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SELECTED DEFOLIATION STUDIES ON
BUTTERNUT Cucurbita moschata, Dunchesne. CV WALTHAM

A Thesis presented in partial fulfilment of
the requirements for the degree of
Master of Agricultural Science
in Plant Physiology at
Massey University

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ABSTRACT

A field experiment was carried out in the summer 1983/84 at Massey University Campus, Palmerston, New Zealand, to study the effect of selective defoliation on both growth and partitioning of dry matter during reproductive growth in Butternut (Cucurbita moschata, Dunchesne).

The plants were trained to grow toward one direction, with one main vine through regular pruning of side branching. Defoliations was carried out at early flowering growth stage, leaving the treated plants with one, two or three block of leaves, at different positions, with different combinations on the stem. Each block has equal number on node, determined at the time of treatment. Newly developed leaves within the defoliated plant section were regularly removed.

Results showed that removal of basal leaves block, significantly increased the total dry weight and yield by 25% and 30% respectively. This was attributed to the high unit leaf rate and leaf area duration in the later period. Removal of one or more block of leaves from other part of the stem, all reduced plant growth and yield. The Butternut plants exhibited a very stable pattern of dry matter partitioning between their organs. The sign of "recovery" which resulted in the proportion of dry matter found in each organs similar to that of CON plants, was observed at the first harvest (7 days) after defoliation. Partitioning of dry matter to fruits was observed to become stronger toward the end of growing period irrespective of pattern of defoliations.

The pattern of fruit distributions on the plant was strongly influenced by the position of leaves. At final harvest, higher total fruit dry weight and fruit number was found on the stem section with leaves presence. High number of fruit abortions reduced the yield in the stem section without leaves.

The overall plant growth was strongly influenced by the age

and the total area of leaf present on the plant after defoliation. Plants with more proportion of younger leaves grew better than plants with older leaves.

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1 INTRODUCTION

Due to limited land resource, maximising the production per unit area has been the most important crop production research objective in Malaysia. This is especially true in the production of cash crops which act as a supplement to small farmers' household incomes. In another words, a technology with quite high labour input is acceptable to a certain degree for the small farmers who normally own between 1.0 to 5.0 hectares only of arable land.

Crops in the family Cucurbitaceae are one of the important cash crops normally grown by farmers. In this family, water melon (Citrullus vulgaris Schrad or Citrullus lanatus (Thunb.) Matsum and Nakai) is the most popular due to its characteristic of being a heavy producer: yields between 23 - 30 t ha⁻¹ are easy to achieve. With present management practices, one crop may give a net profit of M\$2000.00 to M\$4000.00 per ha. This would be a substantial contribution to the farmer's income.

Under the concept of source and sink relationships, water melon production may be limited by three factors namely the source, the sink and translocation (Tanaka 1980). With our present knowledge of these relationships, the capacities of these three factors can be improved practically through breeding work. However, on an area basis, these factors can be altered by increasing the number of individual plants per unit area (Wilson 1972). The number of plants per unit area is however limited by size and the effectiveness of the canopy. More plants per unit area can be grown if the canopy size is reduced through pruning or defoliation, so increasing yield per unit area.

Studies on other crops showed that partial defoliation stimulates the photosynthetic capacity of those leaves that remain on the plants (Sweet and Wareing, 1966; Wareing, Khalifa and Treharne, 1968; Neales, Treharne and Wareing, 1971; Stacey, 1983) and delays the senescence of remaining leaves (Woolhouse,

1976; Alderfer and Eagler, 1976). The principle of reducing the canopy size to allow closer planting has been used in the production of some perennial crops (Yoshida 1980). In Malaysia, cocoa, coffee and some orchards are planted at close spacing while the plant canopies are maintained from overlapping by regular pruning. However, there is no such practice as yet being carried out in annual crops. This probably due to the large number of plants per unit area normally used in annual crops which may increase eventually the cost of labour to a level that will exceed the possible beneficial effect of pruning itself. Nevertheless, the possibility of increase yield through such practices might be a worthwhile study in high value crops such as water melon.

It would appear therefore, that there is a need to study the possible effect of pruning practices on the growth, yield and partitioning of dry matter in water melon. Since the climate at Massey University is too marginal for the successful cultivation of water melon, another Cucurbit, Cucurbita moshata L.cultivar Waltham (a Butternut type of squash), which is quite similar in general characteristic and growth habit to water melon, is used.

2 LITERATURE REVIEW

2.1 INTRODUCTION

This chapter is divided into six sections. The plant under study is introduced in section 2.2. A brief review of plant growth analysis is presented in section 2.3. A comprehensive review of present knowledge in partitioning of dry matter in higher plants is given in sections 2.4 and 2.5. Section 2.4 deals with the long distance transport in plants which includes the loading, inter-organ translocation and unloading while section 2.5 deals with the patterns of assimilates partitioning in plants and the factors that may affect them. In the last section, section 2.6, the agronomic important of dry matter partitioning in crop plants is highlighted.

2.2 THE CUCURBITS: A COMPARISON BETWEEN BUTTERNUT AND WATER MELON

Species of cucurbits have been cultivated for thousands years, and one member of Cucurbitaceae, Lagenaria siceraria (Molina) standley (the white flowered gourd) has the distinction of being the earliest known plant to have been cultivated in both hemispheres. Its widespread use as a container made it indispensable in prepottery times. While not as significant as grain crops, cucurbit species provide many people of tropical and warm temperate climates with food. They are used as cooked vegetables (pumpkins, squashes and marrow), salad items (cucumbers and gherkins) and dessert fruits (rock and water melon). Some cucurbits are grown also as animal feeds (Hume 1980).

The crop used in this study is Cucurbita moschata, Dunchesne; a butternut type of squash. The term "butternut" refers to their bell-shaped fruits. Due to the differences in the morphology of the flowers and leaves, the butternut and water melon (Citrullus vulgaris, Schrad; or Citrullus lanatus (Thunb.) Matsum Nakai) were grouped into different genera (Bailey 1944).

The cultivar Waltham, which is used in this study however, is very similar to water melon in its growth habit which is characterised by indeterminate, trailing vines with tendrils. Their branching habits are similar also, with lateral vines originating mainly from the most basal nodes (Hume 1980, Yamaguchi 1983). The flowers of the genus Cucurbita are solitary in axils, the staminate, long-peduncled, large and yellow, the corolla gamopetalous and lobed about half its way down with anthers united. The ovary is 1-celled, with 3-5 placentae and the stigmas 2-lobed with 3-5 in number. The flower of genus Citrullus is smaller in size, yellow, solitary in axils but their corolla are 5-parted to the base, anthers are free, ovary has 3 plancetae and many ovules and, the stigmas 3-lobed (Bailey 1944).

The male flowers of the genus Cucurbita are usually concentrated toward the base of the stem while the female flowers are toward the shoot (Hume 1980). In the genus Citrullus, female flowers are borne almost at constant intervals along the main vines and lateral branches. The male flowers are found on the rest of the nodes. The number of nodes in between the female flowers varies with cultivars.

The shapes of fruits are different. The butternut fruits are bell-shaped while the shape of watermelon fruits may be round or oblong. They are however, both heavy producers.

2.3 PLANT GROWTH ANALYSIS: FUNCTIONAL AND CLASSICAL APPROACHES

While it is difficult to define growth in a fully comprehensive way, the agronomist and the crop physiologist resolve this problem by emphasising dry weight change with time, either of the whole crop or of selected parts, for example its economic yield. Taken in conjunction with a limited number of other measurements also made over time, this approach constitutes what is termed "growth analysis". It is employed by the agronomist to assess the involvement of both internal and external factors that collectively affect plant growth

(Robertson 1985, pers. com.).

Currently, there are two approaches of growth analysis, namely "functional" and "classical". In the functional approach, plant growth is described by the use of a single analytical function, called "the growth function equation". A general growth function connecting dry weight, W to time, T may be written as follows:

$$W = f(T) \quad (1)$$

where f denotes some functional relationship (France and Thornely 1984).

The development of this area has occurred mostly in plant science and among the early papers is included that of Richards (1959, 1969). More recent publications on this subject are those of France and Thornely (1984), Hunt (1982) and Causton and Venus (1981).

Although the use of growth functions represents one of the simplest approaches to the problem of quantitatively describing plant growth, it has several weaknesses which have been summarised by France and Thornely (1984) as follows:

1. The choice of function is usually fairly arbitrary,
2. Possibly no appropriate analytic function exists,
2. There may be fitting difficulties,
4. Observed growth data often contain discontinuities which cannot be accommodated (due for instance, to sudden changes in nutritional status, the environment or disease). It is for this reason that, the functional approach was not used in the study reported here.

In the classical approach, plant growth is described by the use of computed growth components such as relative growth rate

(R), net assimilation rate or unit leaf rate (E), leaf area ratio (F), leaf area duration (D) and specific leaf area (SLA). Historically, the classical approach was developed much earlier than the functional one. The early papers include those by Blackman (1919), West, Briggs and Kidd (1920a, 1920b) and Watson (1952). More recent publications include those of Evans and Hughes (1962), Whitehead and Myerscough (1962) and Hunt (1978).

2.3.1 Relative Growth Rate (R)

R may be defined as the increase in plant dry weight per unit of dry weight per unit of time (Hunt 1978). It was proposed initially by Blackman (1919) as a direct analogy of interest rates in financial investment and defined as "the efficiency index of dry weight production". The name "relative growth rate" was suggested by West, Briggs and Kid (1920a, 1920b). Fisher (1921) pointed out that R is most simply expressed as an instantaneous value which may be written as:-

$$R = \frac{1}{W} \cdot \frac{dW}{dT} \quad (2)$$

In log scale, this equation can be rewritten as follows (Causton 1977):

$$R = \frac{d(\log_e W)}{dT} \quad (3)$$

This expression tells us that the instantaneous R is the slope of the plot of natural logarithm of dry weight, W against time, T. Mean \bar{R} in a given period ($_1T - _2T$) can be calculated by the following equations:

$$\log_e \frac{_2W}{_1W} = R (_2T - _1T) \quad (4)$$

$${}_{1-2}R = \frac{\log_e {}_2W - \log_e {}_1W}{_2T - {}_1T} \quad (5)$$

In practice, R follows only crudely if the harvest intervals like $2^T - 1^T$, are long, but the two estimates become progressively closer as the intervals become shorter (Hunt 1978).

2.3.2 Unit Leaf Rate (E)

E is the increase in the plant dry weight per unit of assimilatory area (leaves) per unit of time. Initially suggested by Briggs, Kidd and West (1920b) and termed "unit leaf rate", the concept was redefined by Gregory (1926) who termed it "net assimilation rate". Cotemporary usage favours the earlier term (Evans 1972).

The expression of the instantaneous values is:

$$E = \frac{1}{L_A} \cdot \frac{dW}{dT} \quad (6)$$

where L_A is the total leaf area present on the plant. The mean for a period of time $1^T - 2^T$ is:-

$$1-2^E = \frac{2^W - 1^W}{2^T - 1^T} \cdot \frac{\text{Log}_e 2^{L_A} - 1^{L_A}}{2^{L_A} - 1^{L_A}} \quad (7)$$

2.2.3 Leaf Area Ratio (F)

Leaf area ratio is the ratio of total leaf area to whole plant dry weight (Briggs, Kidd and West 1920b). Hunt (1978) notated as F:-

$$F = \frac{L_A}{W} \quad (8)$$

In a broad sense, F represents the ratio of photosynthesizing to respiring material within the plants. Over a harvest interval, it's mean value, F is given by:

$$F = \frac{({}_1L_A / {}_1W) + ({}_2L_A / {}_2W)}{2} \quad (9)$$

$$= \frac{{}_1F + {}_2F}{2} \quad (10)$$

if one assumes that F is linearly related to time (Hunt 1978).

2.3.4 Leaf Area Duration (D)

Leaf area duration, D has been described by Watson (1947) as the "whole opportunity for assimilation" that the crop possesses during the period in question. In other words, it takes account both of the magnitude of leaf area and its persistence in time. The formula for estimation on a plant basis may be written as follows:

$${}_{1-2}D = \frac{({}_1L + {}_2L) ({}_2T - {}_1T)}{2} \quad (11)$$

Graphically, D is the total area in the curve of leaf area plotted against time.

2.3.5 Specific Leaf Area (SLA)

SLA is the mean area of leaf (L_A) displayed per unit of leaf weight (L) (in a sense a measure of leaf density or relative thickness) (Hunt 1978).

$$SLA = \frac{L_A}{L} \quad (12)$$

2.4 PARTITIONING OF DRY MATTER IN FLOWERING PLANTS

The partitioning of assimilates between the sites of production in the photosynthesizing leaves and their sites of utilization in harvestable regions is undoubtedly a major determinant of crop yield (Gifford and Evans 1981). Three important aspects of assimilate partitioning are phloem translocation, loading of assimilates into the phloem system and sink organs. In the foregoing section, some of the latest findings regarding these three aspects will be sequentially considered. An attempt will be made to identify the key processes which might act as control mechanisms in the partitioning. As Giaquinta (1983) has stated, the partitioning is highly integrated and orchestrated throughout plant growth and development, so that control can be exerted potentially at several target sites in both source and sink regions. Understanding of the three aspects mentioned above is therefore essential if one tries to understand the business of partitioning in the plant system.

