lower stomatal frequency was reported to exhibit faster net photosynthesis than a cultivar with greater stomatal frequency (Heichel, 1971). However, Miskin and Rasmusson (1972) found that stomatal frequency did not influence the rate of photosynthesis in barley but did influence transpiration and stomatal diffusive resistance. Low stomatal frequency was also associated with greater drought tolerance in blue panic grass (Dobrenz, Wright, Humphrey, Massengale and Kneebone, 1969), and in greater winter hardiness in American holly (Knecht and Orton, 1970).

Because the initial step in photosynthesis involves entrance of CO_2 into the leaf, a close relationship between them is inferred. Stomatal aperture opening appears to be associated with an excess of turgor pressure in the guard cells over that in the neighbouring subsidiary or epidermal cells although some exceptions have been noted in monocotyledonous species (Fisher, 1973). The mechanism of stomatal opening involves active uptake of potassium ions by guard cells (Willmer and Mansfield, 1969; Thomas, 1970; Fisher, 1971; Fisher and Hsiao, 1971). This in turn induces a turgor change and cause the stomata to open. Fisher (1968) working with *Vicia faba* found that stomatal opening in light was accompanied by a fall in guard cell osmotic potential from -7 to -16 bar, and Humble and Raschke (1971) reported values of -19 bar for closed and -35 bar for open stomata. In *Pelargonium zonale* it has been shown that photosynthesis, pore diameter and average pore area increase together toward maximum values. Illuminated leaves did not begin to

photosynthesise until stomata started opening and thereafter, photosynthesis kept pace with increasing apertures (Scarth and Shaw, 1951; Lurie, 1977).

Stomatal movements provide the leaf with an opportunity to change both the partial pressure of CO_2 at the sites of carboxylation and the rate of transpiration. In order to gain CO_2 most economically, with respect to water loss, stomata should function such that the marginal water cost of assimilating more CO_2 dE/dA is constant during the day (Cowan and Troughton, 1971). Farquhar (1978) has argued that stomata may tend to optimise some index of performance which depends on E and A. He assumed that there is a cost , de (b) associated with an increase in da (a) in assimilation. The optimal conductance is then the one at which $dE/dA = {}^{b}/_{a}$ where dE/dA represents the slope of the relationship between E and A when the conductance is the implicit source of variation. Cowan (1977) defined an optimal time course of stomatal conductance as one which gives rise to the minimum loss of water over a certain period for a particular amount of CO_2 assimilated.

2.4 Chlorophyll, canopy development and photosynthesis

Green plants in terrestrial ecosystems contain pigments, among which are chlorophylls which are essential to the process of photosynthesis. Chlorophylls a and b are the most important in this respect. Leaves may contain up to 1 gm of chlorophyll m^{-2} of surface area. The amount of chlorophylls a and b and that of chlorophyll a:b ratios in plant species vary depending upon such

factors as the nutritional status or other environmental growth conditions (Black and Mayne, 1970; Lawlor, 1987).

Chlorophyll is extracted with fat solubilising solvents, e.g. ether and acetone, for it is a lipophilic molecule only found in membranes containing lipid and hydrophobic protein (Arnon, 1949; Manzerall, 1977). On average, chlorophyll a is present at a ratio of approximately 3:1 of the content of chlorophyll b. C_4 plants show a ratio of chlorophyll a to chlorophyll b of 3.9:1, on average while C_3 plants give a ratio of 2.8:1 (Black, Chen and Brown, 1969; Black and Mayne, 1970; Chang and Troughton, 1972). A given plant species will have a relatively greater a:b ratio if it is grown under higher light intensities (Rabinovitch and Govidjee, 1969

The absorption maxima of chlorophylls a and b are 663 and 645 nm, and 660 and 645 nm in acetone and ether respectively, in the red end of the light spectrum (Arnon, 1949; Machlis and Torrey, 1959; Meidner, 1984). Photosynthesis involves two light harvesting centres with two special variants of chlorophyll a, i.e. photosystems I and II with their absorption at P700 and P680 respectively (Emerson* and Lewis, 1943). It is within this framework that photolysis of water and oxygen evolution occurs coupled with production and transfer of electrons through intermediate compounds to produce energy in the form of ATP and the regeneration of NADPH.

As leaves are the main sources of chlorophyll in plants, it can be inferred that the development and duration of leaf area will

* As quoted by Salisbury and Ross (1978)

affect photosynthesis and hence dry matter production per unit time or seasonally. Watson (1958) working with sugarbeet and kale observed that net assimilation increased with leaf area up to the optimum and then a decline was observed, attributable to mutual shading of leaves. The amount of radiation (PAR) intercepted by a crop over its growing season is important in dry matter production and is influenced by canopy structure and arrangement (Monteith, 1965). Longer leaf area duration is important especially at seed filling. Crop plants vary in their pattern of leaf area development and duration per given season. Baker, Chapman, Bailey and Standish (1983) working with determinate and indeterminate *Vicia faba* observed a delayed leaf senescence in determinate beans as compared to the indeterminate types.

2.5 Source-sink relationships and assimilate partitioning

For growth and development carbohydrate compounds synthesised in photosynthesis must be translocated to various plant organs. Photosynthetic organs, mainly leaves, are the source of photoassimilates while organs of utilisation, e.g. roots, stems, young leaves and grains, become the sinks. Ho, Grange and Shaw (1988) have described source and sink functionally as plant organs or tissues, depending on their ability to supply or use a particular metabolic substance. In general then, source and sink can be defined in terms of supply (losses) and demand (gains) of a particular substance in a plant. Organs may change their status in time depending on the stage of plant development (Evans, 1975; Hall and Milthorpe, 1978; Kursanov, 1984; Ho, Grange and Shaw, 1988).

Consequently, sink-source status of a plant is viewed as dynamic in nature, since an organ may change from a consumer (net importer) to a supplier (net exporter) or *vice versa*, in time (Ho and Shaw, 1977).

The basic pattern of assimilate transport and distribution in an intact plant consists of the growing zones orientating assimilates towards themselves, where each sink creates a sphere of influence for assimilates around itself (Belikov, 1973; Geiger, 1976, 1979).

In studies of ontogenetic distribution of assimilates in soybean, it was observed that in young vegetative plants assimilates moved downwards towards roots and upwards towards the shoot apex (Belikov, 1973). Just before flowering, lower leaves supplied assimilates to roots, mid leaves supplied assimilates upwards to shoot apex or downwards towards roots, and the upper leaves exported assimilates solely to the shoot apex. At the reproductive stage, assimilates from leaves were directed to the nearest pod. Thrower (1962) in another study with soybean plants observed that the expanding leaf imports assimilates from leaves below, this import rising to a maximum and then falling off to zero when the leaf was half-expanded, at which stage it became a net exporter to younger ones. Export both to root and younger leaves increased until the leaf was fully expanded (Thrower, 1962; Thorne and Koller, 1974; Ho and Shaw, 1977).

Crompton, Lloyd-Jones and Hill-Cottingham (1981) working with an indeterminate faba bean found that before flower set most of the ^{14}C-photoassimilates from all expanded leaves moved downwards to the

roots and the stem below the treated leaf after 6 hours. Later, at pod fill, the upper leaves maintained this supply to the roots and lower stem, while most of the ^{14}C-photoassimilates translocated from the lower and midstem leaves went to the pods developing on the same node. ^{14}C-photoassimilates exported from the fed leaf increased over time up to 48 hours but the pattern of distribution did not change. In young corn plants between 80-90% of the assimilated ^{14}C-photoassimilates were translocated from the fed area in 24 hours (Hofstra and Nelson, 1969). Singh and Pandey (1980) working with chickpea plants found that leaves exported 51-56% of ^{14}C-photoassimilates to the pods. They also observed that the total $^{14}CO_2$ fixed by the plants was reduced if the pods or leaves were removed; 45% reduction was observed by complete pod removal and 32-70% by complete leaf removal.

Hume and Criswell (1973) in another study with soybean grown under field conditions, observed that more ^{14}C-photoassimilates were accumulated in actively growing parts. At the vegetative stage, most of the ^{14}C was incorporated into structural tissues of leaf and stem (^{14}C in the roots was not estimated). The amount of ^{14}C in the stem decreased with time in favour of the seeds. They also observed that the amount of ^{14}C recovered at maturity varied with the time of feeding, i.e. if the plants were fed before flowering, only 30-40% of the ^{14}C was recovered at maturity while 65% was recovered if the plants were fed at the stage of rapid seed development. Losses were attributed to both plant respiration and leaf abscission. In cotton, the subtending leaf was found to be the major source of assimilates to the boll while bracts only contributed 5-10% (Ashley, 1972;

Benedict and Kohel, 1975). C_4 plants eg. sugarcane, corn, millet and sorghum have been shown to export ^{14}C-photoassimilates from fed leaves more rapidly than C_3 plants, i.e. 70% after 6 hours (Hartt and Kortschack, 1967; Hofstra and Nelson, 1969; Eastin, 1970).

In *Vicia faba* it was observed that in flowering and pod growth, the patterns of assimilation were similar in determinate and indeterminate beans. In pod growth, leaves were the main contributors of assimilates in both growth types, but the large upper leaves were the main source of assimilates in the determinate type. In the indeterminate type (Maris Bead), more leaves contributed assimilate and no single leaf was a dominant source. Pods were shown to contribute about 20% of the gross assimilation of the crop. It was also observed that the rate of photosynthesis per unit dry weight of pod, judged from ^{14}C fixation, was greater in Topless than in Maris Bead (Austin, Morgan and Ford, 1981).

SECTION 3 : MATERIALS AND METHODS

3.1 Growing of experimental material

Two determinate and one indeterminate types of field bean were grown under glasshouse and field conditions. Plants in the glasshouse were grown in 7 inch plastic pots containing potting compost. A randomised block design was used with four blocks (Cochran and Cox, 1957; Steel and Torrie, 1987). Plants in the field were sown at a density of 21 plants m^{-2}. Plants grown in the glasshouse in autumn and winter when the light intensity (PAR) was low were supplemented with artificial light from 400 W lamps. Routine care of the plants in the glasshouse included regular watering and spraying for insect pests and diseases as the need arose. Nutrient solution was fed to the plants at fortnightly intervals, commencing six weeks after emergence.

3.2 Stomatal measurements

Stomatal frequencies and aperture dimensions were determined on lastic impressions applied on both adaxial and abaxial surfaces of intact leaves. Lastic paste was thoroughly mixed with 1-2 drops of hardener and immediately spread on the leaf surface. Five to seven minutes were allowed to ensure setting of the impression. Leaf surface replicas were then peeled off and preserved for light microscopical examination (Sampson, 1961). Impressions were taken from randomly selected fully expanded leaves on a sunny day, between 9.00 a.m. to 12.00 noon when stomata would be expected to be open.

a



b

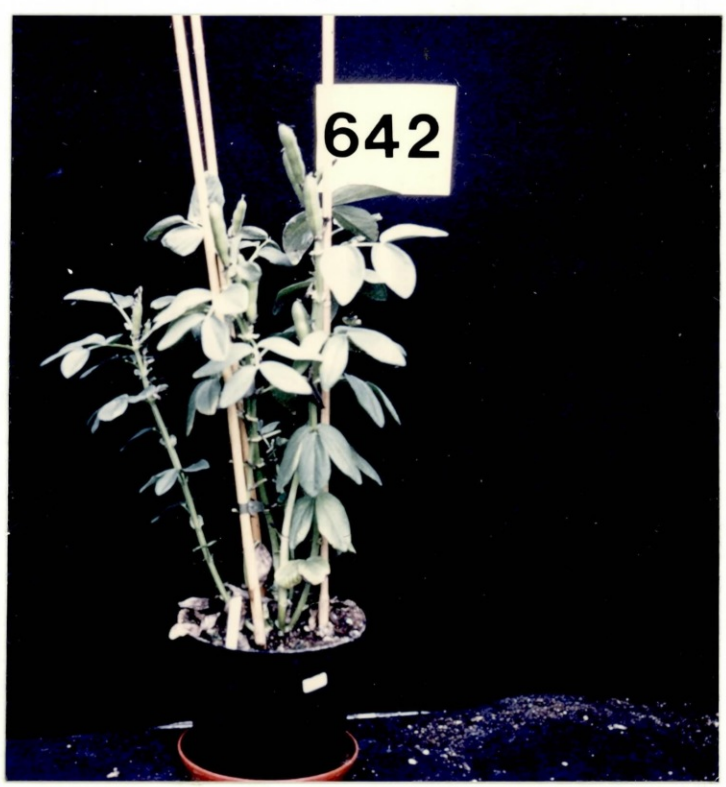
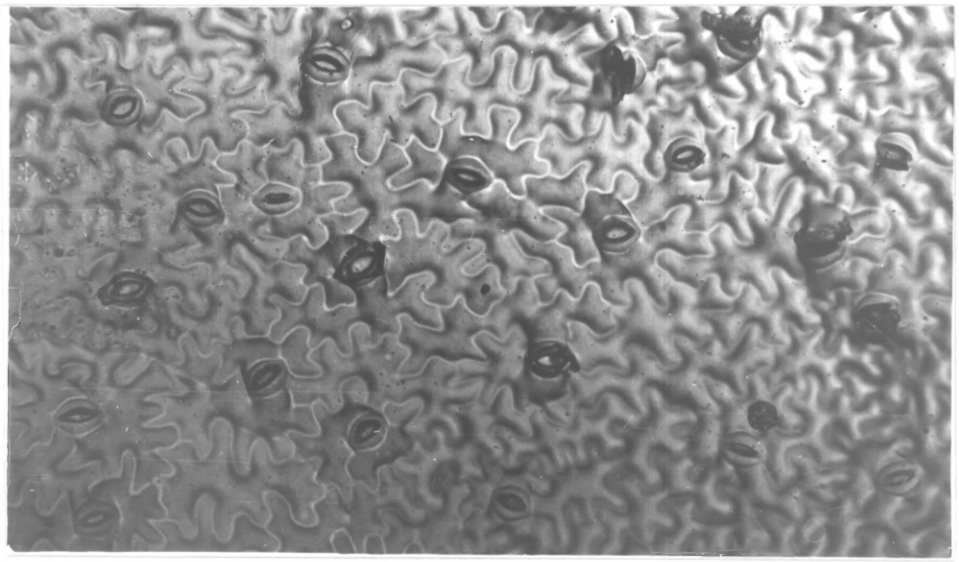


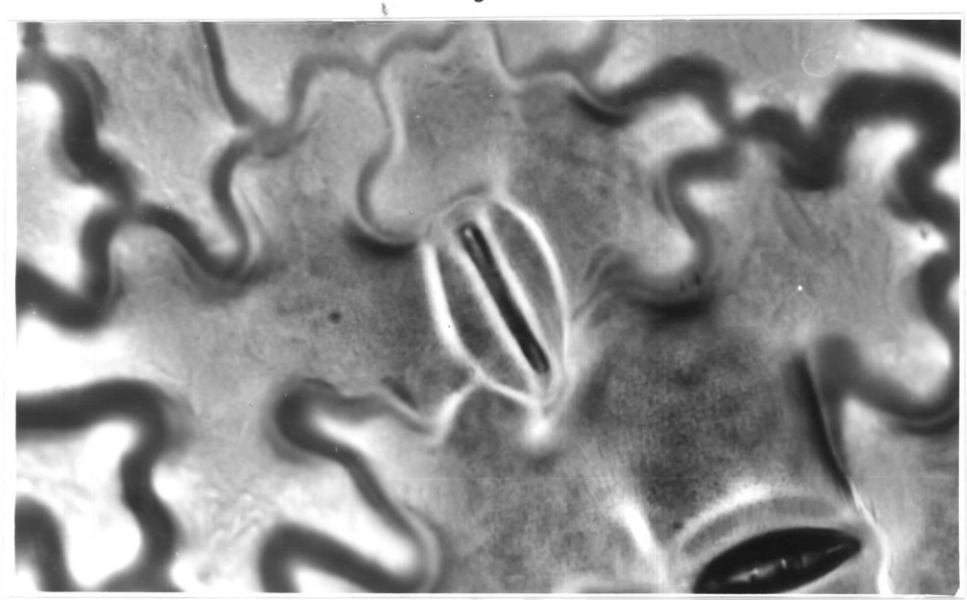


Figure 3.1 Photographs of the two determinate growth habits, 645 (a) and 642 (b) and the indeterminate type, 644 (c) cultivar Maris Bead, taken at pod filling stage

a



b



c

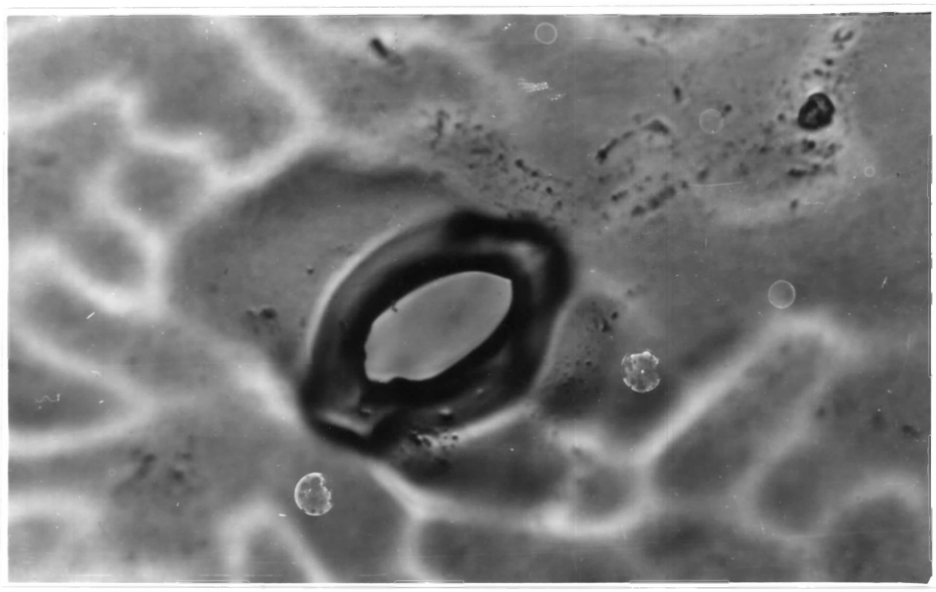


Figure 3.2 Light transmission micrographs of leaf surface replicas showing:-
a) low power (x 12.5) view of the lower surface.
b) and c) closed and open stomata (x 50) with focus on stomata.

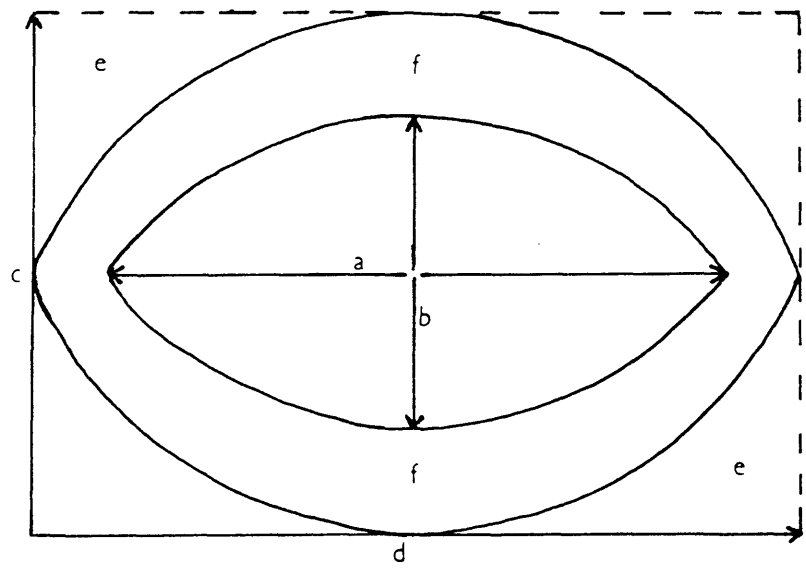


Figure 3.3 Measurements of stomatal dimensions:
a, aperture length; b, aperture width;
c, aperture and guard cell width;
d, aperture and guard cell length;
e, subsidiary cell; f, guard cell.

To facilitate examination in the laboratory, clear nail varnish was applied on the lastic impressions, allowed to dry and set and then peeled off. The nail varnish 'positive' was placed on a glass slide under a cover slip for examination.

To count the number of stomata, 20 views at x40 magnification were randomly examined and the number of stomata in each view recorded. The view area was measured using an eye graticule and scale. Subsequently, numbers of stomata per view were expressed mm^{-2}. Counting was done for both adaxial and abaxial surfaces.

Aperture dimensions, length and width were measured as above and as shown in Fig. 3.3. Stomatal and aperture dimensions were measured in micrometers.

3.3 Leaf area measurements

Plants grown as described in 3.1 were sampled for leaf area determination at intervals of 21 days. Individual leaflet areas were measured by a photographic video leaf area meter; Delta-T devices, model Rs 232C. Total plant leaf area was the sum of all leaflets on the mainstem and branches.

3.4 Chlorophyll determination

Fresh fully expanded leaves of both determinate and indeterminate plants grown in the glasshouse were sampled at intervals of approximately 3 weeks for chlorophyll determination. One gram samples of the fresh leaves were weighed and the area taken,

as in 3.3. The samples were cut into small pieces in a mortar and the contents ground together with a pestle and grinding sand. The ground samples were then introduced into a 50 ml separating funnel. For extraction, 4 ml of acetone were added, the contents well shaken and allowed to stand for 10 minutes. Then 3 ml of distilled water were added, shaken thoroughly and allowed to stand for partitioning to be complete. Finally, 3 ml of petroleum ether were added, shaken thoroughly and allowed to settle. The pigments were found in the petroleum ether layer at the top while the rest of the solution was clear. Extraction with acetone was done in the dark to minimise chlorophyll losses by light degradation.

For spectrophotometric chlorophyll a and b determinations, 1 ml of the ether extract was mixed with 9 ml of acetone in a test tube. Absorbances were read against an acetone blank at wavelengths of 645 nm and 663 nm for chlorophyll b and a respectively, using an SP8-100 UV/vis Beckman spectrophotometer. Absorbance readings were converted to chlorophyll content in μg using Mackinney's method, as modified by Arnon (1949). Chlorophll contents were on the basis of four 1 gm fresh leaf samples and 24 photospectrometric readings.

3.5 Leaf mesophyll anatomy

Scanning electron microscope examination

Fully expanded leaves of glasshouse grown plants were selected and a small area of leaf of about 0.5-1 mm^2 cut out and immediately frozen with liquid nitrogen. The sample was then transferred into a moisture free chamber in a scanning electron microscope where it was

broken transversely with a sharp blade edge to facilitate scanning. Before transferring the sample into the scanning chamber it was coated with gold in order to bring out the details more clearly. Scanning was done at different magnifications and photographs taken. The procedure was repeated for the leaves of both determinate and indeterminate plants. The photographs were used to establish whether differences existed between the leaves of the two types in terms of cell numbers, sizes and arrangement (Steer, 1981; Hajibagheri *et al.*, 1984).

Light and transmission electron microscope examination

An area was selected from fully expanded leaves of experimental beans and a representative sample cut out. From this sample, small tissue samples, 0.5-1 mm^2 were cut for fixation. The method involves killing cells, preserving them and conditioning them to allow the cutting of sections using an ultra-microtome. The tissue specimens were placed in a phosphate buffer immediately after cutting and then immersed in two fixative solutions; glutaraldehyde and osmium tetroxide (OsO_4), followed by dehydration in an acetone series and embedding in epoxy resin and allowing to set.

The resin block containing the specimen tissue was trimmed with a sharp blade and with the help of a stereomicroscope, so that the block face was approximately 0.5 mm across. Sections of 0.5 µm were cut using a high quality glass or diamond knife in an ultramicrotome. The thin sections were floated in water in a small 'boat' attached to the microtome. The sections were later transferred onto grids of copper mesh and covered with formvar

plastic to provide support. The grids were immersed in two heavy metal salt solutions, uranyl acetate and lead acetate, in turn. The heavy metal ions attach to biological materials in general and render them more visible in the electron microscope.

For light microscopy, the resin block containing the specimen was trimmed to shape using a sharp razor blade under a stereomicroscope. Excess resin was removed to produce a 'block face' immediately over or including the tissue specimen. The block was then placed in an ultramicrotome and a glass knife used to cut 1-2 µm sections from the block face. The sections were placed on a glass slide, stained with toluidine blue, washed with distilled water and dried for examination.

3.6 Measurement of CO_2 uptake by infra red gas analyser (IRGA)

Assimilation of CO_2 has been measured by several different techniques, the most common being $^{14}CO_2$-labelling, conductivity and infra-red spectroscopic analysis. The latter, infra-red gas analysis of CO_2, is the most widespread contemporary method of determining photosynthetic and respiratory CO_2 exchange in plants.

In this study, an ADC LCA-2 portable IRGA was used to measure CO_2 uptake in single leaflets selected on the main stem of experimental plants at various stages of growth, i.e. vegetative, flowering and pod filling stages. The equipment consists of an ADC LCA-2 analyser, an ADC Parkinson broad-leaf chamber, an ADC air supply unit and a printer (Fanjul *et al.*, 1980; Parkinson *et al.*,

1980; Parkinson, 1981).

Measurements were taken on sunny days when photosynthetically active radiation (PAR) would not be limiting photosynthesis. In the glasshouse, however, it was possible to supplement natural light with a 150 W source (1350 μmol m^{-2} s^{-1}) to give an average of 1500 u mol m^{-2} s^{-1} on dull days. The selected leaflet was clamped into a broad leaf chamber, ensuring that light falling on the leaf was not less than 900 μmol m^{-2} s^{-1}. An allowance of 30-45 seconds was given for the leaf to stabilise and another 30-45 seconds for CO_2 uptake. The ADC LCA analyser computed figures for net photosynthesis, transpiration and stomatal conductance among others.

3.7 Plant yield measurement

At maturity plants of both types were sampled for yield data. Plants were harvested for various components, i.e. plant dry matter, pod number, seed number, seed weight, average number of seeds per pod, average seed weight and the harvest index. The harvest index was calculated by dividing plant seed weight by the total above ground dry matter (Kambal, 1969a; Donald and Hamblin, 1976).

3.8 $^{14}CO_2$ feeding and ^{14}C-photoassimilate partitioning

Field bean plants of the two determinate and one indeterminate type were fed with $^{14}CO_2$ at the vegetative stage, flowering, early pod set, mid-pod filling and late pod filling stages. Experimental plants were selected for uniformity in batches of three. $^{14}CO_2$ feeding was done on a sunny day when photosynthetically active

radiation (PAR) would not be limiting photosynthesis. Plants at the vegetative stage were fed with $^{14}CO_2$ at the fifth leaf, plants at flowering and early pod formation at the leaf below the first flowering node and plants at mid and late pod filling at the leaf below the first podding node.

Five µl of $NaH^{14}CO_3$ containing 10 µCi (DPM) was applied at the centre of a paper disc a few days before feeding and allowed to dry. This improved the efficiency of $^{14}CO_2$ transfer to the fed leaf. At feeding, the paper disc containing $NaH^{14}CO_3$ was transferred to a transparent polythene bag which was used as a $^{14}CO_2$ chamber. The selected leaf was enclosed in the chamber and carefully secured to the leaf petiole with a wire and a piece of sponge to protect the petiole from damage. Three to five ml of 1% acetic acid were introduced into the chamber with a syringe and needle. The needle hole was carefully sealed with transparent cellotape to avoid leakage of $^{14}CO_2$. Care was taken to release acetic acid onto the centre of the paper disc to ensure complete liberation of $^{14}CO_2$. The leaf was allowed to assimilate $^{14}CO_2$ for 30 minutes before removing the polythene bag. Experimental plants were left to translocate ^{14}C-photoassimilates for 6 hours and then harvested to provide samples of various organs, i.e. fed leaf, leaves, stem, flowers or pods above fed leaf, apical meristem, roots and leaves and stem below the fed leaf. These samples were dried to constant weight at 60°C, ground to powder and sub-samples of 0.2-0.5 g weighed for combustion (Baker, 1984).

Combustion was performed in an OX-400 Biological Material

Oxidiser at 730°C and 930°C in the catalyst and combustion zones respectively. This equipment combusts any biological and most organic materials, wet or dry, in a stream of oxygen gas at 900°C and passes the combustion products through a series of catalysts at 700°C. $^{14}CO_2$ is trapped directly in an external trap containing a scintillation cocktail (27% methylated spirit, 27% phenylethylamine and 46% NE 233). Other gases i.e. halogens, sulphur, phosphorus and nitrogen oxides escape, while metals, salts and high melting point materials remain in the combustion boat. Subsequently, the ^{14}C activity in the scintillation cocktail was determined using an A211 Rackbeta liquid scintillation counter. From these data, it was possible to quantify how ^{14}C-photoassimilates were partitioned between various sinks(DPM).

SECTION 4 : RESULTS AND DISCUSSION

4.1 : Stomatal measurements

The stomatal densities of the two determinate types, 645 and 642 and the indeterminate type, grown in the glasshouse and in the field are presented in Table 4.1. The results clearly reveal that leaves of both growth habits are amphistomatous and also that the abaxial surface has more stomata per unit area than the adaxial surface. For glasshouse grown plants, the determinate type 642 had the highest density for the upper surface, with type 645 showing the lowest densities. The densities for the abaxial surface were similar for types 642 and 644, with that of type 645 being slightly lower. The results for the field grown plants exhibited a similar trend as those for the glasshouse grown plants, in that type 642 evidenced the highest densities for both adaxial and abaxial surfaces, with type 645 showing the lowest densities.

These observations agree with those reported by Meidner and Mansfield (1968) in which stomatal densities for determinate faba beans were 65 and 75 mm^{-2} for the adaxial and abaxial surfaces respectively. Clearly, the determinate type 645, which was observed to exhibit higher leaflet areas, (see Section 4.2, Table 4.3) shows lower stomatal densities for both surfaces when grown in either the glasshouse or in the field. The lower stomatal densities recorded for field grown plants of types 642 and 644 may also probably reflect the fact that the leaflet areas were larger. The observed higher densities for glasshouse grown plants may also reflect the prevailing

Type		Glasshouse		Field	
		Upper	Lower	Upper	Lower
645	Mean	56.50	80.17	35.50	56.00
	SE	0.39	0.97	1.45	3.05
642	Mean	65.70	84.58	47.50	78.00
	SE	0.56	0.51	1.46	2.76
644	Mean	61.75	83.54	45.67	69.50
	SE	0.41	0.73	1.03	1.08

Table 4.1: Stomatal densities (mm^{-2}) of the two determinate types 642 and 645 and the indeterminate type, 644, for upper and lower surfaces of leaves from glasshouse and field grown plants.

Type		Aperture dimensions (μm)		Stomatal dimensions (μm) aperture and guard cells	
		Length	Width	Length	Width
645	Mean	25.28	8.40	40.20	31.85
	SE	0.89	0.05	0.40	0.64
642	Mean	20.7	7.57	38.33	29.50
	SE	0.27	0.313	0.49	0.41
644	Mean	21.10	7.50	39.58	28.58
	SE	0.24	0.22	0.16	0.15

Table 4.2 : Stomatal dimensions, aperture and guard cells, μm, for glasshouse grown plants of the two growth habits.

environmental growth conditions, with glasshouse plants having been well tended and having received higher average temperatures and better nutrition than field grown ones. The stomatal responses to such factors were not investigated in this study. Whether the differences observed here affect net photosynthesis is discussed in Section 4.4.

The stomatal dimensions for open apertures and stomatal apparatus (aperture plus guard cells) measured as shown in Fig. 3.1, are presented in Table 4.2. The results show that the determinate type, 645, which was observed to have lower stomatal density, had not only longer but also wider stomatal apertures than types 642 or 645. The aperture widths for types 642 and 644 were similar. The stomatal apparatus dimensions reveal that although the differences were small, those of type 645 were longer and wider. These results show that the determinate type 645 has larger stomata than types 642 and 644, which resulted in larger apertures when these larger stomata were open.

4.2 Leaf area

Leaf area expansion trends for both the determinate and the indeterminate growth habits are presented in Figs. 4.1, 4.2 and 4.3. The results in Fig. 4.1, measured in the summer of 1987, show that initially, i.e. up to 30 days, the indeterminate type, 644, had a higher leaf area than the determinate type, 642. Afterwards, and up to 70 days, the indeterminate growth habit gave larger leaf areas, although growth had slowed down. This was mainly due to the fact that the terminal apical meristem of the determinate plants had

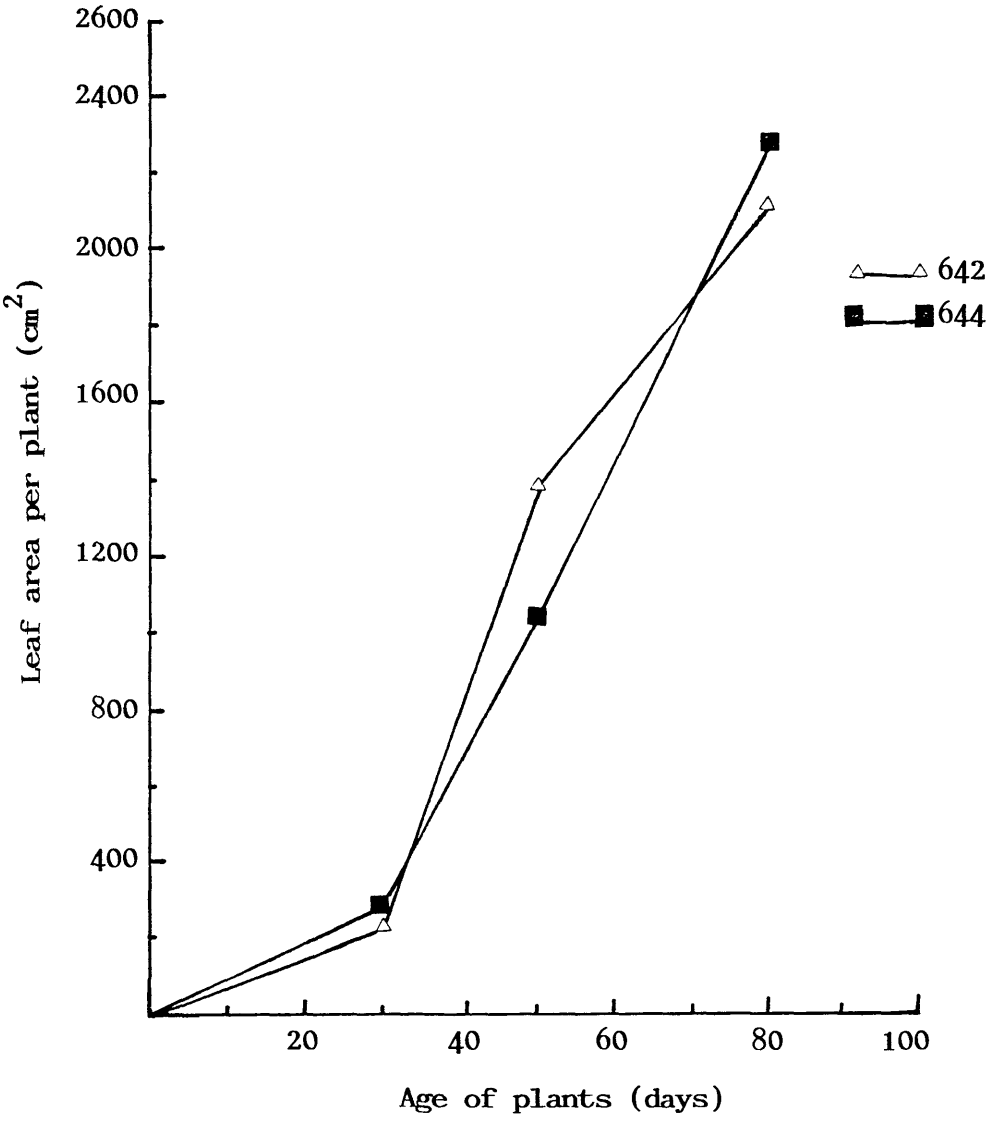


Fig. 4.1 : Plant leaf areas of the determinate growth type, 642, and the indeterminate type, 644, measured at 30, 50 and 80 days from emergence in Summer, 1987. Each value is the mean of 4 plants.