2.4.1. Long Distance Transport

It is commonly known that there are two long distance transportation systems in flowering plants; namely the xylem with the major function of transportation of water and nutrients from root to the rest of plant parts especially leaves, and the phloem with the major function of transporting the assimilates from photosynthetic areas to growing or storage organs.

In the foregoing section, some of recent developments in the understanding of the phloem transportation system especially its ultra-structure, function and mechanisms will be highlighted.

2.4.1.1 Phloem Structure and Function

While the sieve tube was first discovered by Hartig in 1837, it was only from about 1960 that translocation research was strongly directed towards revealing the structure of the sieve tube (Canny 1984). Even though the questions of mechanism and

ultra-structure of sieve tube elements have still not been unequivocally answered up to the present, great strides have been made in understanding the unique structural features of phloem sieve elements and their associated cells (Cronshaw 1981). This success is partly due to the application of new methods of phloem element preservation such as the use of the rapidly penetrating fixative acrolein (Cronshaw and Anderson 1969, Shih and Currier 1969), the rapid freezing of the whole plant in liquid nitrogen and transfer to chemical fixative (Cronshaw and Anderson 1969) or the use of starved or wilted plants for fixation (Anderson and Cronshaw 1970, Evert et al 1973).

Studies on phloem tissue structure have been difficult before, due to the high sensitivity of phloem tissue to manipulation. Normal dissection or manipulation which scarcely affected other tissues destroyed the translocation process and caused visible damage to the sieve tube. A cut into phloem stopped translocation for many centimeters on either side immediately (Canny 1984). This is due to a surge of sieve tube content toward the side pressure release, accumulating "slime plug". These surge artifacts have created controversy as to the internal organisation of mature sieve elements (Cronshaw 1981). The application of new techniques mentioned above has greatly reduced this artifacts problem.

Detailed discussions on the structure of functional sieve cells have been reported elsewhere (Murmanis and Evert (1966), Wheatherly and Johnson (1968), Esau (1969), Johnson (1973), Troughton and Sampson (1973), Schmitz and Srivastara (1974), Fisher (1975), Milaragnu and Walsh (1976), Cronshaw (1981)). Only basic structures that relate to the understanding of the mechanism of translocation will be discussed here.

It has been accepted that in angiosperms, the phloem tissue contains sieve tubes, companion cells, phloem parenchyma and phloem fibre and P-protein (Marshall and Sagar 1978, Cronshaw 1981). Companion cells contain dense cytoplasm with relatively little of their volume occupied by the vacuole. They have an

abundance of organelles (mitochondria, ribosomes, plastid and golgi bodies) as well as large nuclei and endoplasmic reticulum. Sieve-tube elements are typically 20-30 micrometers in diameter and 100-150 micrometers long, and contain on the average 20-100 sieve plates per 1 cm length of phloem. The sieve plate is perforated by sieve pores of approximately 1 micro meter in length and 0.1-5 micrometers in diameter, commonly occupying about 50% of the total plate area (Parthasarathy 1975). Sieve plates are likely to have some function in tranlocation since they are more numerous in evolutionarily "advanced" phloem than that of more primitive species (Esau, 1969). Photographic pictures of sieve element structure can be found in Johnson (1973), Fisher (1975), Esau (1969), Melarangno and Walsh (1976). A good collection of pictures from these authors can be found in Moorby (1981).

One common feature of the sieve element is that it is short-lived in dicotyledon plants. It differentiates quickly from a meristematic cell, passing rapidly through a series of states and within a few weeks to a month or two; or in exceptional cases in some deciduous perennials, two seasons, loses its contents and becomes squashed and obliterated (Canny 1973). Another reason for its short duration is the deposition of callose which enlarges with age, around the sieve pore (Esau 1969). Growing plants solve these problems by producing new sieve elements or by their rejuvenation as occurs in some perennials (Leopold and Kriedman 1975).

The most controversial issue that has not been answered unequivocally up to the present, is the nature of the contents of the sieve tube and sieve tube area pores (Canny 1984). It is known that the sieve element shows a deficiency and degeneracy of the normal cellular organelles but has a characteristic proteinaceous content, originally termed "slime" but now named P-protein (Cronshaw 1981). Phloem exudate analysis has detected a large number of P-protein filaments in species of Cucurbitaceae (Cronshaw et al 1973, Cronshaw 1975), and these have been identified electronmicroscopically as the main structural components of phloem exudates from cucurbits (Eschrich 1963,

Kollmann et al 1970).

Many attempts have been made to explain the ultra-structure of P-protein in relation to its function in translocation. Kleinig et al (1971), Mac Robbie (1971), Ilker and Currier (1974) and Fensom (1975) suggested that P-protein possesses a contractile property which has functional similarities to actin, myosin or tubulin. However, work by Williamson (1972), Hart and Sabnis (1973), Palevitz and Hepler (1975) and as well as data from recent biochemical studies (Sabnis and Hart 1979) have indicated a complete dissimilarity in ion or thiol reagent and ATPase activity between any P-protein studied and known contractile protein. Data from exudate analysis however, showed that P-protein displays a protein with lectin activity. These data with other of their unpublished results, Sabnis and Hart (1978, 1979) show that it is tempting to speculate on functions unrelated to sugar translocation such as recognition or defence systems.

The sieve area pores have also received a lot of attention from investigators. As a result, a better understanding has been achieved in this area. Earlier work (Mishra and Spanner 1970, Siddiqui and Spanner 1970, Spanner 1970) showed that the pores are occluded and these workers believed that this plugged condition represents the normal state in mature functioning sieve elements. However, other workers suggested that when plugged pores are observed, this condition is an artifact created by the sudden release of sieve element hydrostatic pressure (Anderson and Cronshaw 1971, Benhke 1971). Data from recent studies which employ new techniques of fixation show that there is a shift in observation toward more open pores. Freeze-fracture studies by Johnson (1968, 1973) found a uniform network of P-protein continuing from cell to cell through the pores with no dense plugging. Freeze substitution studies by Dempsey et al (1975), De Maria and Thaine (1974), Fisher (1975) showed that the pores are open.

However as Fensom (1981) has stated, there is a wide range of evidence both for partly open and closed sieve plate pores in

angiosperms. They (Fensom 1981 and Spanner 1978) suggested that it is unlikely that all channels in mature sieve elements are open. Therefore both findings are probably true.

Studies on the position of P-protein in the living and functioning tubes also produced inconclusive results. Freeze-etching and more conventional transmission electron micrographs showed a wide range of positions. Some is parietal so that lumens and pores appear open; some is interlaced across the lumen, often with strands that penetrate or pass through the sieve plate pores (Johnson 1978).

Observation of the P-protein in the intact condition has been difficult due to problems associated with the presently available techniques. Fixation requires finite penetration time and also time for disruption of all physical and chemical activity (Mersey and McCully 1978). This almost certainly will distort the position and the arrangement of P-protein in the sieve tube. Even with freeze-etching techniques, the freezing in liquid nitrogen may take 0.5 second (Johnson 1978) and if cell contents are moving at $3 \times 10^{-1} \text{ mm s}^{-1}$ ($=1.0 \text{ m h}^{-1}$) they will move a considerable distance (60 micrometers) during the fixation process alone. This uncertainty about the extent of disruption or position of P-protein in fixed tubes makes identification of its true position difficult (Fensom 1981).

Presently, most workers accept the limitation of existing techniques that block progress in our understanding of sieve tube functioning and attention has turned to the events of loading solutes into sieve tubes and their release (unloading) from them (Canny 1984).

2.4.1.2 Properties of Exudates

The bulk of the translocated substances in the phloem are carbohydrates (Marshall and Sagar 1978, Crownshaw 1981) at concentrations of 10-25% w/v (Leopold and Krideman 1975) and

water. Carbohydrates represent 90% of solid translocate in the phloem (Street and Opik 1976). Nitrogen compounds which are mainly in the form of amino acids are second in the order of abundance (0.2 - 12.0% w/v; some up to 50% depending on the season). Other materials which are found in traces include inorganic ions, enzymes, ATP, vitamins, growth substances, virus particles and artificially applied chemicals (Street and Opik 1976).

The majority of plants studied have true sucrose (unphosphorylated form) as the material in transit (Canny 1984). Of the 500 species listed by Ziegler (1975) all contain sucrose, and about a third contain also the higher alpha-galactosides of sucrose, raffinose, stachyose or verbascose. A few contain one or more of the sugar alcohols, mannitol or sorbitol. In most cases, reducing sugar is absent (Marshall and Sagar 1978). In cucurbits, stachyose is the principal sugar in transit (Geiger 1975).

The ionic content of phloem exudates appears closely regulated. The K^+ (20 - 85 mM) and Mg^{2+} (2.3 - 23mM) contents are very high relative to Na^+ (0.06 - 0.3 mM) and Ca^{2+} (0.25 - 0.5mM) (Mac Robbie 1971).

Another dominant property of phloem sap is its pH, being recorded as strongly alkaline (pH 7.5 - 8.6) (Mac Robbie 1971) in contrast with xylem sap which is always acidic (pH 5.2 - 6.5) (Pate 1980). As regard to rate of movement in the phloem, it is generally agreed in most species, to be in the order of 50 - 100 $cm\ h^{-1}$ (Cronshaw 1981). In some cases, it can be as low as 6 $cm\ h^{-1}$ as in *Pinus* stem or at the extremely high rate of 282 - 600 $cm\ h^{-1}$ in *Zea* leaf (Canny 1984).

There is also an abundance of evidence for the exchange of material between phloem and xylem. The radially orientated ray tissues are well suited to this purpose (Leopold and Kriedman 1975, Holl 1975).

2.4.1.3 Concentration and Pressure Gradient

The presence of a solutes gradient has long been recognised. Among the early workers on this aspect are included Dixon and Gibbon (1932), Zimmerman (1957a, 1957b, 1958) who studied trees while Mason and Maskell (1928a, 1928b) studied cotton and Crafts (1932) cucurbits.

Generally, the sugar concentration in exudates is high, varying from 5 to 15 or 25% (w/v) or even higher, depending on where the sample comes from and on the physiological state of the plants (Canny 1984). The highest concentration is found in the minor veins of leaves where an osmotic potential of 2.29 MPa was measured in the sieve elements of Beta sp by Fellows and Geiger (1974). This corresponds to the potential of 1M sucrose. From this source, the concentration declines along the translocation pathway towards the sinks (Milburn 1974, Canny 1975).

2.4.1.4 In Search of Structural Framework

Any explanation of how translocation works must be soundly based on a knowledge of the internal organisation of the sieve tube. As has been discussed in an earlier section, the search for this knowledge is still continuing. The present technique of sampling and of fixation still cannot solve the problem of possible artifacts created during handling of samples for observation. Until a new technique is found, any major breakthrough in the understanding of the working organisation of the sieve tube is very unlikely (Canny 1984).

2.4.1.5 The Hypothesis

Based on limited knowledge available, several hypotheses have been proposed to explain the possible mechanism of translocation in the phloem by several workers. Details of the proposed mechanisms have been discussed in many publications. The most recent reviews include those by Zimmerman (1969), Mac Robbie

(1971), Canny (1973) and Mac Robbie (1975a, 1975b). Due to limited time and space, only the summaries of these hypotheses will be discussed here.

2.4.1.6 Electro-osmosis Mechanism

Proposed independently by Fensom (1957) and Spanner (1958), this mechanism in its simple, original form pictured the sieve pore as the origin of a force for movement, not an obstruction. This hypothesis presupposes that at least some of the sieve plates have their pores delicately occluded with P-protein. This occlusion provides ultimate channels through the sieve plate small enough to be electro-osmotically effective. The motive force of electro-osmosis is generated through the frictional interaction between potassium ions and other elements of the assimilate stream constituents. This force is generated when potassium ions are driven through the occluded sieve plates by the development of an electrical potential gradient across them. The maintenance of a potential across the sieve plate which is vital for electroosmosis, is achieved through a continuous active uptake of potassium ions from the apoplast above the plate and egress into the apoplast below. Uptake is perhaps by pinocytosis, and utilises the energy of ATP. The hypothesis accepts, that flow is initiated by a Munch-type activity at the source (Spanner 1978). In this way, instead of a pressure gradient falling progressively at each sieve plate, some energy input would make a steep positive jump at each sieve plate perhaps more than compensating for the fall in pressure along the sieve element (Mac Robbie 1971). A new and final version of the theory has been forwarded by Spanner (1979) with some modification. In this new version, the potassium ion pump has been replaced by a proton excretion pump.

This hypothesis suffers many drawbacks. The single most telling objection is that it could not transport ions with both positive and negative charges (Mac Robbie 1971). The polarised potential across the sieve plate has not been found (Canny 1984) and energy consumption to generate the force would be very high such that, the heat produced would be enough to vaporise the

content of sieve tube (Fensom 1972).

2.4.1.7 Transcellular Streaming (Moving Strands)

The presence of intercellular strands described by Thaine (1961) in the sieve tube stimulated Canny (see Canny 1962, Canny and Phillippe (1963)) into advancing an hypothesis of mechanism of translocation involving such a strand. In the model, transcellular strands traverse the sieve tubes from plate to plate and pass through the sieve pores into adjacent sieve elements. The part of the lumen not occupied by strands is filled with a solution (which incidentally is what an aphid would sample, according to this hypothesis) acting as reservoir. There is a rapid exchange between strand and reservoir in this model and the energy required to move the strands is derived from respiration of sucrose in transit. In this model, some strands move in one direction; others in the opposite direction, in the same tube (Canny 1962).

This hypothesis has its problems as well as its virtues in apparently solving movement through sieve plates. Two major drawbacks of this hypothesis are 1) the model is incapable of the speeds observed in some species (Marshall and Sagar 1978, Canny 1984) and 2) the membrane-bound strands have not been found (Canny 1984). The strands seen by Demsey et al (1975), Thaine (1961), are of the right size but are not surrounded by membranes (Canny 1984). 3) The hypothesis gives no explanation as to what happens to the strands when they come to end of their journey (Marshall and Sagar 1978).

2.4.1.8 Transcellular Tubules

Following a similar structural model that involves transcellular streaming, an alternative hypothesis has been developed largely by Thaine, where the strands themselves are essentially membrane bounded fibrillar "tubes" with contractile walls capable of generating movement (peristaltic pumping) (Canny 1984). The model suggests that the moving force comes from long

protein molecules perhaps similar to, but not necessarily identical with, the contractile protein known to occur in cells which show cyclosis, in myxomycetes that move by flowing their cytoplasm and in animal muscle (Marshall and Sagar 1978).

This model has similar drawbacks as transcellular streaming. Work by Williamson (1972), Hart and Sabnis (1973), Sabnis and Hart (1973, 1974) and Palevitz and Hepler (1975) showed the absence of the necessary structural framework for the model to work.

2.4.1.9 Pressure-driven Flow

Proposed by Munch (1930), this hypothesis assumes that the flow of assimilate in the sieve tube is propelled by osmotic potentials generated in the leaves. The materials in the sieve tube travel down the concentration gradient from source (leaves) where the materials are loaded into the sieve tube to sink (growing or storage organ) where the material is unloaded from sieve tube (Zimmerman 1969). It is the most widely accepted hypothesis at present, though there are a number of reservations (Weatherly and Johnson 1968, Crafts and Crisp 1971, Christy and Furrier 1973, Lang 1973, Canny 1984).

This hypothesis apparently solves the problem of high Specific Mass Transfer observed in some species (Troughton and Currie 1977, Thompson et al 1979) but does not satisfactorily explain the presence of P-protein in some species (Mac Robbie 1971) and offers no significant function for the sieve plate (Canny 1975). Two-way movement of materials in the same channel as observed by Trip and Gorham (1967) is absolutely impossible (Mac Robbie 1971, Canny 1973) in this hypothesis.

The credibility of the pressure flow hypothesis depends on whether or not the sieve tube pores are plugged and whether or not the P-protein is directly involved in transportation. The mass flow should, therefore work in those sieve tubes in which the sieve plate pores are wide and open, and pressure gradients are

found (Canny 1984).

2.4.1.10 An Alternative Mechanism

Since all the proposed hypotheses have their weaknesses in one way or another, searching for alternative mechanisms is still continuing. Some other possible mechanisms have been discussed by Fensom (1975) which include the peristalsis of cell walls, micro-electro-kinesis, surface active movement, reciprocating flow and contractile proteins hypothesis. Many other possible mechanisms have been proposed by different workers.

Most of the hypotheses have proposed to explain the working mechanisms in plants without considering the plant species. Therefore, we may have been wrong in the past, trying to seek a single mechanism for all species of higher plants. As has always been observed in other plant systems, one major mechanism may be operating in a given species with another mechanism on standby and will be activated when a situation like stress arises (Robertson 1985, pers. com.).

2.4.2 Phloem Loading

Phloem loading is a process by which the major translocated substances are selectively and actively delivered to the sieve tube in the source region prior to translocation (Geiger 1979). In the process, assimilate is concentrated twenty to hundred times as it moves to the sieve tube of the leaf veins and is the origin of the sucrose pressure gradient in the translocation system (Canny 1984). Most of the loading seems to occur at the smallest veins of leaves (Sovonick et al 1974). In the net-veined leaves, they are first to show accumulation of ^{14}C assimilate above the level in the surrounding mesophyll (Fondy and Geiger 1977). In parallel-veined leaves, where small veins lie in groups between pairs of large veins connected laterally by very small and sparse transverse veins, the specialization of the small veins for loading and the large one for longitudinal movement, is especially clear (Lush 1976, Altus and Canny 1982).

There are two possible routes for the movement of assimilates, namely apoplastic and symplastic routes. The apoplastic route involves the release of sucrose through the plasmalemma of the mesophyll cell into the free space (cell walls), diffusing through all accessible areas of the free space, and concentration by a pump at the cell membrane surrounding the sieve tube/companion cell complex of the minor veins. The symplastic route would confine the sucrose to the cytoplasm of the chain of cells connecting the mesophyll cells via the bundle sheath cells (if in C^4 plants) and sieve elements, travelling from cell to cell in plasmodesmata (Canny 1984).

Kursanov and Bravchenko (1970) have reported that up to 20% of the total leaf sugar, mainly as hexoses, was present in the apoplast of sugar beet leaves. They proposed that the apoplast represents the major route of the assimilate transfer into veins. A similar conclusion was proposed by Sovonick *et al* (1974) and Fondy and Geiger (1977).

In cucurbits, Madore and Webb (1981) have showed that the symplastic pathway is the major, if not sole pathway for loading. Detailed structural studies on Cucurbita pepo L. showed that, plasmodesmata connections can be quite abundant between the bundle sheath and companion cells (Gamalei and Pakhomova 1980, Turgeon and Webb 1976, Turgeon, Webb and Every 1975). The same connections are found to be abundant also in sugarbeet leaves (Geiger *et al* 1973). Thus, the qualitative presence or absence of solute flux data cannot be used to distinguish unequivocally between the two pathways, even although the leaf morphology may affect the type of pathways.

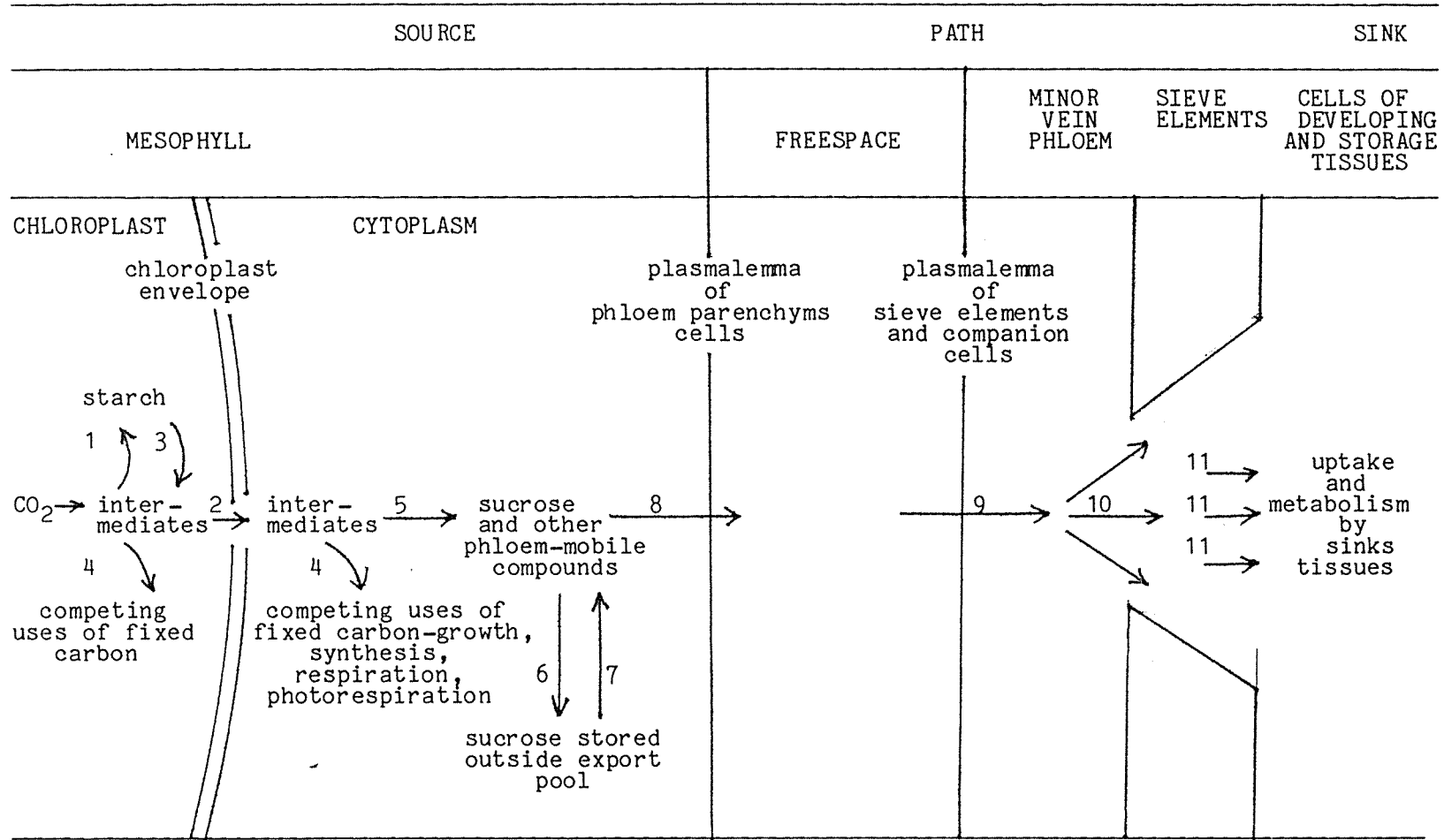
Although an entirely symplastic pathway remains a probability for sugar loading, a symplastic pathway has to be reconciled with several features of loading systems (Giaquinta 1983). First, it is difficult to reconcile selectivity with symplastic transfer, unless some unknown discriminating mechanism exists at the level of plasmodesmata. Second, there is no disagreement that a marked concentration of sugar occurs within

the phloem, suggesting that plasmodesmata contain an active pumping mechanism or act as "one-way valves", or are part of an endoplasmic reticulum-mediated pumping mechanism. Active transport of sugar across the phloem membranes is the simplest explanation for accumulation and these two factors, along with other evidence led Giaquinta (1983) to conclude that loading via the apoplast remains a more distinct possibility.

Geiger (1979) envisaged that both pathways are implicated in both loading processes. According to his model, at some point in the pathway the sugar to be translocated enters the apoplast or free space of the tissue. The point at which the sugar re-enters the symplast is the loading site, probably at the surface of the sieve element companion cell complex.

On the question of loading regulation, Geiger (1979) has suggested there are three groups of processes which regulate export from a source leaf. The first group of processes (Figure 2.1, 7) results in metabolic control of availability of sucrose and other phloem-mobile molecules for export. Products of carbon fixation may be directed into starch synthesis (1) or transported from the chloroplast by a transporter mechanism (2). Under certain conditions, starch may be mobilized (3) and the soluble intermediates pass through the chloroplast envelope (2). Respiration, photorespiration, synthesis and growth (4) divert mobile compound from exports. A portion of the fixed carbon is directed into synthesis of sucrose and other phloem-mobile molecules (5). These compounds may be stored (6) to be mobilised later (7). As a group, these metabolic processes control the availability of sucrose and other molecules for export (Geiger 1979). The second process (Figure 2.1, 8) controls the exit of sucrose or other exportable molecules from the mesophyll into the free space. Molecules destined for export move from sites of synthesis or storage via the symplast to the nearest minor vein sieve tubes and companion cells where they enter the free space, possibly from phloem parenchyma cells. This control process regulates export by compartmental isolation from the sites of phloem loading.

Figure 2.1: Possible control points for regulating the partitioning of assimilated carbon and the export of phloem-mobile compounds. Step 1-9, are discussed in the text; step 10 is the control exerted by the structure features of the path of translocation; step 11 is the control exerted by transport out of the sieve tubes and conversion of transport molecules in sink regions.



The third type of control process (Figure 2.1, 9) directly affects phloem loading by regulating the active uptake of sucrose or other molecules such as amino acids, into sieve tubes. Aspects of this model relating to the exit of sucrose from the mesophyll into the free space and to phloem loading were discussed by Geiger (1975).