NB. The determinate type 645 was not available at this time.

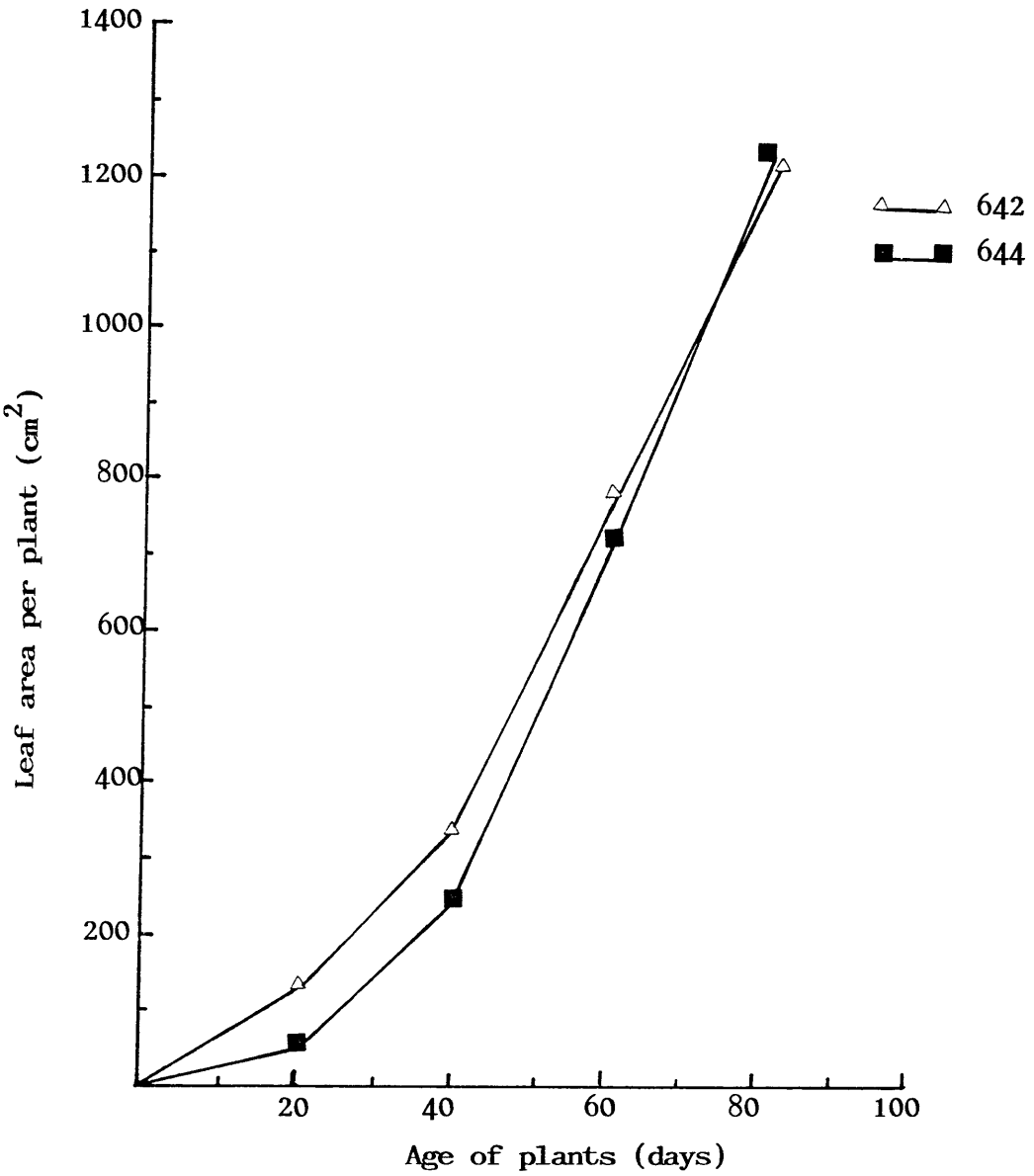


Fig. 4.2 : Plant leaf area of the determinate type, 642, and the indeterminate type, 644, measured at 20, 40, 60 and 82 days in Autumn 1987. Each point is the mean of 4 replicates.

NB. The determinate type 645 was not available at this time.

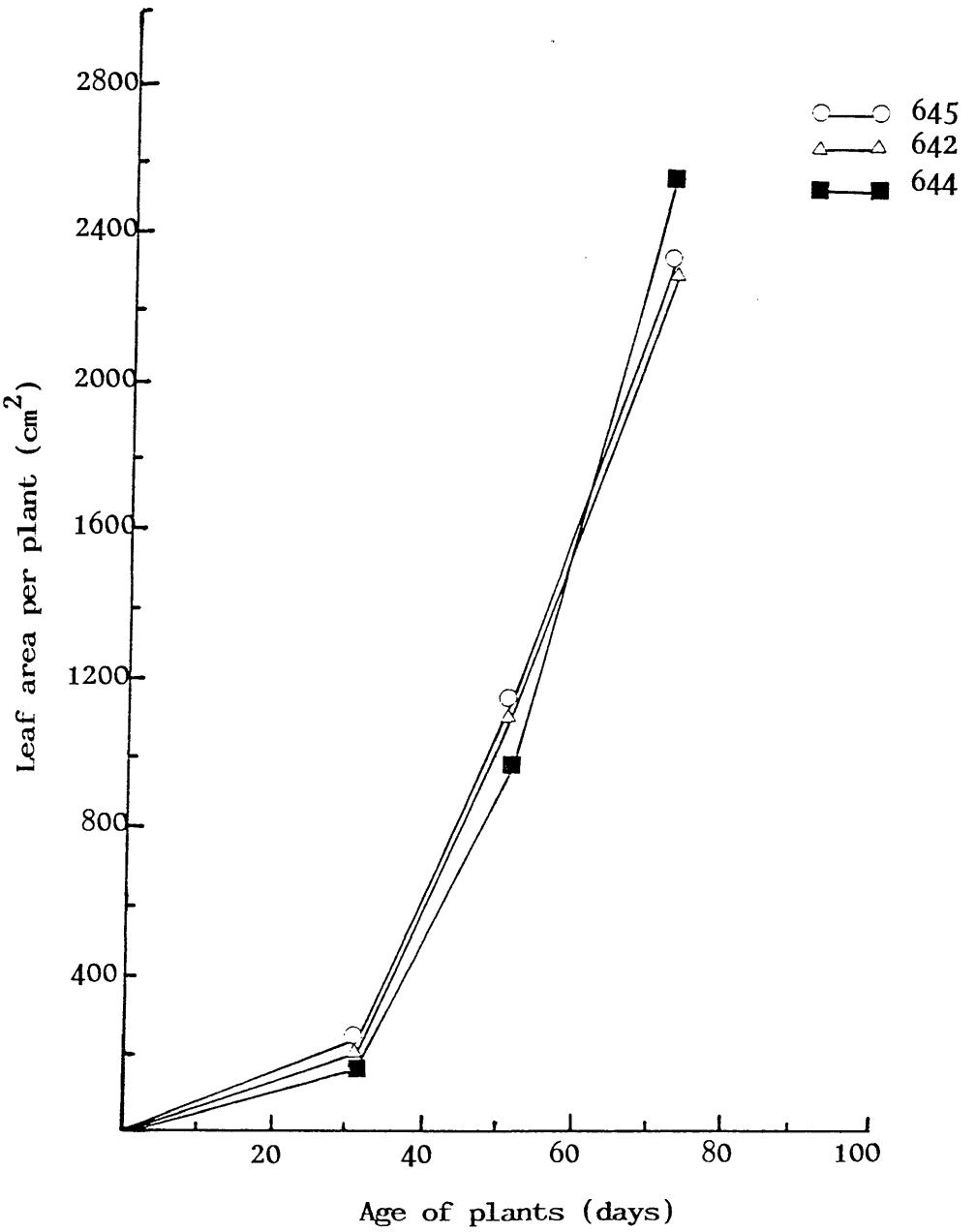


Fig. 4.3 : Plant leaf area of the determinate type, 642, and the indeterminate type, 644, measured at 30, 51 and 72 days in Summer 1988. Each point is the mean of 4 replicates.

become reproductive and any further contribution to area was from leaves on the branches.

The results presented in Fig. 4.2, recorded in the autumn of 1987, show clearly that the determinate growth habit had a larger leaf area per plant up to 75 days. Under the prevailing growth conditions, the determinate type grew faster but the indeterminate one picked up later and its leaf area was larger at 82 days.

The two determinate types show a similar trend for leaf area development, as can be seen in Fig. 4.3. As shown in Fig. 4.3, the determinate types grew faster initially but due to earlier terminal flowering, their areas were lower at maturity; that of the determinate type 645 being higher than type 642, though the differences were not significant.

The results for the average leaflet areas and the number of nodes per plant at maturity are presented in Tables 4.3 and 4.4, respectively. From the data given in Table 4.3, it is evident that the determinate growth types have larger leaflet areas than the indeterminate ones. It was also noted that the leaflet average areas were lower in the indeterminate growth habit at 72 days. This was mainly due to the fact that individual leaflet areas were smaller on later nodes so that although leaflet numbers increased, the overall average leaflet area was reduced. However, the total leaf area per plant was higher for the indeterminate plants.

From these results, it is evident that leaf areas for the

Plant type	Leaflet areas (cm^2)		
	30 days	51 days	72 days
645	17.75	18.91	22.30
	(0.65)	(1.70)	(0.14)
642	13.90	17.03	18.69
	(1.13)	(1.33)	(0.71)
644	11.6	13.99	11.24
	(2.82)	(0.90)	(2.17)

Table 4.3 : Average leaflet areas of the two determinate types, 645 and 642 and the indeterminate type, 644, measured at 30, 51 and 72 days (± SD).

Plant type	Number of nodes
645	13.90
	(2.08)
642	15.10
	(1.52)
644	30.70
	(2.36)

Table 4.4 : Number of nodes at maturity of the two determinate growth types, 645 and 642 and the indeterminate type 644. (± SD)

determinate plants were larger initially than for the indeterminate plants but became lower after terminal flowering of the main stem. Any further increase in total leaf area of the determinate growth was mainly due to the contribution from the branches. The average leaflet areas were higher for the determinate plants and it is possible that the leaf area differences observed between the two growth types before flowering of the determinate plants may not be due to leaflet numbers but more due to leaflet size. It was also observed that the leaflet numbers per leaf were more in the indeterminate plants, albeit smaller in area. Chapman and Peat (1979) have observed also that leaflet number per leaf in the indeterminate growth habit increased with increase in nodes. More branches in the determinate plants compensated for the terminated main stem after flowering so that the final total leaf area was close to that of the indeterminate plants. Austin *et al.*, (1981) observed that there was little difference in the dry matter production between a determinate (Topless) and indeterminate genotypes at maturity. The leaf areas observed here may account for this trend.

4.3 Chlorophyll content

Chlorophyll content measurements at various times is presented in Figs. 4.4, 4.5 and 4.6. These include chlorophyll a and b contents and chlorophyll a:b ratios. The data presented in Fig. 4.4, determined in autumn 1987, show that the contents of chlorophyll a and b increased from 15 to 77 days followed by a decline as the plants aged. It is evident from these results that chlorophyll a content was higher in all stages of growth than chlorophyll b content

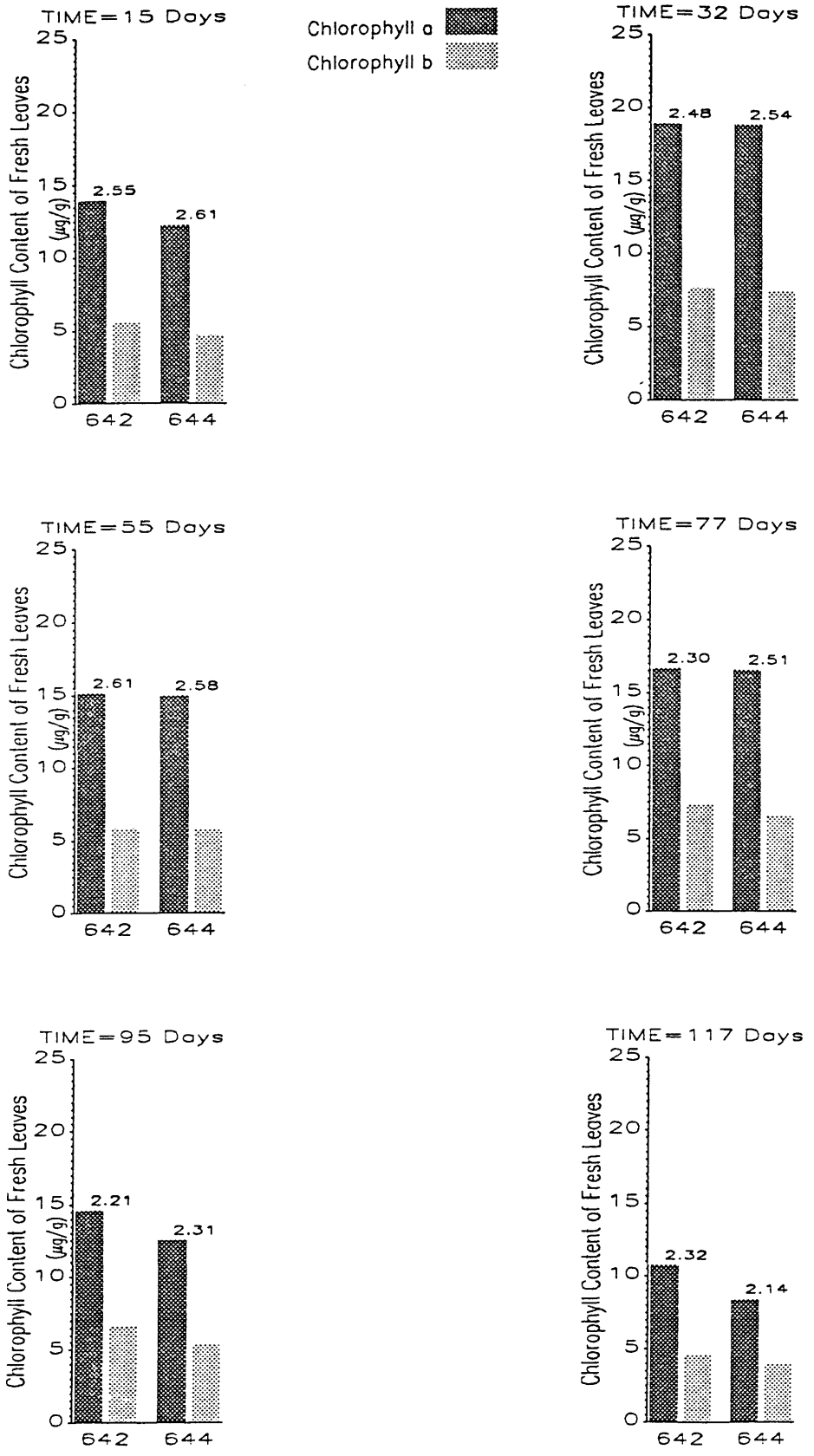


Fig. 4.4: Chlorophyll a and b contents of fresh leaves and chlorophyll a:b ratios (figures above bars), of one determinate type, 642, and the indeterminate type, 644, determined at days 15, 32, 55, 77, 95 and 117 from emergence, in autumn 1987.

Type 645 was not available at this time.