2.4.3 Phloem Unloading

Phloem unloading refers to a process by which assimilates are transported from the sieve elements into sink cells (Ho and Baker 1982). Sieve tube unloading has received little attention in the past (Gifford and Evans 1981) and is less well understood than loading (Ho and Baker 1982). Recent reviews on related subjects include those by Loomis, Robbinge and Ng (1979), Gifford and Evans (1981), and Ho and Baker (1982). Much of the work in the past has been on a restricted range of organs. Organs studied include sugarcane internode segments (Bieleski 1962, Glasziou and Gayler 1972), cotton hypocotyl segments (Hampson et al 1978a, 1978b), wheat kernel (Jenner 1968), expanding cotyledons of Ricinus seedling (Komov 1977, Kriedmann and Beever 1967) developing barley embryos (Cameron Mills and Duffus 1979), soybean seed (Thorne 1980, 1981) and developing ovules of Phaseolus vulgaris L. (Patrick and Mac Donald 1980). Another type of study involves the examination of the behaviour of plant parts parasitized by Cuscuta sp (Wolswinkel 1974a, 1974b, 1975, 1978, 1979, 1984, Wolswinkel et al 1983, 1984), Wolswinkel and Ammerlaan 1983a, 1983b).

The unloading process may take place either via symplastic or apoplastic routes, depending on the nature of storage carbohydrate. The unloading of sucrose from a sieve element in active sinks such as growing leaves and root tips, may be via the symplastic route only. In these organs, there are continuous symplastic connections between the sieve elements and surrounding tissues (Turgeon and Webb 1976), so the osmotic potentials of these tissues are similar (Fellow and Geiger 1974) and no extracellular hydrolysis of sucrose is observed (Chin and Weston

1975). The symplastic unloading of sucrose may be dependent on the gradient of sucrose between the sieve elements and the sink tissue, and be maintained by the metabolic activities of the sink (Geiger and Fondy 1980).

In storage sinks, apoplastic routes may be involved either at the site of unloading, as in sugarcane stems (Gayler and Glasziou 1972) and beet tap roots (Giaquinta 1977), or en route within the sink tissues as in the placento-chalazal tissues of corn kernel (Felker and Shannon 1980) and the endosperm cavities of wheat grain (Jenner 1974). In these sink organs, unloading of sucrose from the sieve elements or the uptake of sucrose into sink cells may involve active transport across membranes. A simple classification of sink organs, based on the nature of a sink, the possible unloading pathway and the postulated control system involved is shown in Figure 2.2 (Ho and Baker 1982).

In concluding their review on regulation of loading and unloading, in long distance transport systems, Ho and Baker (1982) suggest that unloading of sucrose from the sieve elements does not appear to be an energy-dependent process, the rate-limiting step for import into the sink tissues being among the metabolic activities occurring beyond the initial unloading process. Thus the rate-limiting step may not be the same within different sink organs.

2.5 PATTERN OF ASSIMILATES PARTITIONING

The pattern of interorgan partitioning of a plant is changes according to its growth stage. During vegetative growth, young leaves retained all the ^{14}C -labelled assimilates they produced and import from older (expanded) leaves (Turgeon and Webb 1973). After anthesis, the pattern of assimilates partitioning is changed with more assimilates being diverted to reproductive organs (Evans et al 1975, Crompton et al 1981).

The overall pattern of assimilates distribution to plant organs is determined by the photosynthetic activity and by the strength, size and proximity of various sinks (Szynekier 1974, McArthur et al 1975 and Cook and Evans 1978). In Cucurbits, Yishioka and Takahashi (1983) have shown that, each leaf supplied ^{14}C -assimilates to the closest sink. Thus, leaves at the base supply most of their assimilates to the roots and leaves toward shoot contribute to the above ground vegetative growth before anthesis, and to fruit growth after anthesis. When fruit sets at the base of the stem, competition for assimilates between roots and fruits are observed.

Stronger sink strength however may suppress the effect of proximity. Wolswinkel (1974a) has shown a complete inhibition of setting and growth of fruit in Vicia faba L. resulting from the draining of the phloem system by the parasite Cuscuta sp. In an experiment with Tuberolachus salignus (Gmelin), Peel and HO (1970) showed that ^{14}C -assimilates were transported toward a bigger colony at a faster rate than to the smaller one. In Phaseolus vulgaris L., older and bigger fruits were found to compete better than younger and smaller fruits (Tamas et al 1979).

Assimilates produced during vegetative and early reproductive growth may be temporarily stored in the stem (Moorby 1970, Incoll and Neales 1970). The contribution of stem storage to fruit growth is usually higher under low photosynthetic activity (Rawson and Hofstra 1969, Rawson and Evans 1971). Thus, the contribution of assimilates fixed before anthesis to fruit growth is bigger when plants are under stress. Under normal conditions, the contribution of pre-anthesis assimilates to fruit growth is very small (Gallanger et al 1975, Makunga et al 1978).

Environmental factors have been observed also to affect the partitioning of assimilates between above and underground plant parts. Plants grown under water stress (Passioura 1981) or nutrient deficiency (Rufty et al 1984) have more assimilates partitioned to the root system than when they are without stress. The extent of this adjustment depends on the plant species (Gales

1979). The amount of assimilates partitioned to the root system may affect the subsequent plant growth. Plants with a more developed root system has been associated with the ability to withstand drought (Passioura 1981). In the cucurbits, limited root growth due to competition of assimilates with fruits which set at the base of the stem was observed to cause an overall reduction in plant growth (Yishioka and Takahashi 1983).

Figure 2.2: A simplified classification of sink organs

Sink	Routes	Control
1. Growth sinks (Apical meristem).	Symplastic.	Metabolic activity (Rate of growth).
2. Storage sinks	Apoplastic at some point, but not ne- cessarily at step out of sieve elem- ents.	Hydrolysis of sucrose or active uptake of sucrose or starch synthesis.
a) Sugar sink.		
i) Sucrose (sugarcane stem, beet tap root).		
ii) hexoses (grape, berry).		
b) Starch sink (cereal grains, tubers).		
c) Starch-sugar sink (tomato fruits).		

2.6 AGRONOMIC IMPORTANT OF DRY MATTER PARTITIONING IN CROP PLANTS

Dry matter partitioning between organs in crop plants is an important phenomenon in plant physiology. This is because the economic yield comprises selected parts of the plants. The crop yield will increase if more dry matter is diverted to these parts even at the expense of other plant parts.

3 EXPERIMENTAL MATERIALS AND METHODS

3.1 OBJECTIVE

The objective of the study was to examine the effect of selective defoliation during the reproductive stage on the growth and partitioning of dry matter in Cucurbita moschata Dunchesne; cultivar Waltham Butternut.

3.2 TREATMENTS AND LOCATION

Eight patterns of defoliation were chosen for the experiment. To achieve these patterns, the stems were divided into four different sections or blocks based on the equal number of nodes in each section counted at the time the defoliation treatments were carried out. The sections were denoted by capital letters A, B, C and D, where A was the section toward the base and D the section toward the shoot. The eight patterns plus a control, are shown in the Figure 3.1, with each pattern identified by capital letters A, B, C, D, AB, ABC, CD and BCD, which indicate the position of leaf left on the plants after defoliations.

The experiment was carried out in the summer of 1983/84 on a Massey University Orchard area (Plate 1). The site previously carried a corn crop. The soil type was Karapati Brown Sandy Loam and a test by the Soil Science Department, Ministry of Agriculture and Fisheries gave the following analysis:

N	Not done
P	16 $\mu\text{g}/\text{cm}^3$ (Olsen test)
K	0.4 Extractable cations
pH	5.8 bulked sample
Organic matter	1.8%
Cation Exchange Capacity	14 me/100 g

FIGURE 3.1: PATTERN OF DEFOLIATION TREATMENTS

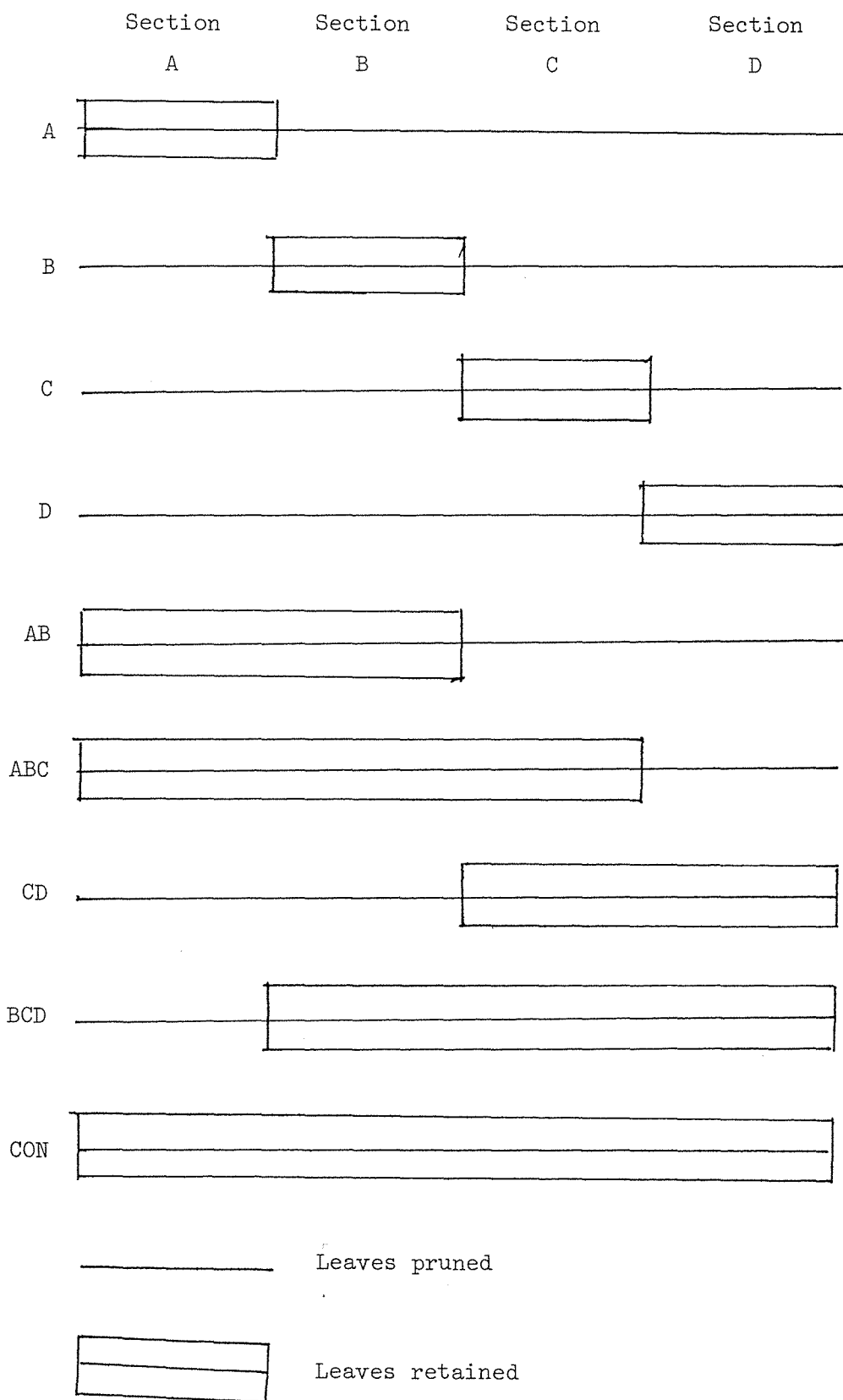




Plate 1 : General view of experimental area

3.3 EXPERIMENTAL DESIGN

The nine treatments were laid down in a Randomised Complete Block Design with four replications. For the purpose of destructive sampling during the vegetative stage, one plot was added to each replicate to give a total of 10 plots in one replication.

Two levels of randomisation using random tables were carried out. Firstly, the 10 plots were randomised in each block. Secondly, the 6 plants in each plot were randomly numbered 1 to 6, representing the 6 destructive samplings. The complete layout of the plot is shown in the Figure 3.2. The plots were separated by two border plants within rows and one row of border plants between rows. Each plot contained 6 plants planted in a row at a distance of 0.6 m. The distance between row was 3.5 m. The total area of experimental plot was 1635.90 m².

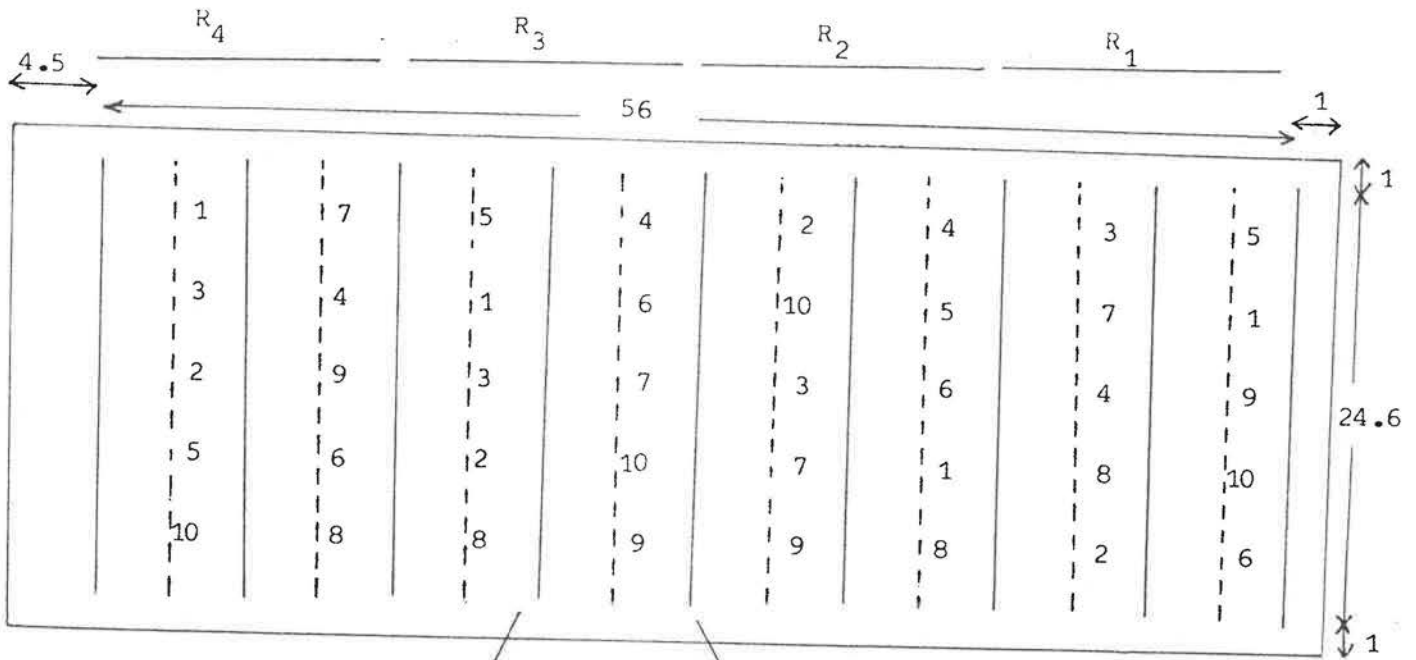
To avoid the experimental area from becoming too big, no border plants were planted within the plot between sampled plants. This led to a situation where a plant could grow without neighbouring plants when destructive sampling started. The effect of "without-neighbours" on the subsequent analysis will be discussed in section 3.8

3.4 SCHEDULE OF DESTRUCTIVE SAMPLING

Destructive sampling was divided into two stages. Stage one was during the vegetative growth stage and consisted of 7 harvests, with the seedling at the time of transplanting as the first harvest. Sampling at the time of treatments was the seventh harvest (Table 3.1).

The second stage of destructive sampling was during the reproductive growth stage which occurred after the plants were treated. It consisted of six harvests with the first harvest seven days after the plants were treated and the final harvest, at maturity.

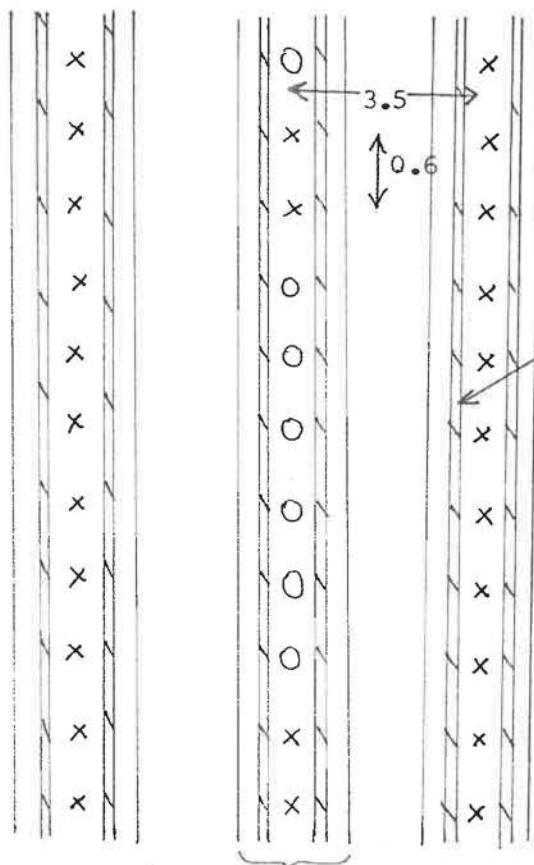
Figure 3.2 : Lay out of the plots



Plot Number Treatments

- 1 = A
- 2 = B
- 3 = C
- 4 = D
- 5 = AB
- 6 = ABC
- 7 = CD
- 8 = BCD
- 9 = CON
- 10 = Vegetative

Single Plot



Planting hole:

X Border plants

O Treated plants

Fertilizer in the furrow

1 meter wide
black polythene sheet

The harvest intervals were longer during the early growth stage, shorter just before and after defoliation treatments and longer again at the end of the growing period. Longer intervals at the beginning and toward the end of the growing periods were selected to coincide with the slow growth rates during these times. Shorter intervals in the middle of the growing period were needed to cover the much faster growth rates then occurring. It was hoped also that the selected intervals would give a better indication of treatment effects immediately after they were applied.

TABLE 3.1 SCHEDULE OF DESTRUCTIVE SAMPLINGS

Stages	No. of Harvest	Date	DAT*	Interval (days)
	1	December 20 1983	0	
	2	January 9 1984	20	20
	3	January 19 1984	30	10
First	4	January 20 1984	40	10
	5	February 8 1984	50	10
	6	February 16 1984	57	7
	7**	February 23 1984	65	8
	1	March 1 1984	72	7
	2	March 8 1984	79	7
	3	March 18 1984	89	10
Second	4	March 28 1898	99	10
	5	April 7 1984	109	10
	6	May 2 1984	134	25

* Days after transplanting.

** Defoliation treatments were carried out.

3.5 EXPERIMENTAL MATERIALS

3.5.1 Wind Breaks

One meter high, 32% light reduction shade cloth was used as a windbreak along the western side of the experimental area to reduce the effect of prevailing southwesterly wind fetch.

3.5.2 The Seeds

The seeds of Cucurbita moschata Dunchesne, cultivar Butternut Waltham were bought from Yates Seed Co., Palmerston North, New Zealand.

3.5.3 The Fertilizer

Fertilizer in the form of Ammophos (12:10:10) at the rate of 1 t ha⁻¹ was used.

3.5.4 The Chemicals

The chemicals used in the experiment were the systemic fungicide Milcurb, a systemic insectide Tamaron and Fumigant Vapona.

3.5.5 Planting Medium and Pots

The planting medium for seed germination in the glasshouse consisted of a mixture of peat and perlite at the ratio of 1:1 v/v. The composition of fertilizers added for one liter of planting medium was as follows:-

3-4 Months Osmocote	180 g
Superphosphate	120 g
Lime	120 g
Dolomite	240 g

Planting pot size 17mm in diameter was used.

3.5.6 Polythene Sheet

One meter wide, 50 μ thick black polythene sheets were used to cover the planting rows (figure 3.2).

3.5.7 Pollination

In order to ensure that complete pollination occurred, three beehives which contained some 20,000 working bees each, were put along the eastern side of experimental area (Plate 2).

3.6 EXPERIMENTAL PROCEDURE

3.6.1 In The Glasshouse

3.6.1.1 Fumigation

One week before the date of sowing, the glasshouse was fumigated three times with Vapona, at 2-day intervals, to kill any spider mites (Tetranychus urticae KOCH) present.

3.6.1.2 Temperature Control

Temperatures of about 25°C and 15°C for day and night respectively were maintained throughout the seed establishment stage.

3.6.1.3 Potting and Sowing

About 800 pots were filled with the prepared planting medium of which a total of 714 pots were used in the experiment. The Butternut seeds were soaked in water at room temperature for about four hours, then wrapped overnight in wet tissue papers. The next morning, the seeds were inspected and 90% of them had developed 1mm-long white radicles. Hand sowing of three seeds per

pot was done in the evening on the same day.

3.6.1.4 Watering

The pots were arranged in groups of 200 pots each on the water absorbent material which covered the glasshouse floor. Immediately after the placement of seeds in the pots had finished, each pot was then carefully watered, followed by soaking the whole glasshouse floor with water to ensure capillary tension between water in the pots and water in the absorbent materials developed. In this way, the water absorbed moved slowly into the pots through capillary action as the pots were drying. The glasshouse floor was flushed with water three times daily (early morning, afternoon and late evening), through hoses with numerous tiny holes running underneath the absorbent materials. The flushing was controlled automatically by a timer.

3.6.1.5 Thinning

Thinning was done on day 9 after sowing, leaving only one medium sized seedling per pot.

3.6.2 In the Field

3.6.2.1 Field Preparation

Two weeks before transplanting, the experimental site was rotavated to kill the existing weeds. The second rotavation and levelling were carried out on day 3 before transplanting. After levelling was finished, furrows of 7-10 cm wide and 4-6 cm deep were dug along both sides of the intended planting rows (Figure 3.2). Fertilizer was applied manually in the furrows before they were covered again with soil by running a horizontal steel bar behind a three wheeler farmbike. The intended planting rows were then covered by polythene sheets (Plate 3). The planting holes were dug later after cutting open the polythene sheets along their central line at the correct planting interval.



Plate 2 : A beehive



Plate 3 : Laying down the polythene sheet

3.6.2.2 Transplanting

Transplanting was carried out when the seedlings reached the one true leaf stage (Plate 4). Screening was done visually in order to ensure the seedlings were uniform for field planting. Due to limited manpower for the destructive sampling later, transplanting was done over two consecutive days. On day 1, only replicates 1 and 2 were transplanted. Replicates 3 and 4 were transplanted on the next day. This sequence was maintained in all destructive sampling later.

3.6.2.3 Irrigation

Immediately after transplanting had finished on each day, the transplanted area was sprinkle-irrigated. Subsequent irrigation was done when there was no rain for about one week (Table 3.2).

3.6.2.4 Trained Pruning

The purpose of trained pruning was to have a butternut plant with only one main vine. This was carried out immediately after side branchings had started. Side branches were cut off when they were about 1 mm long. This procedure was repeated at 3 or 4 day intervals until the experiment finished. Trained pruning was carried out only on the plants in the row plots. The plants in the border row were not pruned. All plants were trained to grow in one direction only (Plate 5).

3.6.2.5 Pest and Diseases Control

Pest control was aimed at preventing the plants from insect damage especially during seedling and early growth stages. Later in the growing period, Powdery Mildew, a fungus disease caused by Erysiphe cichoracearum DC, FLOR. was the main one experienced. Generally, there were no serious outbreak of pests or diseases. The complete sparying programme is shown in the Table 3.2.



Plate 4 : A butternut seedling at transplanting



Plate 5 : The plants, immediately after defoliation treatments

TABLE 3.2: SCHEDULE OF IRRIGATION AND SPRAYING PROGRAMME.

DATE	OPERATIONS*
December 20, 1983	Irrigation
December 21, 1983	Irrigation
January 4, 1984	Insecticide spraying
January 5, 1984	Irrigation
January 10, 1984	Irrigation
January 18, 1984	Insecticide spraying
January 24, 1984	Irrigation
January 27, 1984	Irrigation
February 28, 1984	Fungicide spraying
March 21, 1984	Fungicide spraying
March 22, 1984	Fungicide spraying
March 30, 1984	Irrigation
April 24, 1984	Irrigation

* The rate of spraying is according to the manufacture's recommendation.

3.6.2.6 Defoliation Treatments

Defoliation treatments were carried out when 50% of the plants had produced their first female flowers. This occurred on 65 DAT. The leaf was cut off at the base of the petioles. The pattern of defoliations was described in section 3.2 (Plate 3).

3.7 ANALYTICAL TECHNIQUES

3.7.1 Sampling Method

In the first stage, sampling was easier because the plants were still small. Sampled plants were cut at ground level. The whole plants with all the components still intact were kept in big plastic bags, while being transported to the laboratory.

In the second stage of sampling, the plants were much bigger. Leaves were harvested first and were kept in separate plastic bags according to the plant sections. The stems with fruits and flowers still intact were cut into four predetermined sections (A,B,C and D). Section A which is the base was cut at ground level. Each section was kept later in separate, marked, double-layer big paper bags. All sampled plant components were then transported to the laboratory.

3.7.2 Determination of Leaf Area

Determination of leaf area was carried out on the same day while the leaves were still fresh. Measurement was done on a LI-300 leaf area meter which read the leaf area in square centimeters. Only the area of laminae was measured. The laminae were separated from their petioles before running through the leaf area meter.

3.7.3 Determination of Plant Dry Weight

In the laboratory, the plants were separated into their

components namely leaves, stems, fruits and flowers and were kept in different paper bags. The stems and fruits were cut into small pieces to facilitate drying. All these bags were then carefully arranged in the oven for drying at a constant temperature of 82°C for 24 hours or longer if necessary.

After 24 hours, the samples were carefully inspected to ensure they had been properly dried. The dry weight of each component was taken after the samples had cooled down.

3.7.4 Subsampling

In order to save space and time, all the big fruits were subsampled before drying in the oven. The fruit was cut longitudinally into four pieces after the fresh weight was taken. One of these was used as the subsample. After taking the fresh weight, the subsample was sliced into small pieces and put in a paper bag and later put in the oven for drying together with other plant components.