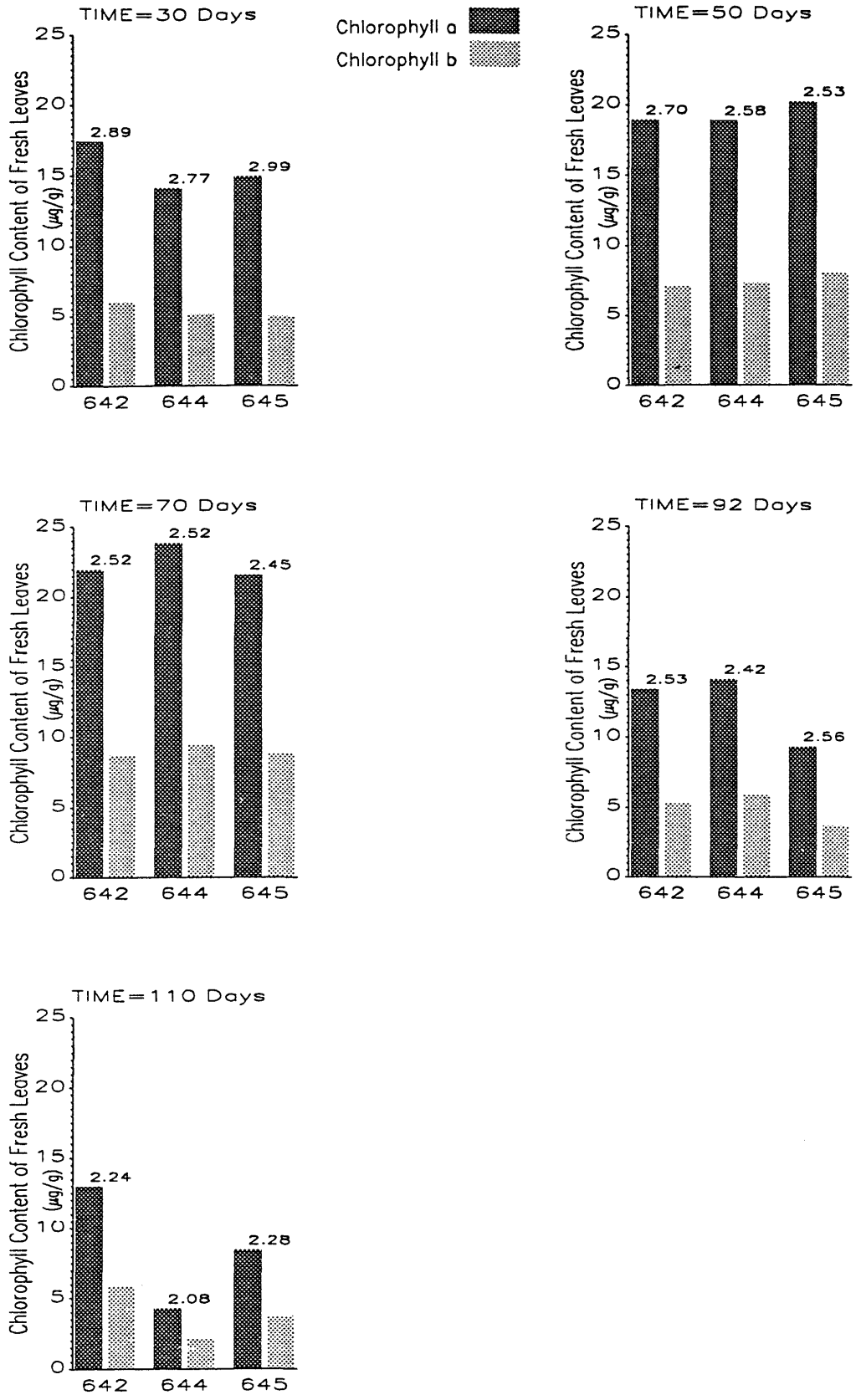


Fig. 4.5: Chlorophyll a and b contents of fresh leaves and chlorophyll a:b ratios (figures above bars), of two determinate types, 645 and 642, and the indeterminate type, 644, determined at days 30, 50, 70, 92 and 110 from emergence, in summer 1988.

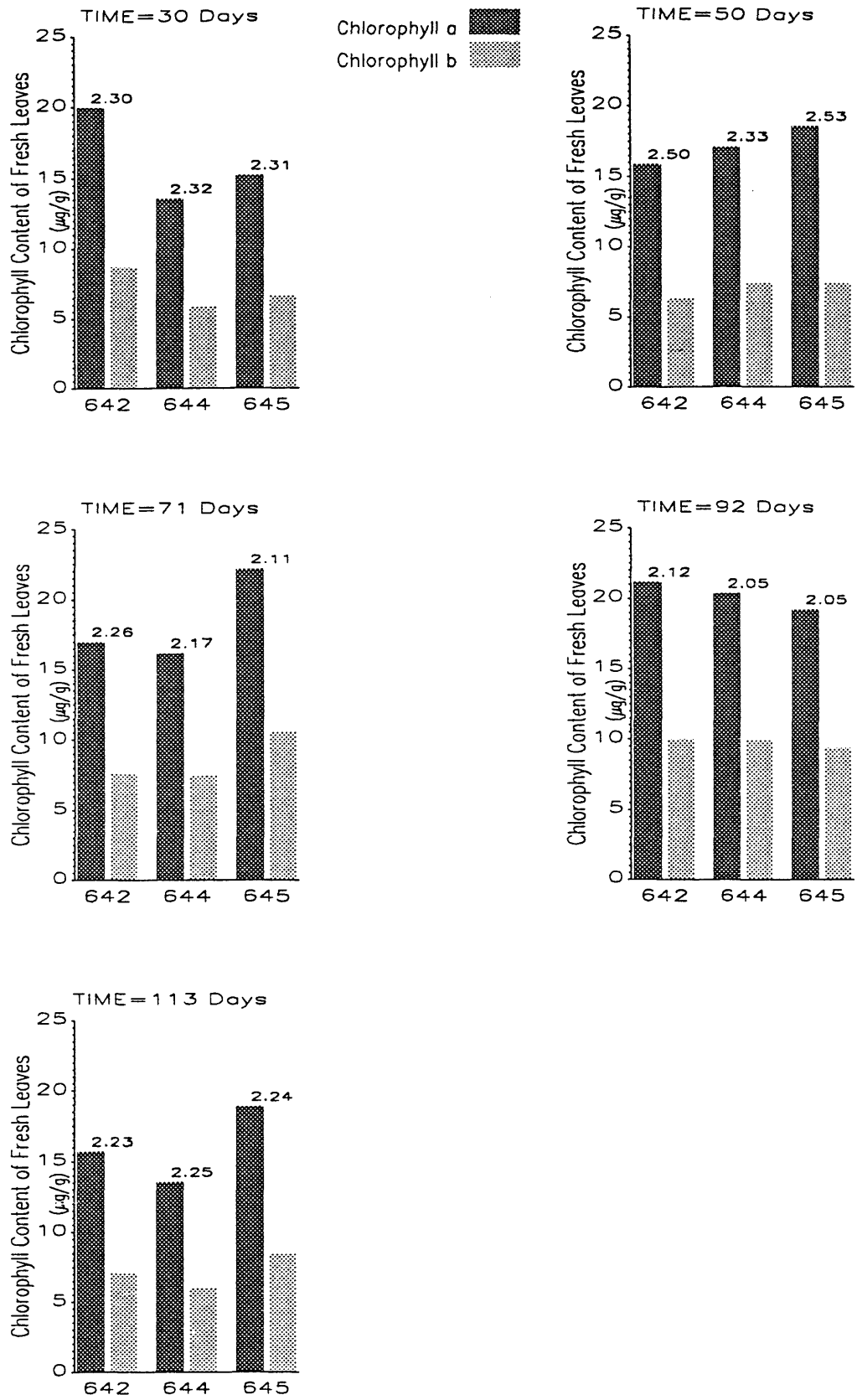


Fig. 4.6 : Chlorophyll a and b contents of fresh leaves and chlorophyll a:b ratios (figures above bars), of two determinate types, 645 and 642, and the indeterminate type, 644, determined at days 30, 50, 71, 92 and 113 from emergence, in autumn 1988.

and ratios of a:b declined faster in the indeterminate growth habit than in the determinate one.

The data presented in Fig. 4.5 determined in the summer of 1988 show more clearly the trends described above. In this case plants, especially those of the indeterminate growth habit, senesced earlier, i.e. at 70 days. Leaves of the determinate plants were still green 30 days later. It is also notable from a comparison of the data in Fig. 4.4 and 4.5 that plants grown in the summer had higher chlorophyll a:b ratios, but senesced faster than the autumn grown plants. The chlorophyll content for the determinate plants was initially higher than for the indeterminate plants, reaching a maximum at 30 days. The ratios of chlorophyll a:b had reached a maximum at 30 days and then declined gradually in the season.

In Fig. 4.6, chlorophyll content data determined in the Autumn of 1988 show that as in Figs. 4.4 and 4.5, there was a general increase in chlorophyll content with time, but the pattern was not as distinct as in the summer grown plants. While chlorophyll content remained higher as compared with Fig. 4.5, the chlorophyll a:b ratio was relatively low. There is some evidence here to show that autumn grown plants of the two growth habits remained greener longer with a more gradual decline in chlorophyll level but nevertheless showed lower chlorophyll a:b ratios.

These results therefore clearly show that in all cases the chlorophyll a content was higher than that of chlorophyll b. There was a marked increase of chlorophyll content of fresh leaves towards

an optimum depending on season and growth habit, followed by a decline towards senescence. Summer grown plants (Fig. 4.5) of both habits exhibited higher chlorophyll a:b ratios, as compared with the autumn grown plants, but these ratios declined with the age of leaves, irrespective of the season. The ratios of chlorophyll a:b observed for the summer grown plants is consistent with the value of 2.8:1 for C_3 plants reported by Black and Mayne (1973). The lower chlorophyll a:b ratios observed for autumn grown plants reflects the view of Ribinovitch and Govidjee (1969) and Reger and Krans (1970) that plants of a given species will have a greater chlorophyll a:b ratio if they are grown under high light intensities. Baker *et al*., (1983) working with determinate and indeterminate faba beans observed that the chlorophyll content of indeterminate plant leaves was higher initially but declined earlier than that of the determinate type. However, they also observed that the ratio of chlorophyll a:b was the same in both types. There was also an indication that leaves of the determinate plants retained chlorophyll at higher levels for a longer duration than leaves of indeterminate plants, and that leaves of the indeterminate plant abscised after 66 days while those of the determinate plants did not abscise until 40 days later.

These results clearly show that chlorophyll a:b ratios in both growth habits are similar and that the chlorophyll contents were not significantly different. Chlorophyll degradation was earlier in the indeterminate growth habit and chlorophyll a declined faster than chlorophyll b in both growth habits. The extended leaf area duration in the determinate growth habit may be advantageous if more podding nodes are achieved either on the mainstem or on the branches.

4.4 Leaf mesophyll anatomy

The results of cell counts in the palisade and spongy mesophyll layers, Table 4.5, show that the leaves of the indeterminate plant, 644, have a higher number of palisade mesophyll cells per unit area than those of determinate plants. The determinate type, 642, has a significantly lower number of palisade mesophyll cells ($P = 0.05$). On the other hand, type 645 showed the highest average number of spongy mesophyll cells, with type 642 giving the lowest counts.

Counts obtained from a 400 μm transect on scanning electron microscope (SEM) photographs are presented in Table 4.6. These results show that the indeterminate type, 644, had more palisade mesophyll cells while the determinate type, 645, had the lowest number. Types 645 and 644 gave the same number of spongy mesophyll cells which was higher than that of type 642. The average number of cells for the lower and upper epidermis was the same for both growth types.

The SEM photographs shown in Figs. 4.7, 4.8 and 4.9 for the transverse sections of leaves of both growth habits clearly show that the leaf mesophyll has the same basic structure. They show a single layer of palisade mesophyll and a spongy mesophyll with extensive air spaces. Observations during this study showed that leaves of the determinate plants are more succulent and thicker than the indeterminate ones. This view is illustrated in Figs. 4.10, 4.11 and

Plant type	Number of palisade mesophyll cells mm^{-2}	Number of spongy mesophyll cells mm^{-2}
645	128.65	480.45
	(5.41)	(11.93)
642	122.15	415.95
	(4.87)	(13.23)
644	133.85	430.85
	(4.42)	(14.11)
SE of means	1.85	7.55
LSD (0.05)	(6.15)	(11.85)

Table 4.5 : Number of palisade and spongy mesophyll cells in the leaves of the two determinate types 645 and 642 and the determinate type 644. (± SD)

Plant type	No. of palisade cells	No. of upper epidermis cells	No. of spongy mesophyll cells	No. of lower epidermis cells
645	14.40	14.80	15.40	14.80
	(0.55)	(0.84)	(0.89)	(1.30)
642	16.20	14.80	13.40	15.40
	(1.64)	(1.30)	(2.07)	(1.14)
644	19.20	14.80	14.80	15.60
	(1.30)	(0.45)	(1.92)	(1.14)
S.E. of means	1.59	0.36	0.73	0.36
LSD (0.05)	6.84	1.59	(3.14)	(1.57)

Table 4.6 : Number of cells in the spongy and palisade layers and the upper and lower epidermis, counted over a 400 µm transect on scanning electron microscope photos of the two determinate types, 645 and 642 and the indeterminate type, 644. (±SD)

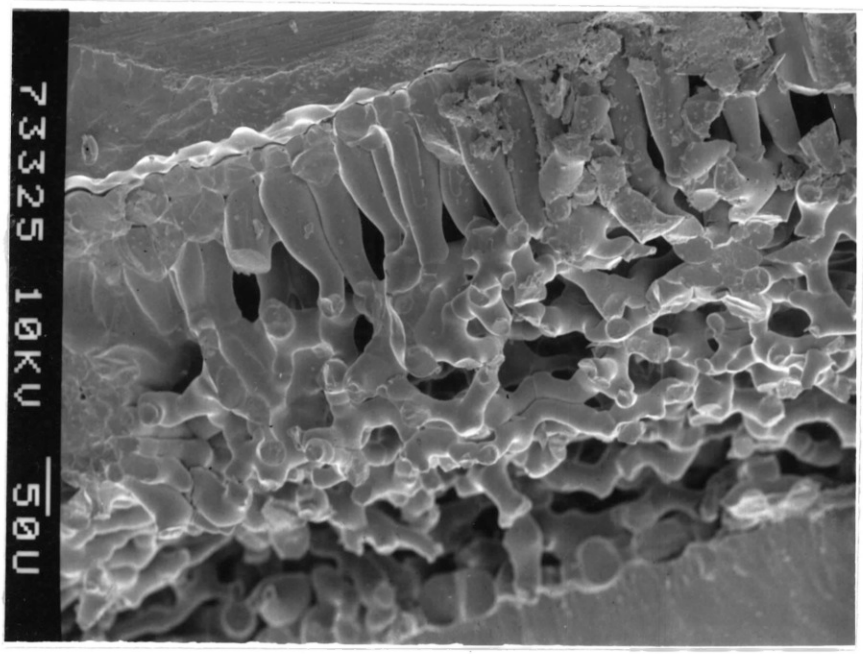


Fig. 4.7 : A scanning electron micrograph (x 300) of the transverse section of a leaf from the determinate type, 645.

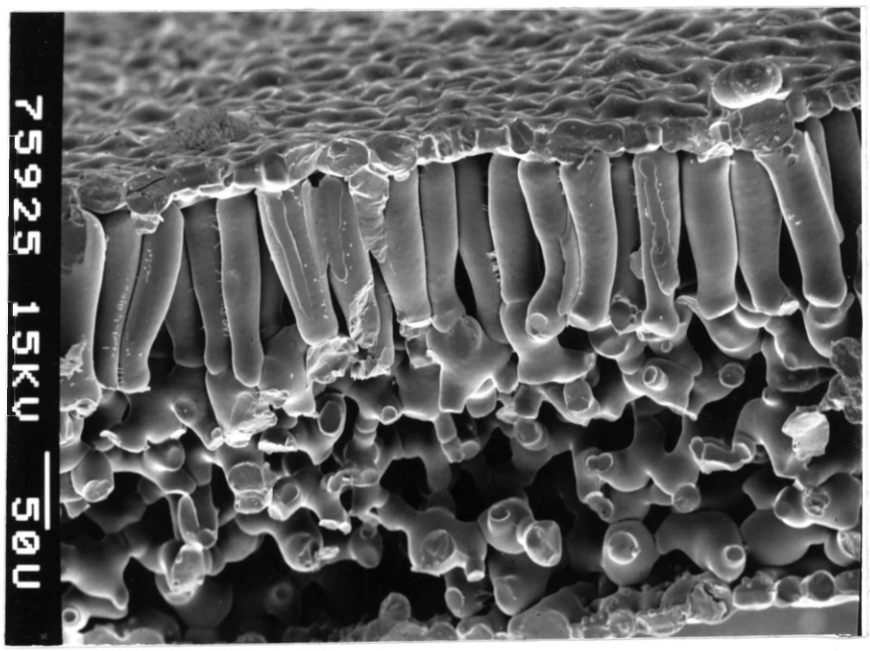


Fig. 4.8 : A scanning electron micrograph (x 300) of the transverse section of a leaf of the determinate type, 642.

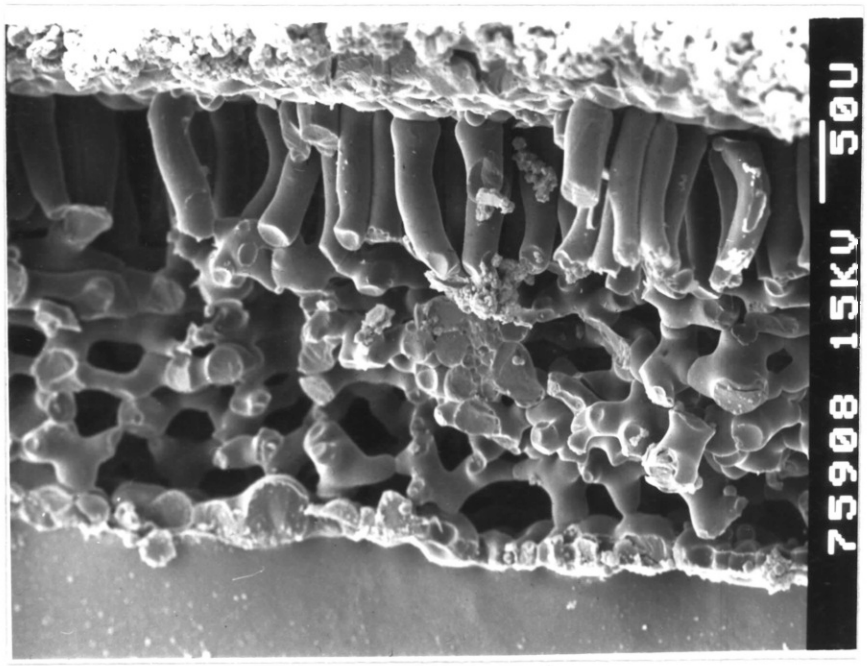


Fig. 4.9 : A scanning electron micrograph (x 300) of the transverse section of a leaf from the indeterminate type, 644.

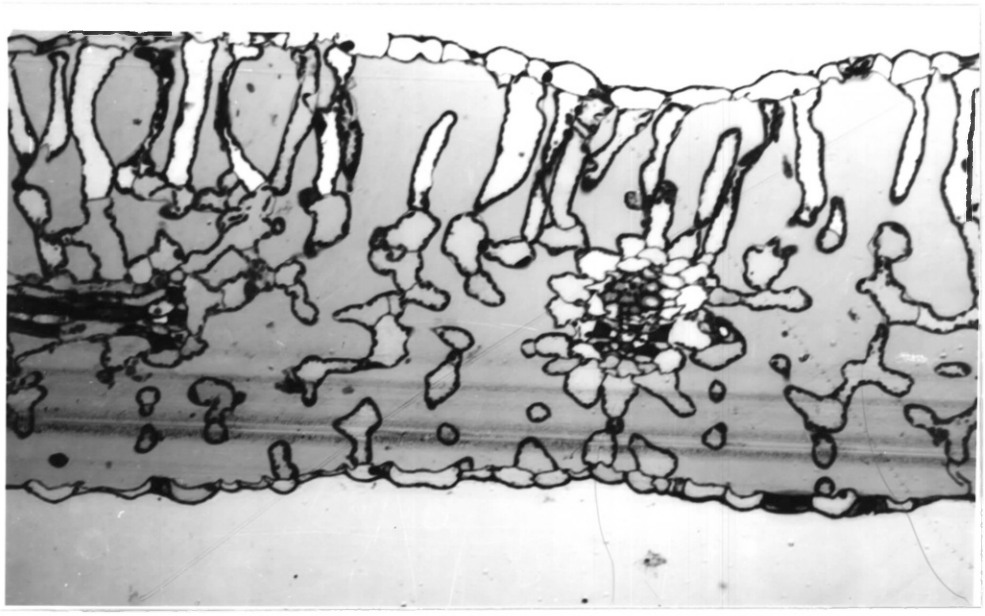


Fig. 4.10 : A light micrograph (x 400) obtained from a thin (2 μm) microtome transverse section of a leaf of the determinate type, 645.

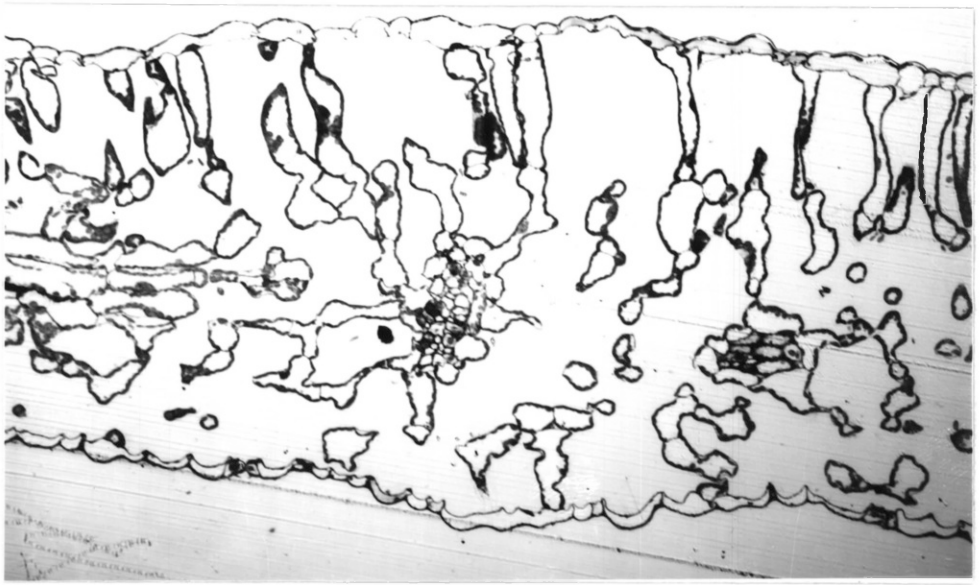


Fig. 4.11 : A light micrograph (x 400) obtained from a thin (2 µm) microtome transverse section of a leaf of the determinate type, 642.

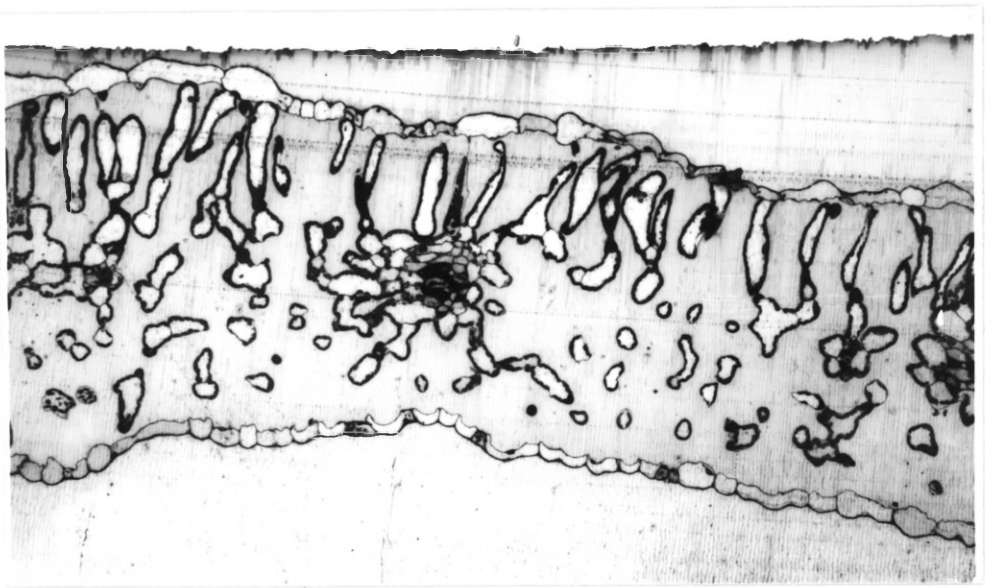


Fig. 4.12 : A light micrograph (x 400) obtained from a thin (2 µm) microtome transverse section of a leaf of the indeterminate type, 644.

4.12 which show light microscope transverse sections of both growth types. A comparison between these sections show some indication that leaves of the indeterminate plants are narrower (Fig. 4.12) However, this difference did not affect the basic leaf structure.

Therefore, the observations made in this study give some indication that the leaves of the indeterminate plants have more palisade mesophyll cells than those of the determinate plants. On the other hand, the determinate type, 645, has more spongy mesophyll cells than either type 644 or 642. The determinate type, 642, has the lowest number of spongy mesophyll cells, which suggests that it could possibly have a larger air space area. There is an indication from these results that leaves of the determinate plants have thicker leaves.

Leaf anatomy studies have been performed by a number of investigators on a variety of species to attempt to assess the role of specific anatomical characteristics in the determination of photosynthetic rates. Jellings and Leech (1983) working with five Triticum genotypes found no correlation between either the proportion of mesophyll cell surface exposed to airspace or the ratio of exposed mesophyll cell surface to leaf surface, and the photosynthetic capacity. Mesophyll cell surface area parameters have been found to correlate with photosynthetic rate in other species, i.e. in soybean leaves (Dornhoff and Shibbles, 1976) and *Plectranthus parviflora* (Nobel, Zaragoza and Smith, 1975). Mesophyll cell size has been considered to be an important factor in many species but the question of how photosynthetic rate is influenced by cell size has been more

difficult to assess (Jellings and Leech, 1983). Negative correlations have been found between mesophyll cell size and leaf photosynthetic rate in several species of monocotyledons and dicotyledons (El-Sharkaway and Hesketh, 1965), in ryegrass genotypes (Wilson and Cooper, 1967) and also between diploid, tetraploid and hexaploid wheat varieties (Dunstone and Evans, 1974; Austin *et al.*, 1982; Parker and Ford, 1982). On the other hand, Byne, Nelson and Randall (1981) when comparing polyploid species of tall fescue found the mesophyll volume and CO_2 exchange rate to be positively correlated.

CO_2 uptake data presented in Section 4.4 show some indication that the photosynthetic rates of the two growth types may not be different, as was observed by Baker *et al.*; (1983) working with faba beans of both growth types. The slight differences in net photosynthesis observed in this study may be the result of many internal and external factors, mesophyll anatomy being one of them, as discussed above. The lower number of spongy mesophyll cells in type 642, coupled with a wider transverse section, could have resulted in a more efficient diffusion of CO_2. However, Wilson and Cooper (1967) working with the grass *Lolium* observed that the rate of photosynthesis at saturating light intensities depended on the thickness of leaves and the size of the mesophyll cells. They also showed that photosynthesis per unit volume of mesophyll increases as total mesophyll cell surface increases, because the surface to volume ratio will increase as cell size decreases. Increase in photosynthetic rate with increasing cell surface area at high light intensities when CO_2 is limiting results from lowered mesophyll

resistance because an increased surface area will presumably promote transfer of CO_2 to reaction centres in chloroplasts. The number of mesophyll cells per unit surface area (N) and leaf thickness (T) interact to determine the rate of apparent photosynthesis per unit leaf area (Wilson and Cooper, 1972). As such, where two leaves have the same number of mesophyll cells per unit area but different thickness, the leaf with the greater thickness will have the greater photosynthetic rate in spite of a larger mean cell size. With the same thickness, the photosynthetic rate will be determined by cell size if all other factors are equal.

Outlaw *et al.*, (1975, 1976) have noted that the photosynthetic CO_2 fixation in the leaves of *Vicia faba* is similar in the different mesophyll tissues. The relative rates of photosynthesis in the palisade and spongy parenchyma were found to be dependent upon the intensity of the incident $\overset{\text{light}}{\}}$ (PAR). It was also noted that the differentiation of the mesophyll into palisade and palisade parenchyma does not reflect any significant qualitative difference in the photosynthetic carbon metabolism of the two layers; and that the quantitative differences in relative photosynthetic rates are due largely to a light intensity gradient through the leaf.

4.5 CO_2 uptake and transpiration

The infra-red gas analysis data presented in Tables 4.7 to 4.13 clearly indicate that the rates of photosynthesis, stomatal conductance and transpiration varied with the time of measurement, type of growth habit and stage of development of the plants (Kent,

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	16.01	250.0	4.72
	(0.72)	(17.33)	(0.18)
642	14.06	189.50	4.17
	(0.51)	(10.93)	(0.14)
644	16.98	261.45	5.27
	(0.46)	(12.45)	(0.18)
SE of means	0.47	12.23	0.03
LSD (0.05)	2.02	52.57	0.13

Table 4.7 : Mean rates of photosynthesis, stomatal conductance and transpiration for glasshouse-grown plants at the flowering and early pod formation stage measured in Spring 1988 (+ SE)

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	8.85	256.0	8.73
	(0.63)	(12.81)	(0.26)
642	10.96	307.13	9.45
	(0.60)	(14.42)	(0.22)
644	10.125	248.87	8.43
	(0.75)	(19.05)	(0.29)
SE of means	0.39	11.60	0.19
LSD (0.05)	1.68	49.89	0.82

Table 4.8 : Mean rates of photosynthesis, stomatal conductance and transpiration of glasshouse grown plants at the vegetative stage, measured in Spring 1988 (+ SE)

1972; Kassam, 1973). Crompton *et al.*, (1981), working with the indeterminate cultivar Maris Bead, found that the amount of $^{14}CO_2$ taken up by individual leaves at initial pod set, rapid pod-fill and when the lower pods were maturing did not differ significantly ($P = 0.05$), from the mean value for the plant. There was an indication that the same amount of radioactivity was taken up initially by each leaf regardless of its position on the stem and the presence of pods at a node.

At the vegetative stage, it was observed that photosynthetic rates were lower for glasshouse grown plants, than for field grown plants (Tables 4.8 and 4.12). The photosynthetic rates for types 642 and 644 were similar, with that of the former being slightly higher. Type 645 had the lowest rates. Observed rates of stomatal conductance and transpiration were lower in the field than for glasshouse grown plants. Overall, the determinate type, 642, was more effective in CO_2 fixation at this stage both in the field and under glasshouse conditions.

For plants at the flowering and early pod formation stage, the indeterminate type exhibited a higher rate of photosynthesis, stomatal conductance and transpiration (Table 4.7). These rates were higher than for the plants at the vegetative stage. It was also noted that the higher the photosynthetic rate, the higher were the rates of stomatal conductance and transpiration.

At the mid-pod filling stage, the two determinate types exhibited higher rates of photosynthesis but that of type 642 was

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	12.35	280.53	5.38
	(1.28)	(33.63)	(1.59)
642	10.42	177.27	5.01
	(0.76)	(19.88)	(0.33)
644	11.51	199.30	5.25
	(1.06)	(20.69)	(0.33)
SE of means	0.35	19.86	0.06
LSD (0.05)	1.52	85.39	0.29

Table 4.9 : Mean rates of photosynthesis, stomatal conductance and transpiration of glasshouse-grown plants at the mid pod filling stage, measured in Spring 1989 (+ SE)

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	10.84	267.53	6.96
	(0.85)	(29.95)	(0.42)
642	13.01	301.87	8.42
	(0.61)	(22.14)	(0.29
644	12.07	292.47	7.54
	(0.77)	(26.48)	(0.38)
SE of means	0.39	6.48	0.27
LSD (0.05)	1.71	27.86	1.15

Table 4.10 : Mean rates of photosynthesis, stomatal conductance and transpiration for glasshouse grown plants at the mid pod filling stage, measured in Summer 1989 (+ SE)

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	14.68	247.40	3.65
	(1.01)	(15.44)	(0.13)
642	15.19	218.25	3.25
	(1.41)	(19.43)	(0.15)
644	15.74	275.30	3.73
	(0.65)	(14.23)	(0.83)
SE of means	0.17	9.02	0.08
LSD (0.05)	0.72	38.79	0.35

Table 4.11 : Mean rates of photosynthesis, stomatal conductance and transpiration of field grown plants at the pod filling stage, measured in Summer 1989 (+ SE)

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	15.23	208.60	3.62
	(0.67)	(8.36)	(0.12)
642	15.71	205.95	3.27
	(0.29)	(11.99)	(0.10)
644	15.40	210.27	3.74
	(0.31)	(12.35)	(0.13)
SE of means	0.08	0.49	0.08
LSD (0.05)	0.33	2.09	0.33

Table 4.12 : Mean rates of photosynthesis, stomatal conductance and transpiration of field grown plants at the vegetative stage, measured in Spring 1989 (+ SE)

higher (Table 4.9). However, at the pod-filling stages, it was observed that photosynthetic rates were higher for glasshouse grown plants (Tables 4.10, 4.11 and 4.13). The determinate type, 642, exhibited higher rates of photosynthesis, stomatal conductance and transpiration for glasshouse grown plants. Type 645 had lower rates. In the field, type 644 exhibited the highest rate of the three factors, although not significantly different from that of type 642. Photosynthetic rates presented in Table 4.13 were the highest recorded for any time where type 645 had the highest rate of photosynthesis. Type 642 had a higher rate of stomatal conductance while type 645 exhibited the highest rate of transpiration. In Table 4.11 the higher rates of photosynthesis observed for type 644 could have resulted from the fact that it was still Producing young pods, creating a higher demand for photoassimilates than the determinate types whose pods were almost mature. Crompton *et al.*, (1981) observed in an indeterminate type, Maris Bead, that more $^{14}CO_2$ was translocated from the fed leaf to pods both on treated nodes and other nodes at initial pod fill than when the lower pods were maturing. This suggests that young pods are stronger sinks for assimilates and have an influence on leaf photosynthetic rates.

The rates of photosynthesis, stomatal conductance and transpiration observed in this study were slightly different in some cases but there was no unequivocal evidence to suggest that either of the two growth habits was more efficient in CO_2 assimilation. These views agree with those of Baker *et al.*, (1984) who noted that the photosynthetic rates of detached leaves of two determinates (Wye 19280/1 and 19260/19) were not different from that of the

Type	Photosynthesis μMol CO_2 m^{-2} s^{-1}	Stomatal conductance mMol m^{-2} s^{-1} volume flow	Transpiration mMol H_2O m^{-2} s^{-1}
645	18.14	391.90	7.04
	(0.33)	(10.34)	(0.07)
642	18.09	416.20	7.00
	(0.31)	(24.36)	(0.09)
644	17.89	375.60	6.98
	(0.34)	(15.48)	(0.07)
SE of means	0.04	6.46	0.01
LSD (0.05)	0.17	27.78	0.04

Table 4.13 : Mean rates of photosynthesis, stomatal conductance and transpiration of field grown plants at the pod filling stage, measured in Summer 1989 (+ SE)

indeterminate cultivar Maris Bead. Thus, both growth types are similar in the production of dry matter and their differences in the production of yield may lie in their efficiency to produce yield components (Austin *et al*., 1981).

4.6 Yield and yield components

Yield and yield component data for glasshouse grown plants are presented in Tables 4.14, 4.15 and 4.17. The determinate type 642 had slightly higher values for these data (Table 4.14). However, its harvest index was lower, mainly due to its higher shoot dry matter resulting from the greater number of less productive branches. For the data presented in Tables 4.15 and 4.17, the indeterminate type gave higher values of the measured yield components. The yields of the two determinates were not different and their average single grain weight was higher as compared to the indeterminate type. Type 645 tended to have a higher harvest index for the glasshouse grown plants. Overall, the indeterminate growth habit had more seed weight per plant, mainly because it had more podding nodes than the determinate types and also due to the fact that most branches in the determinate plants, particularly type 642, were less fertile.