Dry weights of the whole fruits were calculated based on the percentage moisture content in the subsamples.

3.8 STATISTICAL METHODS

3.8.1 Data Transformation

Appropriate transformation was done on data which did not meet the basic assumptions for Analysis of Variance (ANOVA). All transformed data resembled more or less bell-shaped distribution curves indicated by their histograms and approached a near straight line as shown in their normal probability plots (Daniel 1959, Bliss 1967). The formula of transformation is presented as a footnote to the related table of means in Chapter 4.

In the table of means, only original data were presented. In the situation where ranking was not similar to the original means, the retransformed means were used (Gomez and Gomez 1984).

Retransformation was carried out by applying an inverse operation to the transformed means (Steel and Torrie 1981).

3.8.2 Covariance Analysis

Covariance analysis as described by Gomez and Gomez (1984) was used to adjust the effect of "without-neighbour" in all variables. The total number of day the treated plants grew without neighbouring plants was used as a covariate. All the computations was performed by the general statistical programme GENSTAT (Alvey et al 1980).

The relative efficiency (RE) of covariance analysis was calculated by formula:

$$RE = \frac{EMS \text{ (unadjusted)}}{EMS \text{ (adjusted)}}$$

where EMS = error mean square.

3.8.3 Analyses of Variance (ANOVA)

Standard ANOVA for RCBD as described by Steel and Torrie (1981) was used in the comparison of treatment means. All computations were performed by the general statistical programme, GENSTAT (Alvey et al 1980).

3.8.4 Duncan Multiple Range Test

Tests of significance between all means of each time were carried out for all variables using the Duncan Multiple Range Test (DMRT) (Duncan 1955) as this is more appropriate than the Least Significant Differences test in comparing a large number of treatments (Gomez and Gomez 1984).

3.8.5 Coefficient of Variation

The formula used for calculating the coefficient of variation (CV) is as described by Steel and Torrie (1981):

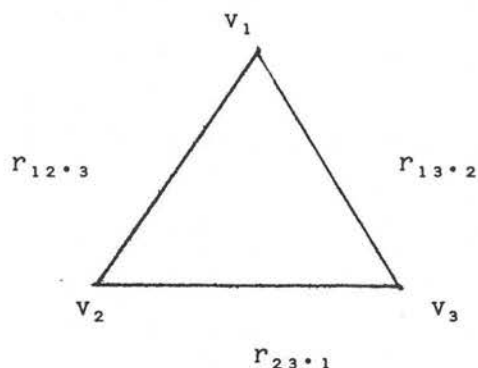
$$CV = (\sqrt{EMS/\bar{x}}).100 \%$$

where EMS = error mean square,

\bar{x} = grand mean.

3.8.6 Partial Analysis

Partial correlations as described by Steel and Torrie (1960) and Nie et al (1975) were calculated to make comparisons of the relationships between pairs of variables. Only the first order of partial correlation coefficients which was calculated between pairs of variables while holding the effect of a third variables constant, were used. The partial correlation coefficient is diagrammed as follows:



where:

v_1 , v_2 and v_3 represent variables 1, 2 and 3.

$r_{12.3}$ is the partial correlation coefficient between variables 1 and 2, with the effect of variable 3 held constant.

$r_{23.1}$ and $r_{13.2}$ are, similarly, the partial correlation coefficient between variables 2 and 3, 1 and 3 with the effect of variables 1 and 2 respectively held constant.

3.8.7 Regression Analysis

A simple regression analysis was used to examine the relationship between total dry weight accumulation at final harvest and total leaf area duration. The dependent variables are predicted from a linear function of the form (Draper and Smith 1981):

$$\hat{y} = a + bX$$

where \hat{y} = estimated value of the dependent variables y,

a = intercept,

b = regression coefficient,
which is the slope,

X = independent variable.

The analysis was carried out by SPSS (Nie et al 1975) which also determined the coefficient of multiple determination (R^2) by formula:

$$R^2 = (SS_{yy} - SS_{res}) / (SS_{yy})$$

where SS_{yy} = sums of squares in y,

SS_{res} = residual sums of squares.

The homogeneity of the two regression coefficients of the regression lines, $\hat{y}_1 = a_1 + b_1X_1$ and $\hat{y}_2 = a_2 + b_2X_2$, was analysed using the t-test formula (Gomez and Gomez 1984):

$$t = \frac{(b_1 - b_2)}{\sqrt{[S_p^2(1/\Sigma x_1^2 + 1/\Sigma x_2^2)]}}$$

$$\text{where } S_p^2 = \frac{(n_1 - 2) S^2_{xy_1} + (n_2 - 2) S^2_{xy_2}}{n_1 + n_2 - 4}$$

S_p^2 = pooled residual mean squares,

$S^2_{xy_i}$ = residual mean square for lines

$$\Sigma x_i^2 = \frac{S^2_{xy_i}}{(SEb_i)^2}$$

This is equivalent to establishing that $b_1 = b_2$; that is, the slopes of the regression lines are the same.

4 EXPERIMENTAL RESULTS*

4.1 INTRODUCTION

In this chapter, the experimental results are presented in four major sections. Sections 4.2 and 4.3, deal with climatic data during the experimental period and adjustment for "without-neighbour effect". In Sections 4.4, 4.5 and 4.6, data regarding the growth and development of Cucurbita moshata Dunchesne; cultivar Waltham Butternut, partitioning of dry matter and correlation and regression data will be considered sequentially.

The use of capital letters A, B, C, D, AB, ABC, CD, BCD, CON (as previously introduced in Chapter 3) to denote the nine treatments is continued here and throughout the rest of the thesis.

Since root sampling was not included in this experiment, only data from above ground parts are available. Consequently, all data presented throughout the thesis will represent the above ground plant parts only. Furthermore, unless otherwise stated, all data presented are on a per plant basis.

All the mean separations were carried out by the use of the Duncan Multiple Range Test (DMRT) method at $P < 0.05$ levels. In the tables, this is denoted by small letters attached to each means. At a given column or time, mean values followed by different letters show they were different significantly. Columns without any letters show the means were not significantly different.

4.2 CLIMATIC DATA

The weekly rainfall and irrigation, maximum and minimum temperature, and bright sunshine hours are shown in Appendix 1a,

* All ANOVA data are deposited in Massey University Library.

1b and 1c respectively. Low rainfall was recorded in the week during defoliation treatments and toward the end of the growing period (week 14, 15, 17, 18). Supplementary irrigation was given during the low rainfall periods (Appendix 1a)

Fluctuating temperatures were recorded until a maximum of 25°C in the week 11 was reached followed by progressive reductions. Nevertheless, abrupt reductions in temperatures were recorded in weeks 4, 10 and 14. Similar patterns of reduction were recorded in the weekly minimum temperatures.

A big weekly fluctuation was observed in bright sunshine hours, with a maximum of about 10 hours/day in week 10. However, in week 9 and 11, the recorded values were very low. There was a trend of high sunshine hours toward the end of the growing period (week 18) (Appendix 1c).

4.3 ADJUSTMENT FOR "WITHOUT-NEIGHBOUR EFFECT"

Relative efficiency (RE) of covariance analysis for all variables was found to be less than 100% meaning that the experimental precision was reduced when adjusted for "without-neighbour" effects. This result implied that the increase in space between plants in the planting rows had no effect on all variables. This was due probably to the nature of experiment which allowed each plant to grow with only one main stem and without side branching. Thus the side growth was reduced to a minimum.

No adjustment was made therefore to all data.

4.4 PLANT GROWTH AND DEVELOPMENT

4.4.1 Whole Plant Data

4.4.1.1 The Control Plants

Initially, growth component data of CON plants which represent the plant growth without treatment effects were examined. Figure 4.1 shows the total dry matter accumulation of CON plants plotted against time. To show the instantaneous plant growth rate, the mean of total dry weight is plotted on \log_e scale. The figure shows that, CON plants entered their grand period at about 75 DAT and finished at about 100 DAT.

The computed R, E, and F values are shown in Figures 4.2a, 4.2b and 4.2c. The formulae of computations are shown in Chapter 2. Figure 4.2b shows that, E values confirm the normal trend which increased toward the maximum in the middle of the growing period (between 50 to 60 DAT), then dropped quite abruptly after 80 DAT. The R values reached a maximum during 20 to 30 DAT, then dropped progressively till they reached a minimum value during 99 to 109 DAT. The F values were at maximum during 20 to 30 DAT then, reduced progressively toward a minimum at maturity.

In general, the growth of CON plants appeared to be smooth, except for a sudden fall in E during 57 to 65 DAT and 99 to 109 DAT (Figure 4.2b). As a result, a substantial fall in R occurred in the same periods (Figure 4.2a).

4.4.1.2 Total Dry Matter Accumulation

The most direct effect of defoliation was to reduce the total dry weight of treated plants to values significantly lower than those of CON plants (Table 4.1). These values were however increased again at different rates depending on the treatments (Figure 4.3). The effect of these differences showed at final harvest (134 DAT). The highest total dry weight was $1763.97 \text{ g plant}^{-1}$, accumulated by treatment BCD plants. CON

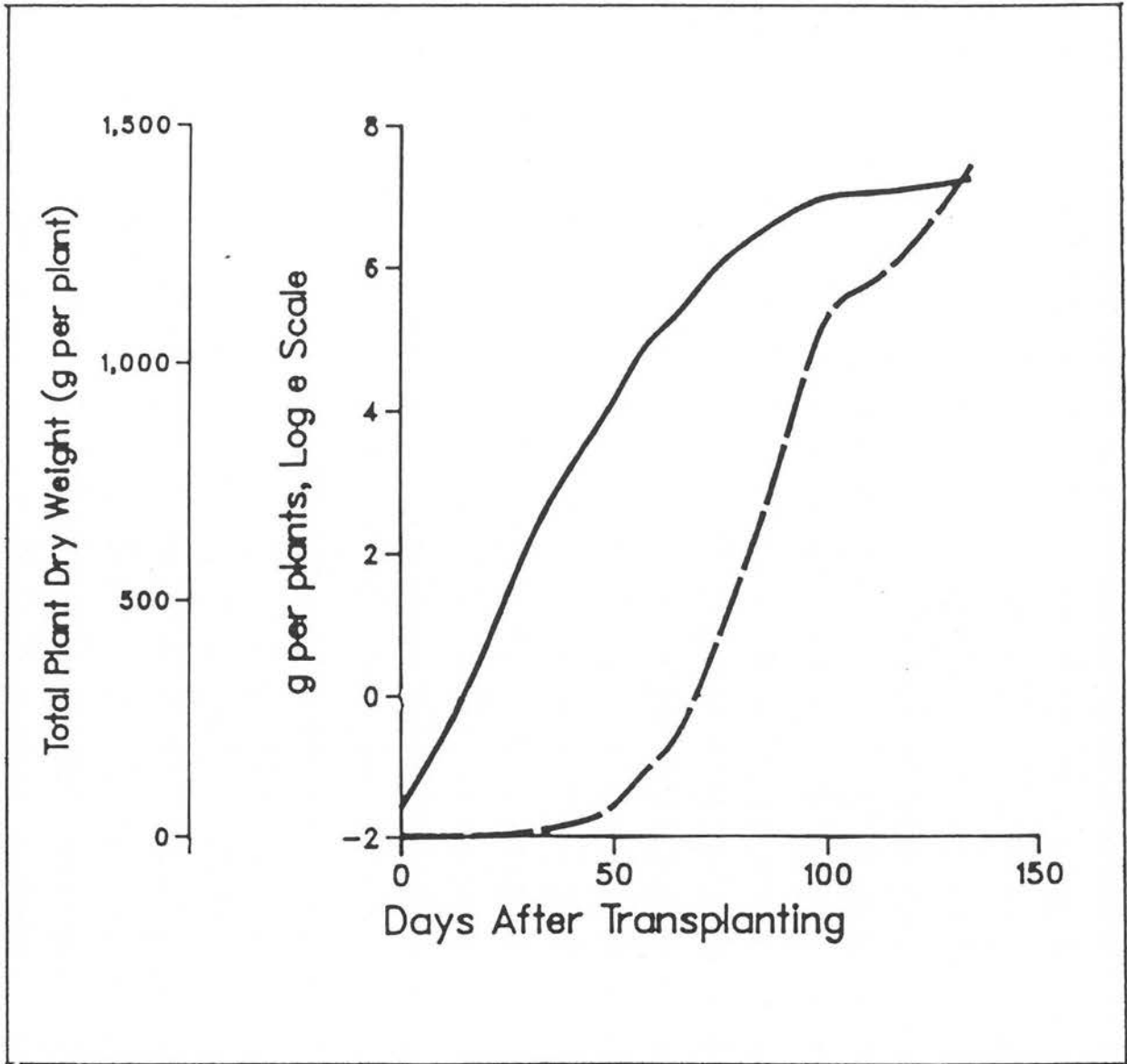


Figure 4.1: Changes in total dry weight of CON plants with time (——). The broken line (-----) shows dry weight on \log_e scale.