Data are presented in Tables 4.16 and 4.18 for field grown plants from the summers of 1988 and 1989, respectively. The indeterminate type had higher values of all yield components, as compared to the determinate types, although these differences were not statistically significant (Lsd 0.05). The two determinate types were similar in their plant yield. As in the glasshouse grown

Plant type	Average number of pods per plant	Average number of seeds per plant	Average number of seeds per pod	Total seed weight per plant (g)	Average shoot dry weight (g)	Total plant dry matter (g)	Harvest index	Average seed weight per seed (g)
642	9.60	26.66	2.60	10.15	16.02	26.17	0.38	0.42
	(2.09)	(6.88)	(0.50)	(3.43)	(3.56)	(5.09)	(0.09)	(0.09)
644	8.10	23.70	2.90	8.90	11.25	22.76	0.41	0.38
	(2.70)	(8.40)	(0.46)	(2.71)	(2.35)	(9.59)	(0.07)	(0.05)
SE of means	0.39	0.77	0.13	0.32	0.95	0.88	0.01	0.01
LSD (0.05)	(1.73)	3.22	0.61	0.40	4.10	3.80	0.03	0.04

Table 4.14 : Yield data for the determinate type 642, and the indeterminate type 644, grown in the glasshouse in summer 1987 (± SD). n = 15 plants

The determinate type 645 was unavailable at the time these measurements were done.

Plant type	Average number of pods per plant	Average number of seeds per plant	Average number of seeds per pod	Total seed weight per plant (g)	Average shoot dry weight (g)	Total plant dry matter	Harvest index	Average seed weight (per seed) (g)
645	10.75	25.83	2.33	14.24	30.92	*ND	0.47	0.57
	(4.45)	(9.65)	(0.49)	(4.85)	(8.19)		(0.07)	(0.17)
642	8.92	20.75	2.33	10.31	30.89	ND	0.33	0.59
	(5.14)	(13.07)	(0.49)	(5.37)	(9.21)		(0.09)	(0.28)
644	13.33	30.16	2.25	16.05	33.68	ND	0.44	0.50
	(2.53)	(7.88)	(0.45)	(4.09)	(9.23)		(0.06)	(0.09)
SE of means	0.82	2.00	-	1.43	0.65	ND	0.03	0.02
LSD 0.05	3.51	8.60	-	6.17	2.81		0.13	0.08

Table 4.15 : Yield data for the two determinate types, 645 and 642, and the indeterminate type, 644, grown in the glasshouse in the summer of 1988. (± SD). n = 12 plants

* not determined

Plant type	Average number of pods per plant	Average number of seeds per plant	Average number of seeds per pod	Total seed weight per plant (g)	Average shoot dry weight (g)	Total plant dry matter	Harvest index	Average seed weight (per seed) (g)
645	10.05	25.25	2.29	11.67	*ND	ND	ND	0.40
	(4.05)	(9.17)	(0.55)	(5.20)				(0.09)
642	12.50	30.50	2.58	13.44	ND	ND	ND	0.43
	(4.28)	(10.85)	(0.50)	(6.26)				(0.08)
644	16.33	42.04	2.62	16.31	ND	ND	ND	0.39
	(5.07)	(14.02)	(0.57)	(5.81)				(0.07)
SE of means	0.76	2.64	0.11	0.67	ND	ND	ND	0.06
LSD (0.05)	3.28	11.37	0.50	2.91				0.02

Table 4.16 : Yield data for the two determinate types 645 and 642 and the indeterminate type 644, grown in the glasshouse in summer 1989. (± SD) n = 24 plants

* ND - not determined

Plant type	Average number of pods per plant	Average number of seeds per plant	Average number of seeds per pod	Total seed weight per plant (g)	Average shoot dry weight (g)	Total plant dry matter	Harvest index	Average see weight (per seed) (g)
645	27.00	77.00	2.89	33.15	*ND	ND	ND	0.43
	(9.42)	(30.01)	(0.60)	(12.73)				(0.05)
642	27.62	78.12	2.75	30.57	ND	ND	ND	0.37
	(10.94)	(36.24)	(0.71)	(19.16)				(0.06)
644	49.55	156.22	0.30	65.65	ND	ND	ND	0.41
	(22.49)	(73.05)	(0.50)	(32.89)				(0.06)
SE of means	5.55	20.27	0.05	8.74	ND	ND	ND	0.01
LSD (0.05)	23.90	87.16	0.24	37.59				0.05

Table 4.17 : Yield data for the two determinate types, 645 and 642 and the indeterminate type, 644, grown in the field in summer 1988 (± SD) n = 10 plants

* Not determined

Plant type	Average number of pods per plant	Average number of seeds per plant	Average number of seeds per pod	Total seed weight per plant (g)	Average shoot dry weight (g)	Total plant dry matter	Harvest index	Average seed weight (per seed) (g)
645	47.60	147.30	3.10	135.03	*ND	ND	ND	0.97
	(18.28)	(52.72)	(0.57)	(24.56)				(0.20)
642	46.80	135.70	2.90	120.08	ND	ND	ND	0.89
	(9.68)	(24.41)	(0.57)	(13.50)				(0.11)
644	86.90	282.30	3.10	163.74	ND	ND	ND	0.62
	(29.60)	(101.50)	(0.32)	(28.50)				(0.16)
SE of means	10.25	36.45	0.02	9.92	ND	ND	ND	0.08
LSD (0.05)	4.41	156.72	0.11	42.70				0.35

Table 4.18 : Yield data for the two determinate types, 645 and 642 and the indeterminate type, 644, grown in the field in summer 1989 (± SD). n = 10 plants.

* ND - not determined

plants, the average single grain weights were higher for the determinate plants.

These results clearly indicate that plants of both growth habits yield more in the field than under glasshouse conditions. Except for the data presented in Table 4.14, the indeterminate plant had higher values in most of the yield components measured, although the differences were not significant. Apart from the number of seeds per pod, values obtained for most yield components varied between plant type and within seasons. Kambal (1969a) working with indeterminate field beans noted that the primary components of yield in this crop are number of pods per plant, number of seeds per pod and seed size. The primary components are themselves influenced by a number of secondary components, such as the first flowering node, first podding node, number of nodes, plant height and number of branches.

The results emerging from this study may be viewed as only representative of actual field data under optimum plant density and other agronomic specifications (Ishag, 1973; Igram, 1976; Pandey, 1981; Poulin, 1984). Ishag (1984) observed that yield in indeterminate field beans was closely correlated with the number of pods per plant. In the same study, doubling of plant population from 30-58 plants m^{-2} increased yield by 30%.

Results presented here show that there are fundamental differences in yield components of the two growth habits. The determinate type has a limited number of podding nodes and the higher

number of branches associated with it tend to be less fertile. However, this fact is ameliorated by its inherent benefits, i.e. early flowering, shorter life cycle and a shorter plant, less prone to lodging. Baker *et al*. (1984) noted that the greater yield of the indeterminate plant type on an individual plant basis merely reflects the greater size, the determinate type being one quarter in size and producing one quarter the amount of seed of the indeterminate type. In this study, yields of determinate plants were 50.5 and 46.5% for 1988 and 70 and 82% in 1989 for type 645 and 642, respectively, as compared to the indeterminate one. Austin *et al*., 1981) observed that a determinate genotype (Topless) in irrigated and non-irrigated studies gave yields of 89% as compared to the indeterminate type Maris Bead. The yield of the dry matter in Topless depended on the production of tillers and axillary branches, many of which did not bear grain and were sinks for assimilates during grain filling.

Allowing for between plant and seasonal variation, it is apparent that the determinate growth habit is not inherently inferior in yield production, and if more podding nodes were incorporated and more branches were fertile, this neotenous plant type would offer a more reliable option in terms of yield production and performance (Chapman and Peat, 1979; Austin *et al*., 1981; Baker *et al*., 1983).

4.7 ^{14}C-Photoassimilate partitioning

The pattern of ^{14}C-photoassimilate partitioning and the related specific activities is presented in Figures 4.13 to 4.18. These results clearly indicate that the pattern of distribution of the ^{14}C-photoassimilates varied with the plant growth habit and the stage of development. However, the general pattern of partitioning was basically similar in that the most actively growing organs not only imported more ^{14}C-assimilates but also exhibited higher specific activities per unit of dry matter.

At the vegetative stage, Figs. 4.13 and 4.14, the bulk of ^{14}C-photoassimilates was exported to the roots, stem and the shoot apex. For the data presented in Fig. 4.13, for plants treated in the summer of 1988, it were observed that the two determinate growth types exhibited a similar pattern in distribution. The roots, stem and the shoot apex were the major sinks for assimilates. The branches in the determinate variety, 642, received more assimilates than those of type 645. On the other hand, the distribution in the indeterminate type was similar to that of the determinate types. In the data presented in Fig. 4.13, for the summer of 1989, again the pattern of assimilate distribution of the two growth habits was similar as most of the assimilates were exported to the roots, stem and the shoot apex. The roots in the indeterminate type were observed to be particularly strong sinks at the time of feeding. There was an indication, especially in Figs. 4.13 and 4.14a that younger leaves attracted more ^{14}C-photoassimilates than older ones. Rapidly growing organs, i.e. shoot apex, roots and the stem had higher specific activities per

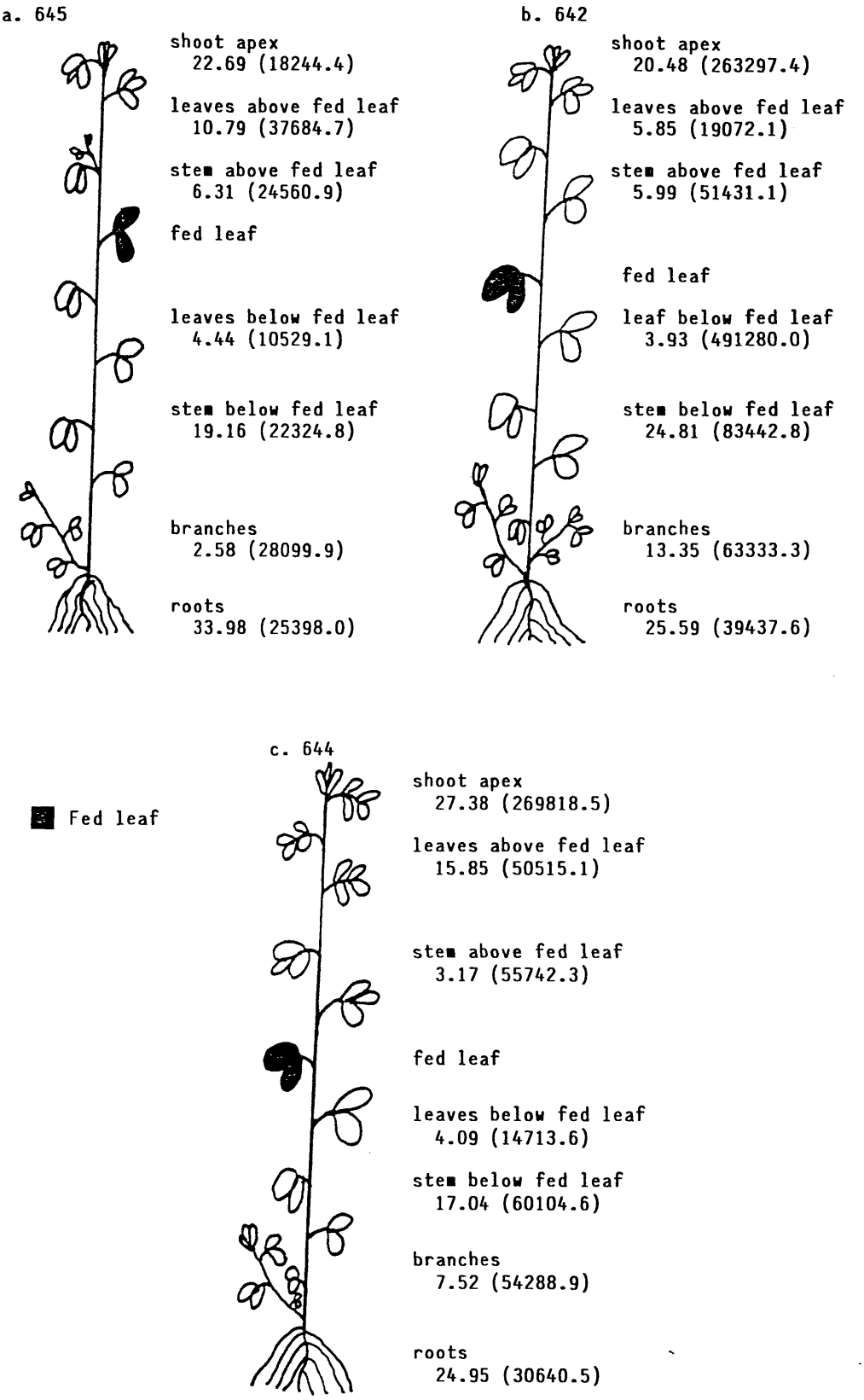


Figure 4.13: The % distribution of translocated ^{14}C-photoassimilates and the activities min^{-1} g^{-1} dry matter, for the two determinate growth habits, 645 (a) and 642 (b) and the indeterminate type 644 (c) at the vegetative stage in summer 1988. Values in parenthesis are the activities. Values are means of 3 replicates.

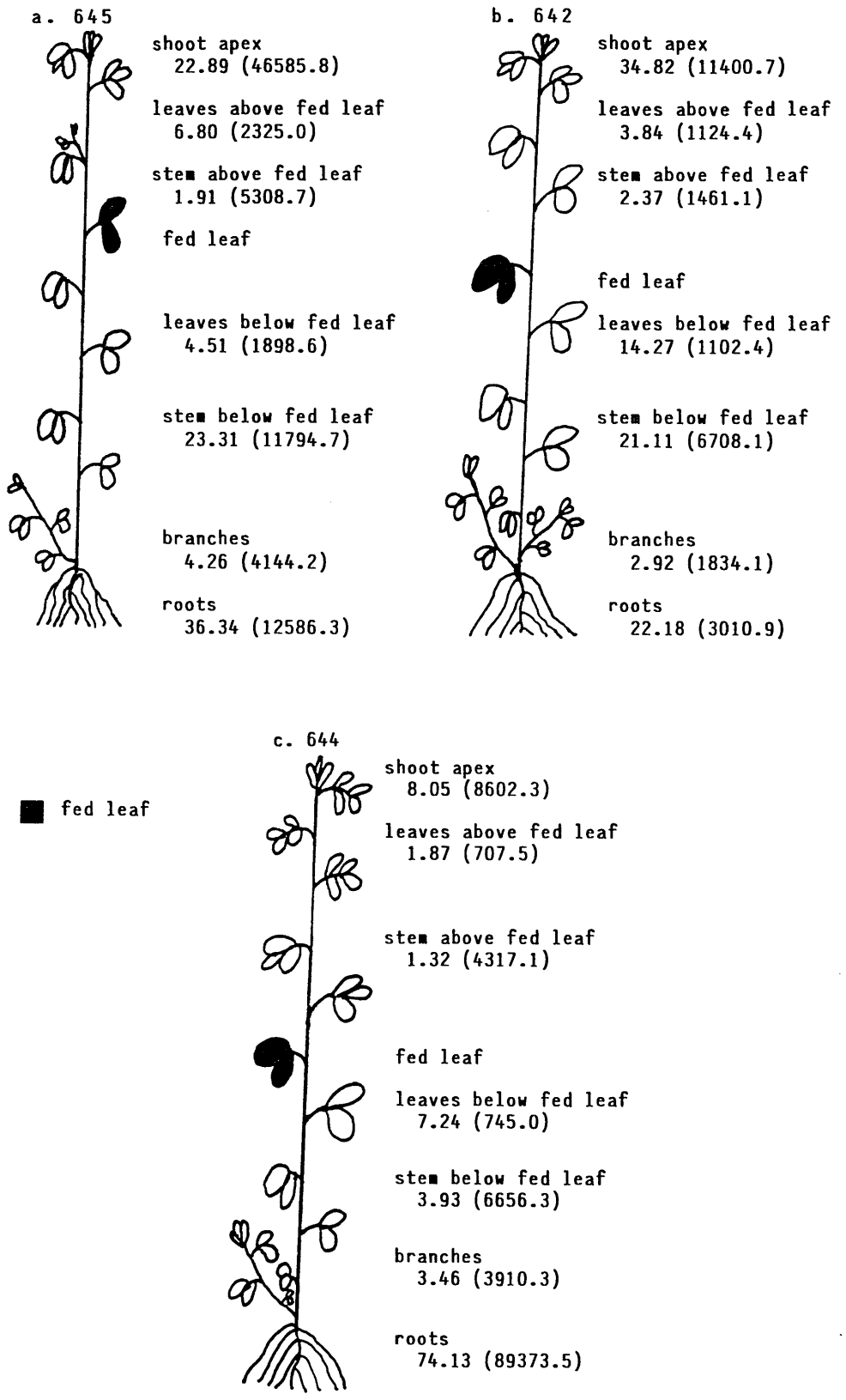


Figure 4.14 : The % distribution of translocated ^{14}C-photoassimilates and the activities in counts min^{-1} g^{-1} of dry matter (in parenthesis) for the two determinate growth types, 645 (a), 642 (b) and the indeterminate type 644 (c) at the vegetative stage in summer 1989. Values are means of three replicates.

unit of dry matter (for organ dry weights, see Appendices 1-6). The relatively higher activity that was observed in the stem than in several other organs may be an indication that some storage was taking place.

Crompton *et al.* (1981) working with the indeterminate cultivar, Maris Bead, noted that the direction in which assimilates moved varied with the stage of development of the plants. It was observed that at pod set, i.e. at the vegetative and the flowering stages, most of ^{14}C-assimilates were exported downwards from the expanded leaves to the lower stem and roots with little going to the growing shoot. These results are to some extent divergent from the results presented here, especially with reference to the amount going to the shoot apex which was found to not only import quite a considerable percentage of ^{14}C-photoassimilates but also had, in most cases, higher specific activity. The results presented in this study are consistent with those of Belikov (1973) in vegetative soybean plants in which lower leaves exported assimilates to the roots, mid-stem leaves to the roots and shoot apex while upper leaves capable of exporting assimilates were entirely under the influence of the shoot apex. Hume and Criswell (1973) also working with soybeans observed that at the vegetative stage, ^{14}C-photoassimilates were incorporated into structural leaf and stem tissues. In young corn plants, 3 to 6 weeks old, the bulk of assimilates was exported mainly to the roots after 24 hours and young expanding leaves retained most of the label (Hofstra and Nelson, 1969).

The relatively high percentages of ^{14}C-assimilates observed in

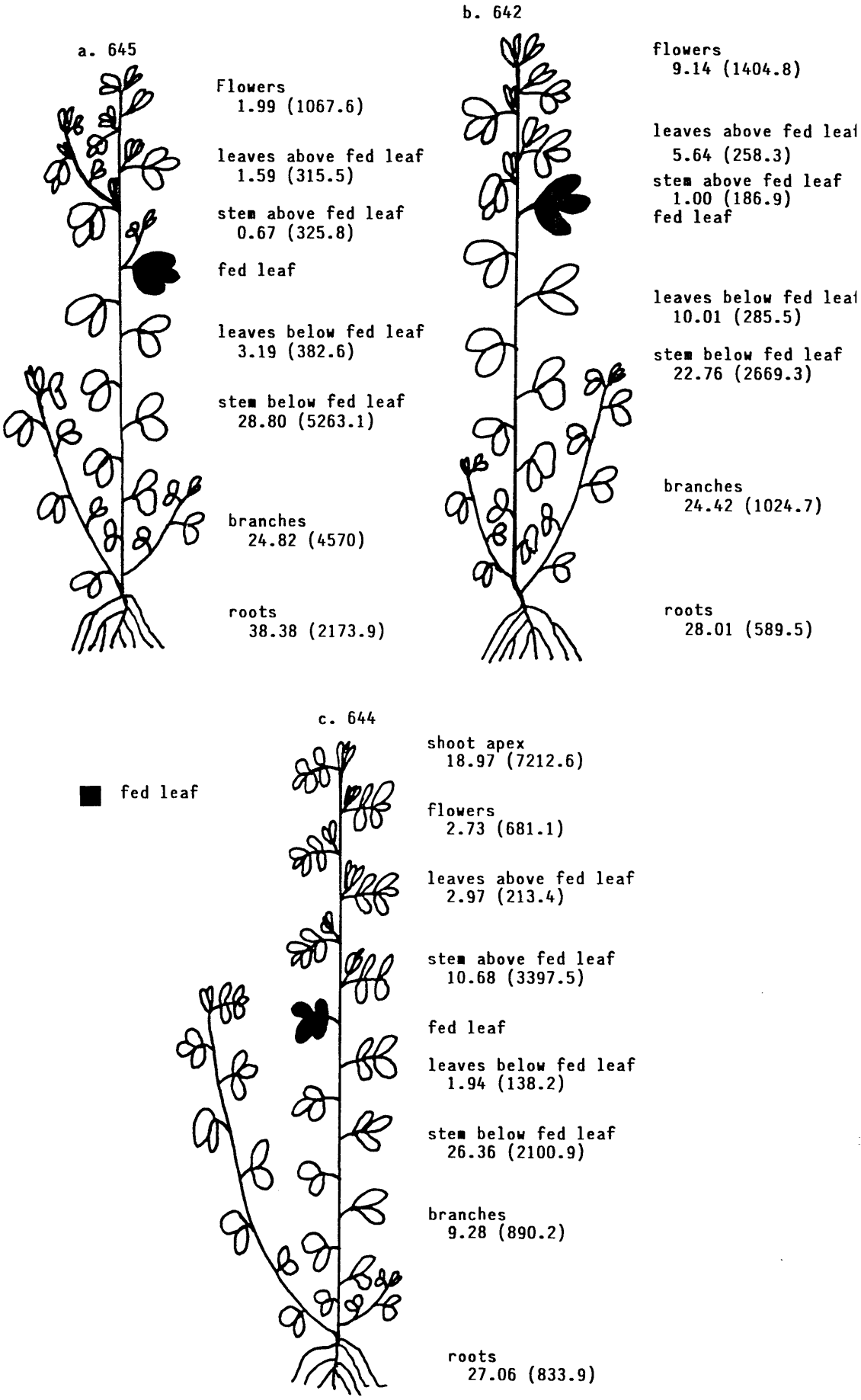


Figure 4.15: The % distribution of translocated ^{14}C-photoassimilates and the activities in counts min^{-1} g^{-1} of dry matter (in parenthesis) for the two determinate growth types 645 (a) and 642 (b) and the indeterminate type 644 (c) at the flowering stage. Values are means of 3 replicates.

the stem, particularly the stem below the fed leaf, may reflect that some storage was taking place. Ishag (1973) noted that the loss in dry matter of an indeterminate growth type was associated with increased dry weight of seed, and that the slow growth rate of the stem at pod filling indicated that dry matter was translocated from the stem to seeds or, as Allison and Watson (1967) observed in maize, more dry matter was lost from the stem by respiration than could be replaced, because assimilates were preferentially diverted to the grain. That the stem might be the site of storage and remobilisation is indicated by the work of Peel and Weatherly (1962) who showed that with the change from light to dark, the source of sugar for phloem translocation in Salix species changed from the leaf to the stem tissue which indicates that the stem has an important role in the carbon economy of the plant.

The pattern of ^{14}C-photoassimilate partitioning at the flowering stage reveals that it was dependent on the growth habit (Fig. 4.15). This difference is due to the fact that the shoot apex of the determinate plants was now reproductive and hence most of the assimilates were exported to the roots, stem and branches, unlike in the indeterminate growth habit where the shoot apex remained vegetative. The low percentage of assimilates exported to the flowers is an indication that they are weak sinks which could have significant implication for the pod set, and hence the often observed flower abscision in this crop (Kambal, 1969b; Bond and Toybee-Clarke, 1976; Jacquirey and Keller, 1980; Gates, Smith, White and Boulter, 1983). Tillers and axillary branches were now growing vigorously and received more assimilates, especially in the determinate plants.

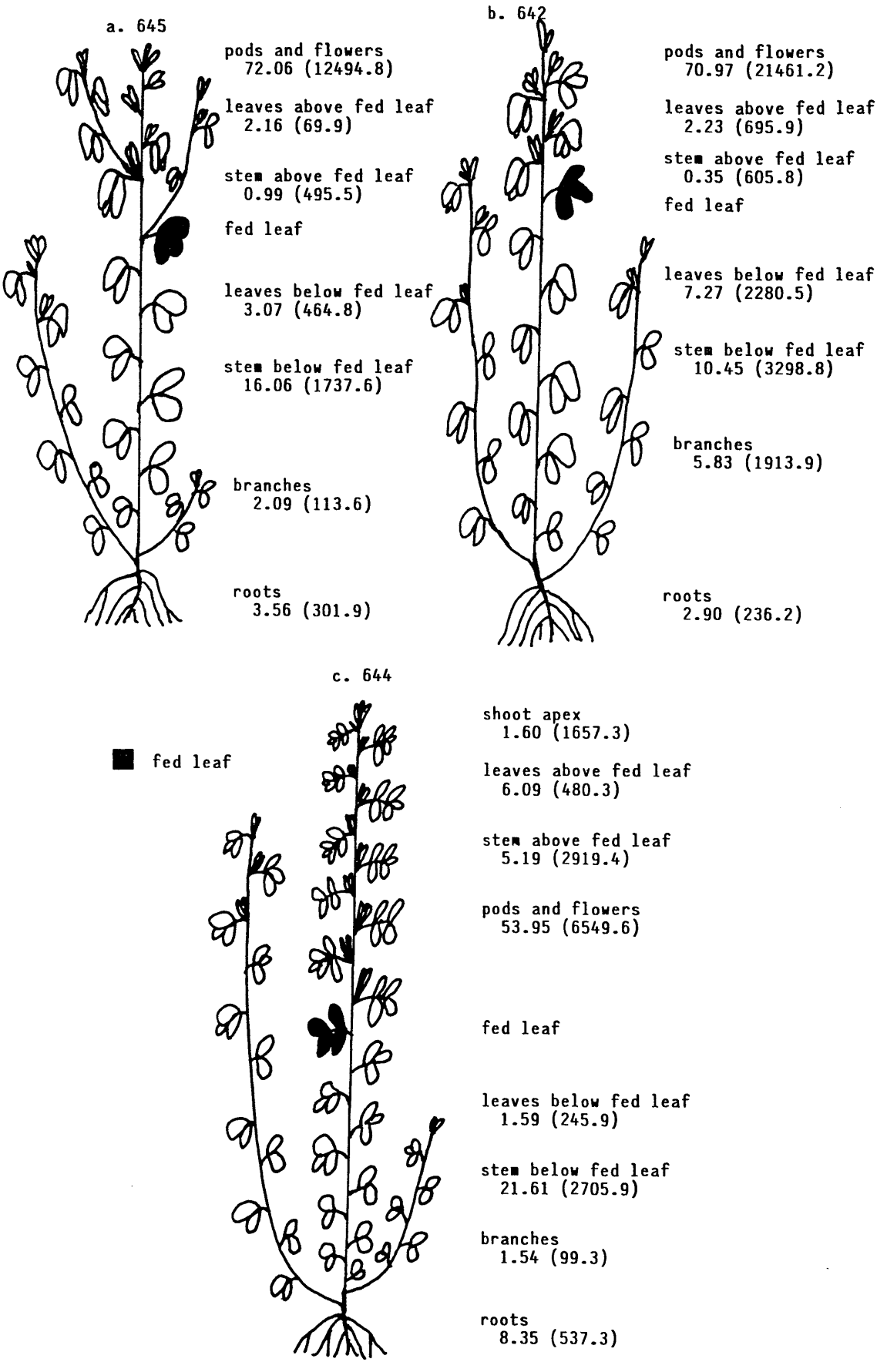


Figure 4.16 : The % distribution of translocated ^{14}C-photoassimilates and the activities min^{-1} g^{-1} of dry matter (in parenthesis) for the two determinate growth habits 645 (a) and 642 (b) and the indeterminate type 644 (c) at the flowering and early pod growth stage in summer 1988. Values are means of 3 replicates.

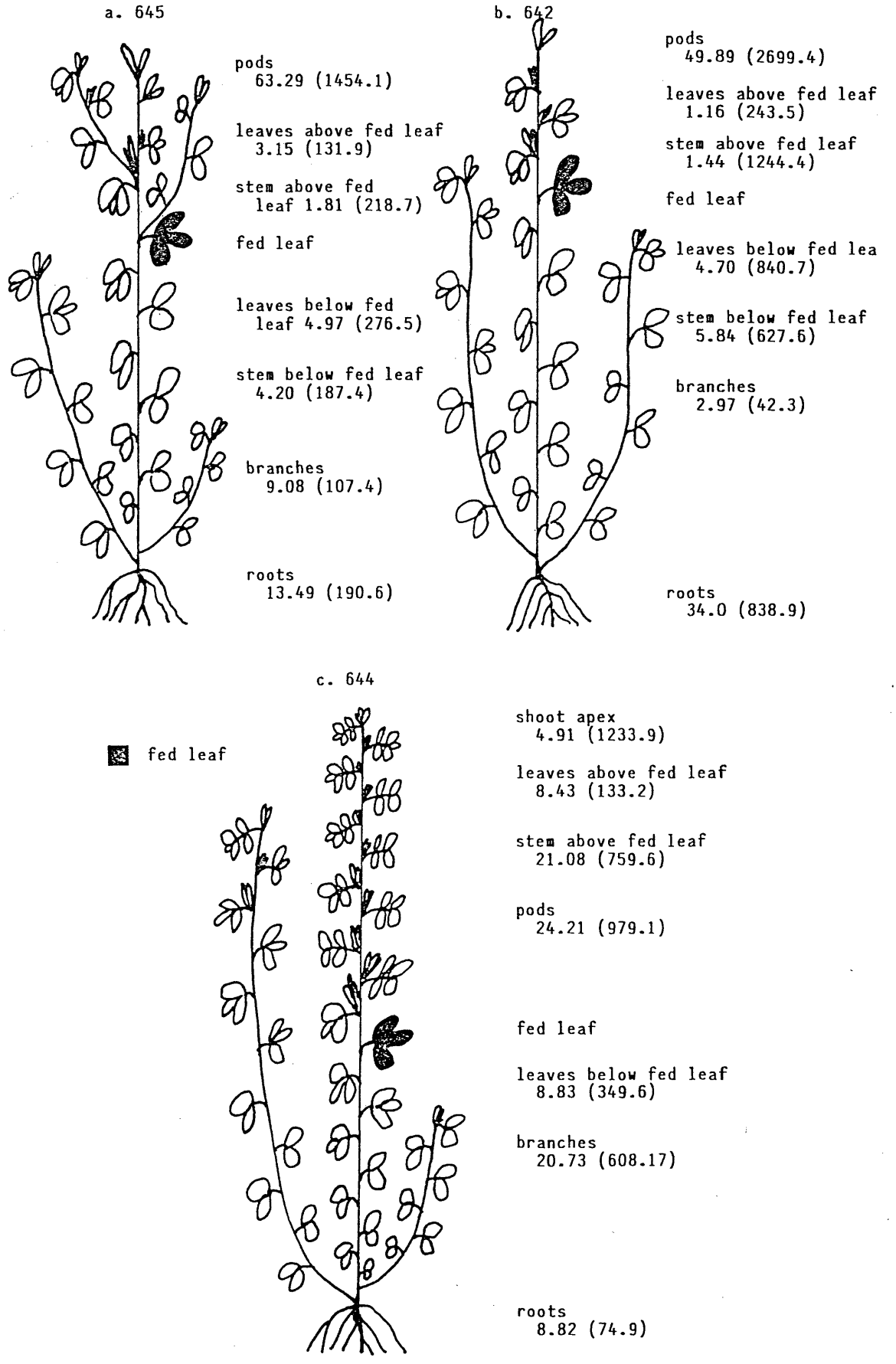


Figure 4.17: The % distribution of translocated ^{14}C-photoassimilates and the activities min^{-1} g^{-1} of dry matter (in parenthesis) for the two determinate growth types 645 (a) and 642 (b), and the indeterminate type 644 (c) at the mid-pod filling stage in summer 1989. Values are means of 3 replicates.

This observation concurs with that of Baker *et al*. (1983) in which they noted that in the determinate plant, the tillers and branches on the main stem behave in a similar fashion to the indeterminate apical growth in that they are both sources of sinks for assimilates to and from the main stem. On the other hand, most of the ^{14}C-assimilates in the indeterminate plant were exported to the stem, roots and shoot apex. For the determinate plants, the stem below the fed leaf had the highest specific activity while the shoot apex had more activity in the determinate plant. Although flowers received less assimilates, their specific activity indicates that they were more active than some sinks, especially in the determinate growth habit.

At flowering and early pod growth, figure 4.16a, b and c, the reproductive organs (pods and flowers) were the main sinks for ^{14}C-photoassimilates. Clearly, the emphasis on assimilate demand had shifted to the pods and now less was exported to the roots, stem and shoot apex. In the determinate types, over 70 and 50% of assimilates were exported to the reproductive organs in the determinate and the indeterminate types, respectively. More assimilates were found in the stem of the determinate types, while diminishing amounts were exported to the other organs. Specific activity counts show that the pods were the most active sinks in both growth habits, followed by the stem. The branches for determinate plants had more specific activity. Overall, there was a general decrease of assimilate export to other organs in favour of the growing pods.