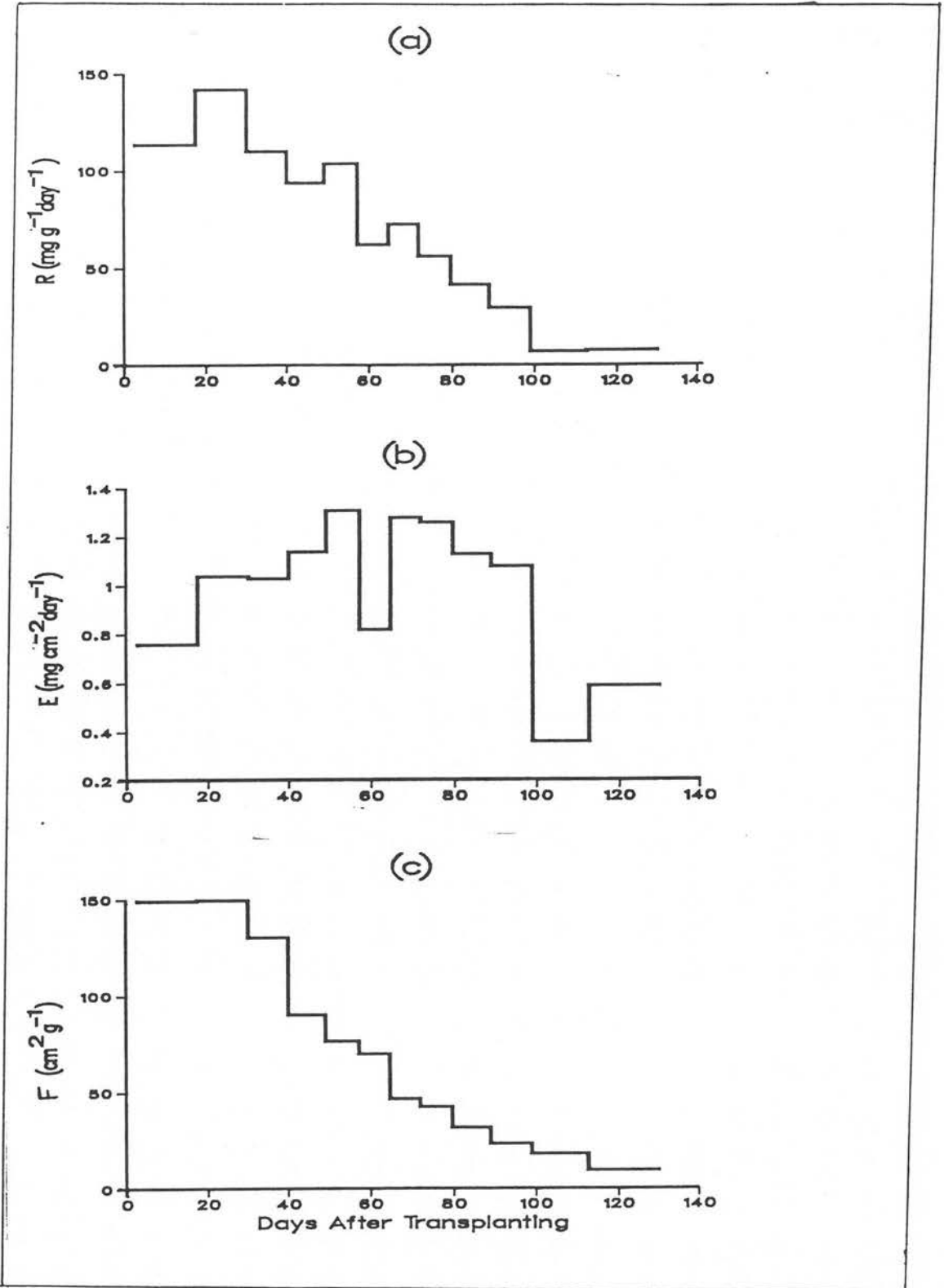


Figure 4.2: Relative growth rate (a), unit leaf rate (b) and leaf area ratio (c) of CON plants.

TABLE 4.1: MEAN VALUES OF TOTAL DRY MATTER (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING						
	72	79	89	99	109	134	
A	147.7 ab	143.4 b	196.9 a	161.8 a	170.3 a	150.38 a	(10.69)*
B	143.3 ab	190.6 ab	270.0 a	281.8 ab	340.9 ab	269.72 ab	(19.1)
C	187.5 b	216.4 ab	310.5 a	421.2 b	545.6 bc	492.77 bc	(34.9)
D	112.1 a	137.5 a	227.9 a	365.7 ab	534.0 bc	627.23 cd	(44.4)
AB	211.0 bc	251.3 bc	272.9 a	432.2 b	406.7 ab	410.43 abc	(29.0)
ABC	284.5 d	376.2 d	661.3 bc	796.9 cd	793.6 cd	835.78 de	(59.1)
CD	209.1 bc	291.8 cd	567.0 b	727.8 c	934.8 de	1044.32 e	(73.9)
BCD	254.9 cd	500.5 e	696.7 cd	970.6 de	1197.1 e	1763.97 g	(124.8)
CON	357.4 e	529.4 e	801.5 d	1077.7 e	1159.4 e	1413.23 f	(100.0)
CV%	20	21	16	23	28	25	

* Value in the bracket shows the percentage of dry weight as compared to CON.

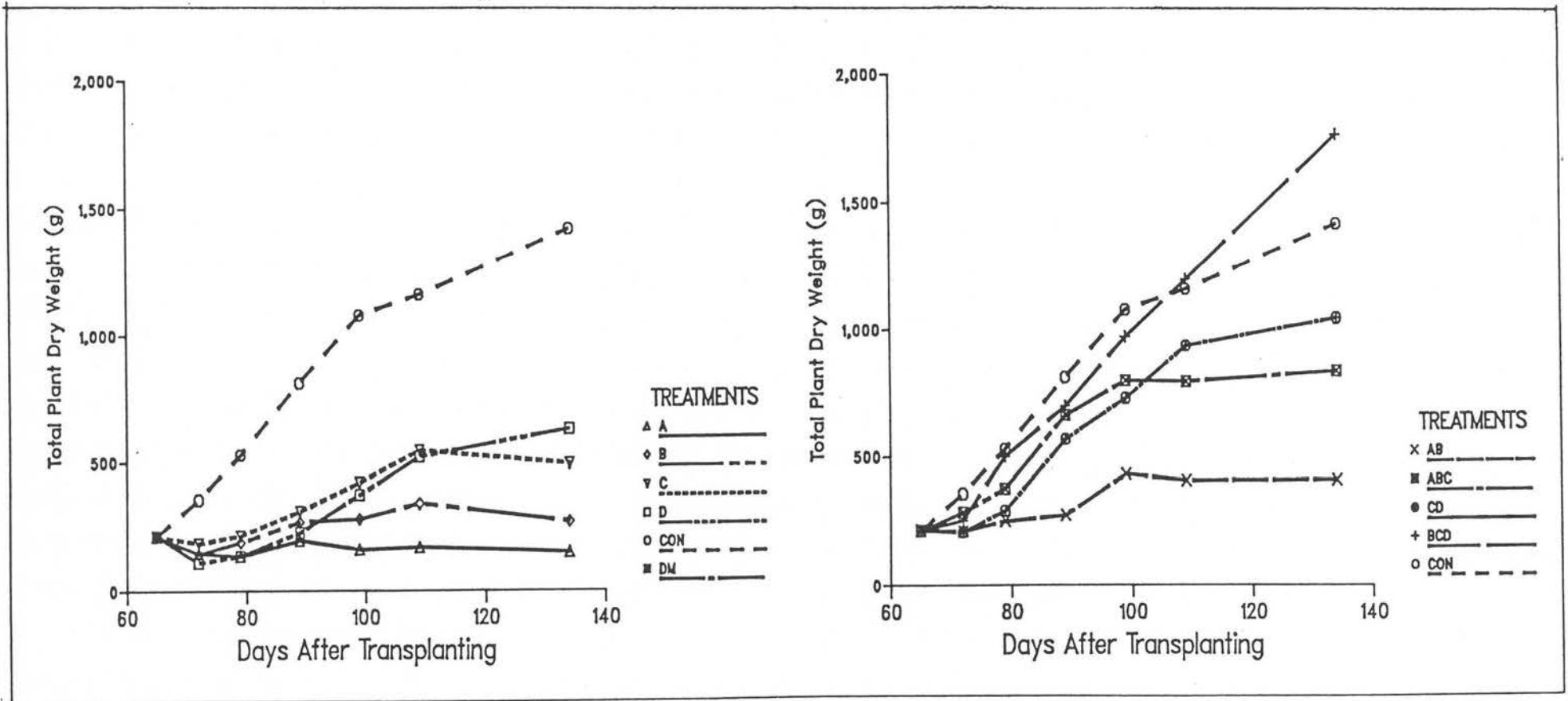


Figure 4.3: Effect of treatments on total plant dry weight accumulation.

plants accumulated only 1413.23 g plant⁻¹ and were significantly lower than that of BCD plants. The lowest dry weight was accumulated by treatment A plants which was only 150.38 g.

The results above plus significant differences observed at all harvests suggest that the total dry weight accumulation was greatly affected by defoliation treatments.

4.4.1.3 Relative Growth Rate (R)

As expected, the most obvious effect of defoliation was to bring down the R values of all treated plants to those lower than the control plants (Table 4.2). The highest fall was found in plants receiving treatment D (Figure 4.4). However, their R increased again at a very fast rate to reach a maximum in P5 (89 to 99 DAT) before slowly declining.

The R values of plants receiving treatment BCD also increased again after defoliation, reaching a maximum in P3, then declined at about the same rate toward P4 where thereafter, they decreased at a much slower rate (Figure 4.4). They were significantly higher than the control plants in P3 and P7 (Table 4.3).

Generally, there was a trend of increased R values after a sharp fall due to defoliations with different treatments reaching different values before declining again.

4.4.1.4 Unit Leaf Rate (E)

There was an increase in E values for all treated plants, after a sharp fall due to defoliations. Very unstable E values were recorded in plants receiving treatment A. They increased to a maximum in P4 and then declined to a very low value in P5 before increasing again in P6. Thereafter, they reduced abruptly to a minimum in P7 (Figure 4.5). It was also observed that the fluctuation of E values became less obvious in treatments ABC, CD, BCD and CON plants (Figure 4.5).

TABLE 4.2: MEAN VALUES OF UNIT LEAF RATE (E) ($\text{mg cm}^{-2} \text{ day}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	-1.2875 b	-0.4974 a	1.9965 e	-2.1498 a	1.8345 a	-2.3200
B	-1.0531 c	1.2017 bc	1.5299 d	0.1770 b	1.6849 a	-3.2664
C	-0.3875 d	0.5620 b	1.2985 cd	1.5157 bc	1.9024 b	-0.5333
D	-1.6592 a	0.5175 b	0.8762 b	1.1064 bc	1.3066 a	0.4394
AB	-0.0578 e	0.7715 b	0.3438 a	2.4617 c	0.4332 a	-1.2537
ABC	0.7051 g	0.9873 bc	2.0607 e	0.9225 bc	0.0071 a	0.2259
CD	-0.0669 e	0.8412 b	1.5519 d	0.8319 bc	1.1135 a	0.3102
BCD	0.3807 f	1.9532 e	0.8844 b	1.1807 bc	0.9949 a	1.1808
CON	1.2763 h	1.2568 bc	1.1322 bc	1.0824 bc	0.3586 a	0.5906
CV%	17	73	18	125	403	541