For data presented in Fig. 4.17 for plants at the mid-pod filling stage, it was observed that pods were the major sinks. More

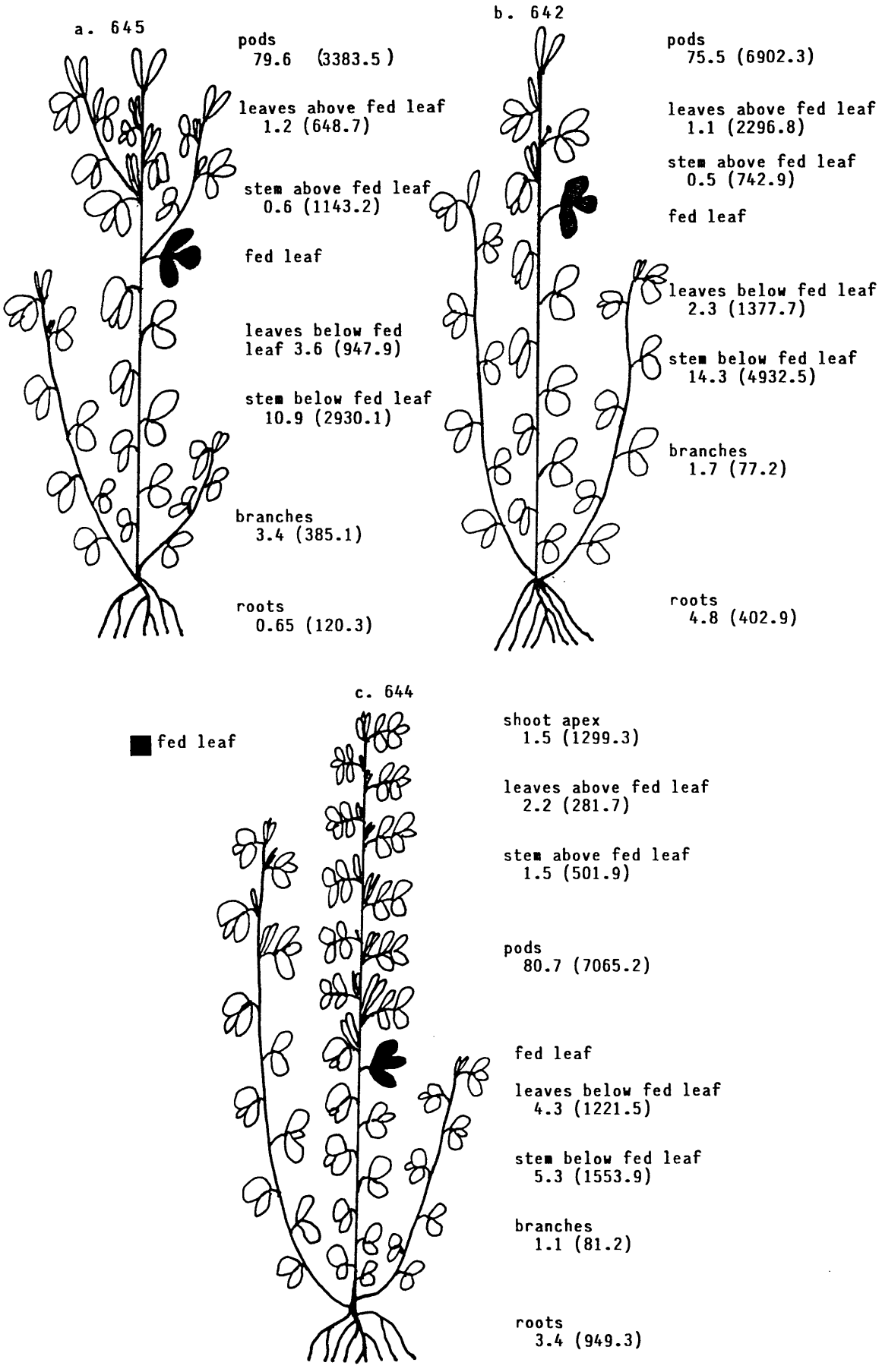


Figure 4.18 : The % distribution of translocated ^{14}C-photoassimilates and the activities min^{-1} g^{-1} of dry matter (in parenthesis) for the two determinate growth types 645 (a) and 642 (b) and the indeterminate type 644 at the late -pod filling stage in summer 1988. Values are means of 3 replicates.

assimilates were exported to the pods in the determinate plants than the indeterminate ones. This reflects the fact that determinate plants set pods earlier. Overall, the stem received more assimilates in the indeterminate plants, while roots were stronger sinks in the determinate growth habit. These observations agree with those of Crompton *et al*. (1981), who noted that at pod fill much of carbon from the lower and mid-stem leaves moved into the pods in the indeterminate type. At young pod development, Baker *et al*. (1981) noted that 6.26, 64.4 and 62.6% of translocated ^{14}C-photoassimilates were exported to pods when plants were fed at 1st, 2nd and 3rd flowering nodes, while in the indeterminate plants the pods received 64.9, 66.6 and 50.7% respectively. The pods and the shoot apex had more specific activity than the other organs in the determinate and the indeterminate plants respectively. The difference is most probably due to the fact that the determinate plant set pods earlier than the indeterminate one.

At the late pod filling stage, Fig. 4.18, it was observed that over 75% of the ^{14}C-assimilates were exported to the stem in both growth types. As expected, the pods had the highest specific activity, followed by the stem and leaves. The stem, apart from receiving an appreciable percentage of ^{14}C-assimilates, also gave relatively higher activity than other organs.

The results presented here therefore clearly indicate that the distribution pattern of ^{14}C-photoassimilates changed with the stage of development, type of growth habit and even the time of feeding, depending on the prevailing environmental conditions (Austin *et al*.,

1981). The general pattern of distribution of assimilates for both growth types was similar at the vegetative stage but as the shoot apex of the determinate plants became reproductive at flowering, the subsequent pattern of assimilate distribution was different from that of the indeterminate plant. At the reproductive stages the pods were the major sinks for assimilates. In all stages of development considered in this study neither of growth habits was observed to be unequivocally more efficient in the uptake and distribution of photoassimilates.

The activities in the fed leaf (see Appendix 7) after 6 h were higher than in the other organs. Crompton *et al*. (1981) observed that the amount of radioactivity moving out of a source leaf at a fruiting node increased over successive samplings up to 48h; the pattern of distribution however remained unchanged.

SECTION 6 : GENERAL DISCUSSION

This study was instituted with the important objective of appraising the relative advantages and disadvantages of two *Vicia faba* growth habits, with reference to photosynthesis and photoassimilate partitioning. Chapman and Peat (1978, 1979) have enumerated the phenotypic advantages which accrue to a determinate habit compared with an indeterminate one. The results presented here provide some physiological quantification of the relative performance and effectiveness of the two forms to utilise growth resources under similar conditions.

As Baker *et al.*,(1983) have pointed out, the development of a neotenous determinate field bean offers the potential for a protein yielding break crop which could readily fit into modern, cereal-dominated agricultural systems. However, there is still ground to be covered, particularly when we consider that this new type is still under improvement programmes. A feature requiring urgent attention is the tendency of the determinate type to develop infertile branches on the main stem which results in reduced plant yields. This is aggravated by the fact that the main stem has only 4 to 6 podding nodes (Sjodin, 1971). Gates *et al.*,(1983) have pointed out that although the determinate type offers a promising alternative for achieving yield stability, the concomitant loss of photosynthetic leaf area has resulted in lower potential yield than in the indeterminate one. However, the patterns of leaf area development observed in this study for both types were similar, although that of the determinate plants was initially more rapid. Austin *et al.*,

(1981) observed the same trend, and also noted that the pattern of leaf area and dry matter increase was similar for both growth types. Possibly, the lower plant yields observed for the determinate growth habit are mainly due to the lower number of pods per plant as compared with the indeterminate type. Is it possible then that the determinate type is sink limited? The fact that the plant has fewer podding nodes compared with the presence of infertile tillers leads us to believe that the photosynthetic capacity of the leaf area (source) may not be fully utilised. Moreover, it was observed that leaf area duration was longer in the determinate type and with the limited sink capacity this may well have encouraged the late growth of tillers. In fact, the tillers acted in the same way as the indeterminate growth habit but without sinks (pods) to provide economic benefit from the imported assimilates. As Chapman and Peat (1979) observed, however, there were no significant differences in the average yields of the two phenotypes, although the normal indeterminate plant did have the highest average performance (Tables 4.16 to 4.18). Moreover, neither growth habit showed any major differences in its relative effectiveness in the uptake and assimilation of CO_2, even if slight differences existed in their stomatal densities.

It is therefore suggested that the future of the neotenous growth type in enhancing yields lies in the incorporation of more pod-forming nodes on the main stem and on the currently infertile tillers. Otherwise, this factor will continue to dilute the relative advantages of this type as compared with the conventional determinate types. The results for assimilate partitioning studies presented

here have elucidated to some exent how the two growth habits behave in their pattern of assimilate distribution at different developmental stages. Before and at flowering, the pattern of assimilate distribution was similar in both growth habits. Interestingly, flowers were observed to be only weak sinks for the current assimilates, judging by the amount of ^{14}C-assimilates transported to them. Heavy flower shedding was observed in both growth habits. It has been observed in a number of studies that fertilisation is not a major cause of flower shedding (Kambal *et al.*, 1976; Chapman *et al.*, 1979; Gates *et al.*, 1981). In other cases, a variety of stress conditions was found to increase abscission, especially in the racemes of the middle and upper regions, with basal flowers invariably setting pods (Smith 1982). In their study, Gates *et al.*,(1981) pointed out that the pattern of flower abscission may be directly related to sequential acropetal anthesis within racemes and to the architecture of the vascular system within raceme peducles. The development of basal pods of racemes was found to induce cellular changes in the abscission layers of the apical flowers, resulting in shedding, even if fertilised. They also suggested that the physiological interaction between pods and flowers with the same raceme may be circumvented by selecting for synchrony of anthesis within racemes, or for independent vascular traces to each flower, so that direct interaction between flowers and young pods cannot occur. As synchrony of anthesis is strongly influenced by environmental factors such as temperature, the presence of an independent vascular supply to each flower within a raceme is the most reliable means of improving pod set, in which case any loss of yields would only be attributable to pod and ovule abortion.

Charlesworth (1989) in answering the question "why do plants produce so many more ovules than seeds?" has suggested that abortion of ovules and fruits may result due to lack of enough pollen for fertilisation, competition over limited resources where excess flowers and fruits are produced and more importantly, due to high genetic loads, causing many fertilisation products to abort randomly early in development. Alternatively, Bawa *et al*. (1989) have proposed that both embryo and fruit abortion which are distinctly different contribute to the lowered maturation of ovules; which is caused by parent-offspring conflict over resource allocation and sibling rivalry. The production of extra ovules may be a means of selecting embryos in the face of diversity of pollen genotypes reaching the stigmas resulting in non random abortions.

As detailed studies have yet to be performed on the anatomy of the new determinate types, especially on the anatomy of flowering, the area of independent vascular supply to individual pods remains plausible and there is justification to believe that the massive flower and pod set observed in both growth types may have a bearing on the timeliness and pattern of vascular development in the racemes. Concerted and detailed studies in this area in future programmes may help in solving this puzzle and enhance the effectiveness of producing yields. It is the close coordination between the knowledge of anatomical development of photosynthetic tissue, vascular development, especially at the reproductive stage, and the pattern and availability of assimilates, that will help enhance the potential for yield of existing and new phenotypes in this crop.

Further, it is suggested that such future studies should also include a detailed analysis of the C:N relations. This will elucidate how these major metabolic constituents are partitioned within the growing season. Such information may be invaluable, especially in the timing of fertiliser applications for maximum effect. Whichever course the future investigations assume, they would need to consider the points discussed here with a view to broadening and improving the scope of this legume crop.

It is therefore concluded that the relative advantages of the determinate growth habit over the indeterminate one are to a greater extent cancelled by the fact that these types produce fewer pods on the main stem, coupled with the asynchronous production of infertile tillers. With this background, it is suggested that the breeders may consider in the future an intermediate growth habit which will combine the existing advantages of the determinate plants, while exhibiting a superior yield status. Perhaps lines with independent vascular traces to the individual pods on racemes will enhance the possibility of increased yields. Certainly, this type of plant will have to exploit the existing photosynthetic capacity in such a way that extended or current leaf area will be utilised more effectively than at present. It is assumed that the proposed intermediate determinate phenotype will have more pod-bearing nodes on the main stem and fewer tillers, with an improved capacity to set pods. It will also fit within a framework of optimum field agronomic practices of density, nutrients and other environmental factors. However, it is appreciated that this is not a simple task and it is admissible that for the interim, the indeterminate conventional types will

continue to outyield the neotenous determinate ones. It is also appreciated that there is still scope for improvement of the existing types by exploiting the existing potential by injecting desirable characters for enhancement of better yields.

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Plant component \ Plant type	645	642	644
Apical meristem	0.229	0.181	0.168
±SD	0.057	0.094	0.031
Leaves	2.878	1.360	1.221
±SD	0.434	0.342	0.279
Stem	1.619	1.675	1.777
±SD	0.337	1.151	0.381
Reproductive parts	-	-	-
Branches	0.203	0.376	0.279
±SD	0.072	0.153	0.150
Roots	2.989	1.729	1.609
±SD	0.739	0.394	0.499
Plant total	7.914	5.321	6.054
±SD	1.497	2.072	1.207

Appendix 1 : Dry weights (g) of various plant components of the two determinate types, 645 and 642 and the indeterminate type, 644, measured at the vegetative stage (see Fig. 4.13).

Plant component \ Plant type	645	642	644
Apical meristem	0.215	0.170	0.176
±SD	0.077	0.060	0.025
Leaves	1.831	2.218	2.239
±SD	0.731	0.348	0.221
Stem	0.658	0.766	0.867
±SD	0.171	0.102	0.142
Reproductive parts	-	-	-
Branches	0.426	0.533	1.033
±SD	0.138	0.372	0.511
Roots	1.564	1.598	1.959
±SD	0.675	0.324	0.252
Plant total	4.637	5.286	6.275
±SD	1.520	0.470	0.637

Appendix 2 : Dry weights (g) of various plant components of the two determinate types, 645 and 642 and the indeterminate type 644, measured at the vegetative stage (see Fig. 414).

Plant component \ Plant type	645	642	644
Apical meristem	-	-	0.281
			0.101
Leaves	2.915	3.393	4.503
±SD	0.681	1.349	0.796
Stem	1.598	1.447	2.374
±SD	0.632	0.471	0.344
Reproductive parts	0.232	0.353	0.706
±SD	0.091	0.025	0.227
Branches	0.667	2.564	2.510
±SD	0.528	1.718	2.413
Roots	2.794	3.821	4.990
±SD	0.603	1.082	1.667
Plant total	8.193	11.507	15.365
±SD	1.290	2.680	4.950

Appendix 3 : Dry weights (g) of various plant components of the two determinate types 645 and 642 and the indeterminate type 644, measured at the flowering stage (see Fig. 4.15).

Plant component \ Plant type	645	642	644
Apical meristem	-	-	0.340
±SD			0.098
Leaves	4.244	2.609	5.672
±SD	2.537	0.069	1.129
Stem	4.116	1.728	4.181
±SD	3.081	0.079	1.078
Reproductive parts	1.991	1.569	1.972
±SD	0.252	0.394	0.819
Branches	6.684	11.150	6.183
±SD	2.830	3.795	1.644
Roots	3.692	6.258	5.440
±SD	1.325	3.017	1.693
Plant total	20.726	24.314	23.788
±SD	9.832	4.921	1.628

Appendix 4 : Dry weights (g) of various plant components of the two determinate types, 645 and 642 and the indeterminate type, 644, at the flowering and the early pod growth stage (see Fig. 4.16).

Plant component \ Plant type	645	642	644
Apical meristem	-	-	0.275
±SD			0.090
Leaves	5.126	3.309	7.571
±SD	1.520	0.450	1.281
Stem	5.108	2.560	5.983
±SD	2.800	0.600	0.651
Reproductive parts	5.926	5.330	3.540
±SD	1.255	2.230	0.741
Branches	11.798	13.392	11.274
±SD	3.450	2.550	3.410
Roots	7.540	9.970	9.480
±SD	0.948	0.975	2.060
Plant total	35.502	34.564	37.128
±SD	3.540	1.590	5.090

Appendix 5 : Dry weights (g) of various plant components of the two determinate types, 645 and 642 and the indeterminate type, 644, measured at the mid-pod filling stage (see Fig. 4.17).

Plant component \ Plant type	645	642	644
Apical meristem	-	-	0.330
±SD			0.052
Leaves	4.300	1.997	5.317
±SD	2.640	0.436	0.337
Stem	4.628	1.759	4.055
±SD	2.640	0.436	0.337
Reproductive parts	14.711	4.688	7.819
±SD	3.112	1.042	1.648
Branches	7.549	15.921	9.982
±SD	4.639	7.997	1.116
Roots	4.966	6.176	5.329
±SD	1.399	3.099	1.594
Plant total	36.161	30.542	32.831
±SD	4.757	10.909	5.138

Appendix 6 : Dry weights (g) of various plant components of the two determinate types, 645 and 642 and the indeterminate type, 644, at the late pod filling stage (see Fig. 4.18).

Fig No. / Plant type	Activities of fed leaf per g(DPM)		
	a (645)	b (642)	c (644)
13	1222518.025	2604259.107	1808803.143
14	372938.845	360732.786	883823.990
15	167418.498	235609.745	221995.538
16	364447.425	381194.760	365526.356
17	205816.323	249636.992	227063.538
18	149140.245	238693.306	324182.471

Appendix 7 : Activities per minute per g of dry matter of the fed leaf of plant growth habits at various stages of growth as per indicated figures.

Plant type \ Time (days)	Leaf areas (cm^2) 30	50	80
642	239.90	1382.27	2105.75
	(18.38)	(2.77)	(86.25)
644	271.90	1021.75	2361.70
	(5.32)	(86.87)	(43.69)

Appendix 8 : Leaf areas of the determinate type 642 and the indeterminate 644, measured at 30, 50 and 80 days from emergence in Summer 1987. (± SE). See Fig. 4.1

Plant type \ Time (days)	Leaf areas (cm^2) 20	40	61	82
642	122.62	348.30	785.20	1206.57
	(8.05)	(55.95)	(81.01)	(88.38)
644	55.25	243.57	729.48	1288.25
	(13.25)	(15.69)	(28.17)	(115.44)

Appendix 9 : Leaf areas of the determinate type 642 and the indeterminate type 644 measured at 20, 40, 61 and 82 days from emergence in Autumn 1987. (± SE). See Fig. 4.2.

Plant type \ Time (days)	Leaf area (m^2) 30	51	72
645	238.40	1157.80	2340.40
	(9.37)	(14.68)	(44.40)
642	201.05	1105.60	2291.55
	(7.81)	(17.38)	(59.35)
644	117.25	997.50	2526.00
	(24.60)	(32.81)	(98.45)

Appendix 10 : Leaf areas of the two determinate types 645 and 642 and the indeterminate 644, measured at 30, 51 and 72 days after emergence, in Summer 1988. (± SE). See Fig. 4.3