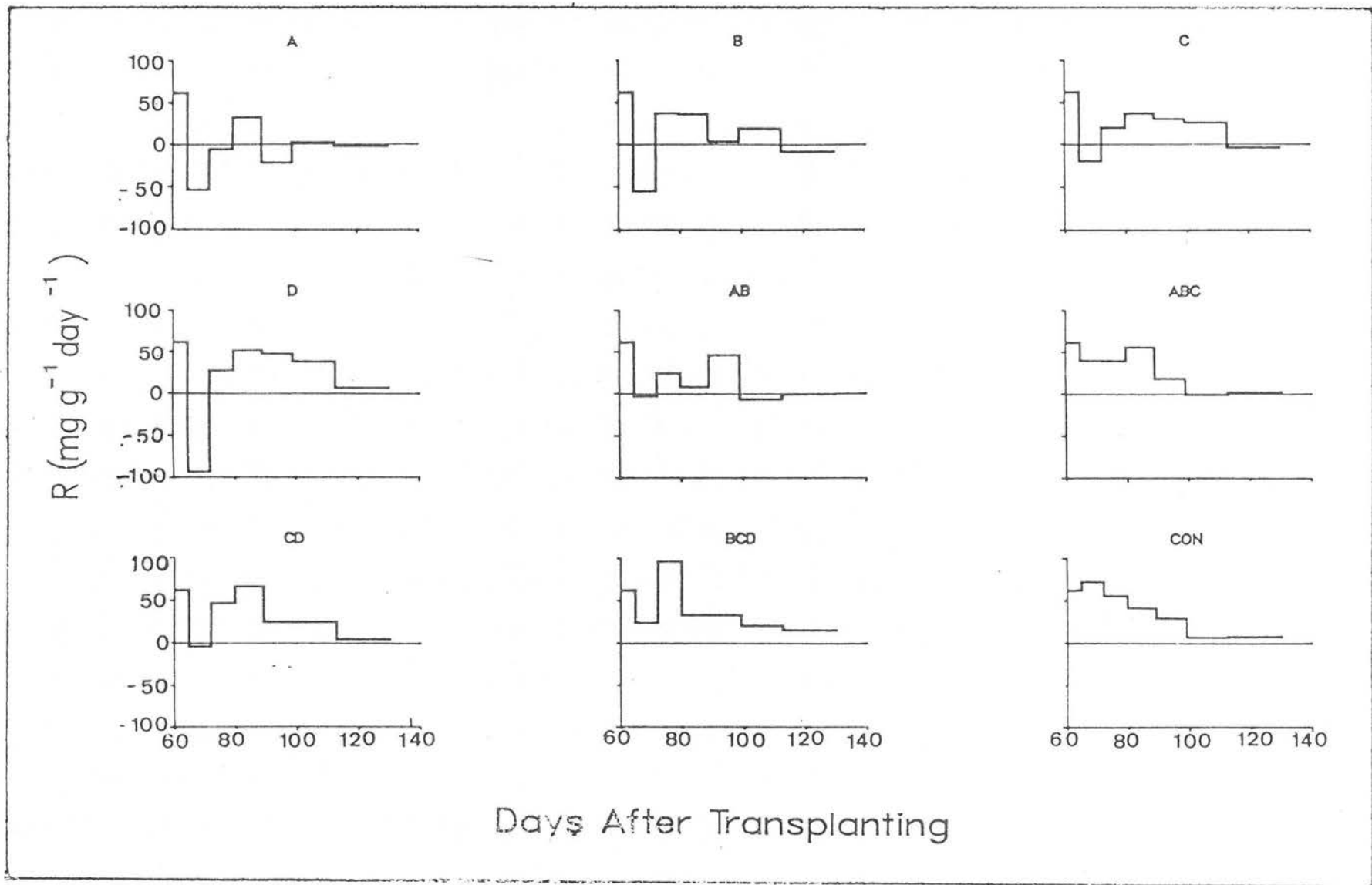


Figure 4.4: Effect of treatments the relative growth rates (R).

TABLE 4.3: MEAN VALUES OF RELATIVE GROWTH RATES (R) ($\text{mg g}^{-1} \text{day}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	-53.969 b	-5.992 a	32.455 b	-22.116 a	2.306 ab	-3.111 abc
B	-55.289 b	36.870 cd	35.264 b	3.600 b	18.771 abc	-9.034 a
C	-19.799 c	19.776 b	36.433 bc	30.302 cd	25.837 bc	-3.931 ab
D	-93.450 a	27.290 bc	51.577 d	47.182 f	37.950 c	6.602 de
AB	-2.893 d	24.433 bc	8.367 a	45.863 ef	-6.527 a	-0.749 bcd
ABC	39.860 f	39.673 cd	56.540 d	18.585 c	-0.486 ab	2.132 bcde
CD	-4.166 d	47.236 de	66.657 e	24.891 cd	25.023 bc	4.485 cde
BCD	24.127 e	96.318 f	33.129 b	33.121 de	20.961 abc	15.540 f
CON	72.451 g	56.015 e	41.533 c	29.577 cd	7.275 ab	7.955 e
CV%	22	27	10	37	121	230

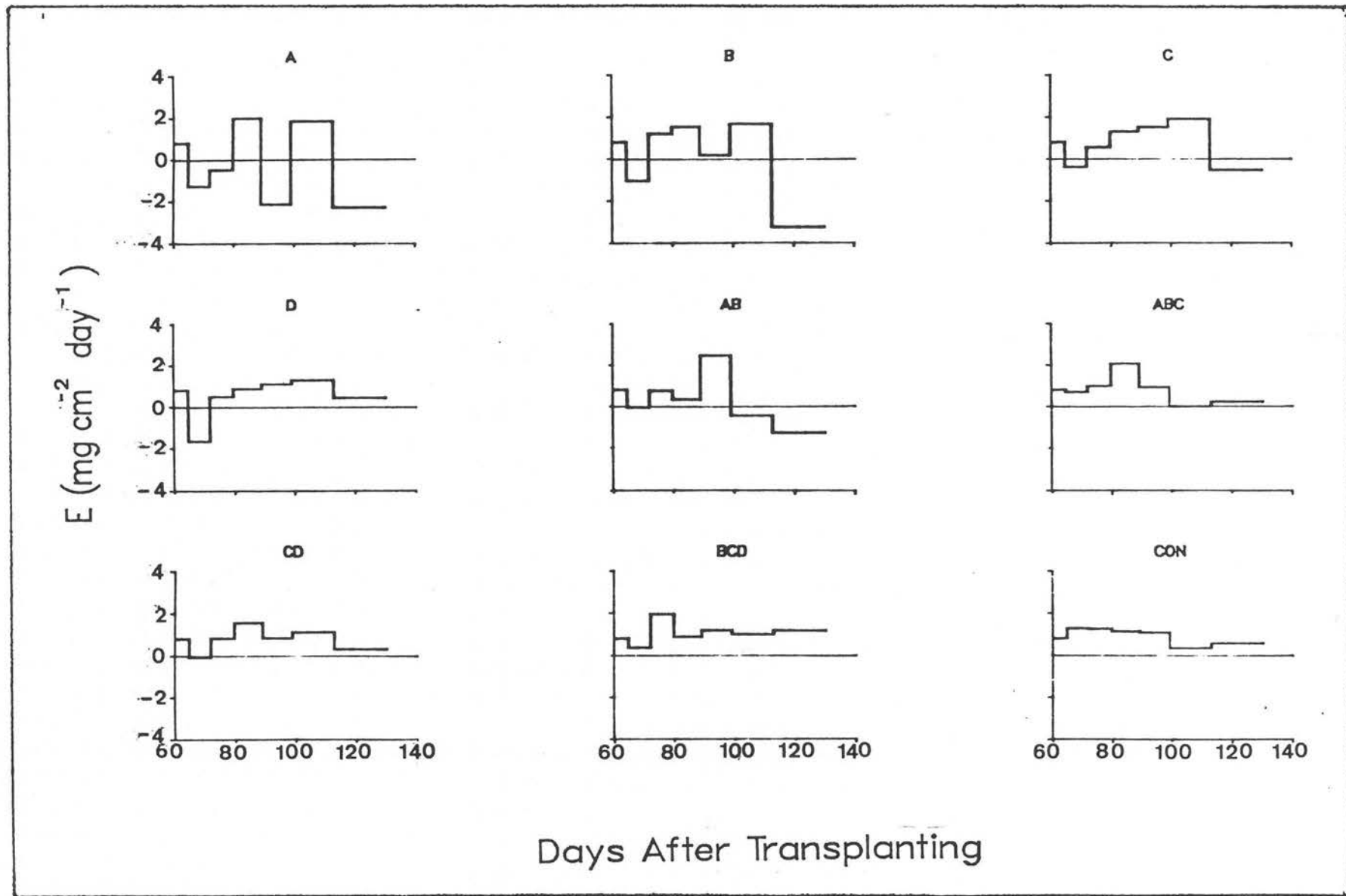


Figure 4.5: Effect of treatments on unit leaf rates (E).

Significant differences amongst treatment means observed in P2, P3, P4, and P5 (Table 4.3) suggest that the E values of treated plants were affected by defoliation treatments in these periods.

4.4.1.5 Leaf Area Ratio (F)

Except for plants receiving treatment D, the F values of plants receiving other treatments followed the same trend as the control plants (Figures 4.6), with values decreasing constantly with time.

The F value of plants receiving treatment D increased at a very high rate after defoliation treatments to reach a maximum in P3. Thereafter, it reduced progressively until final harvest but was still significantly higher than the rest of the treatments until P6. Except in P2, the F value of plants receiving treatment BCD was found to be not significantly different from the control.

Significant differences amongst treatment means observed in all periods suggest that the F of treated plants was greatly affected by defoliation (Table 4.4).

4.4.1.6 Leaf Area Duration (D)

The D of treatment A plants showed constantly lower values while on the other hand, except in period 2, the D of CON and BCD plants maintained significantly higher values in all periods (Table 4.5). Even though not significantly different, the D of treatment BCD plants was slightly higher than that of CON plants in the last period.

4.4.1.7 Specific Leaf Area (SLA)

Treatment D plants maintained the highest SLA from periods 3 to 7 (Table 4.6). In period 2, the SLA of treatment C and D plants was the highest. In period 7, the SLA of treatment CD reached the same level as that from treatment D plants.

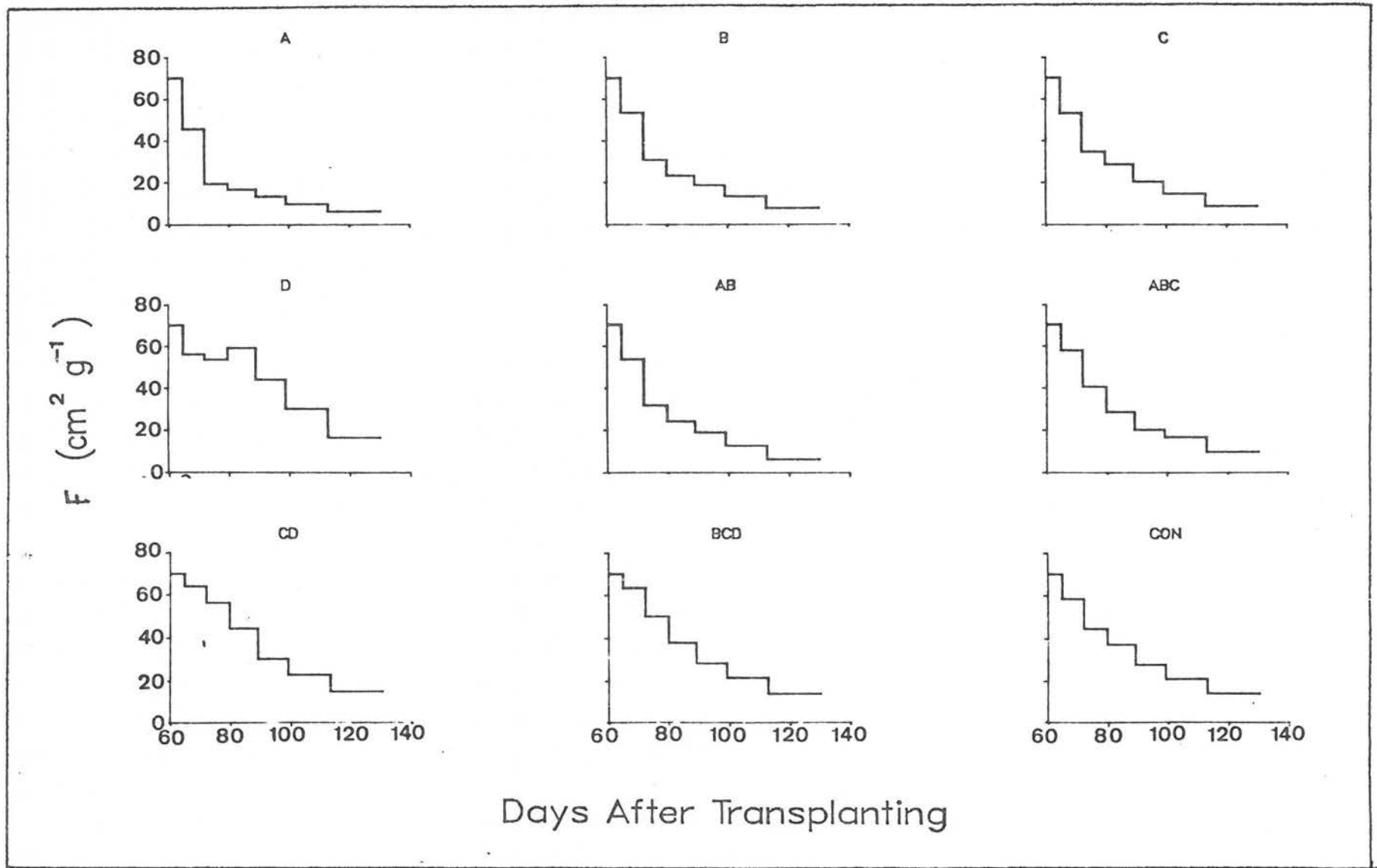


Figure 4.6: Effect of treatments on leaf area ratios (F).

TABLE 4.4: MEAN VALUES OF LEAF AREA RATIO (F) ($\text{cm}^2 \text{g}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	21.076 a	17.337 a	15.606 a	10.669 a	8.583 a	3.643 ab
B	36.880 b	24.675 b	21.642 b	15.748 b	11.199 abc	4.639 ab
C	35.896 b	33.448 c	23.604 b	16.918 b	12.272 bc	5.397 b
D	42.506 c	64.970 f	53.604 e	34.831 d	25.647 e	7.551 c
AB	37.205 b	26.211 b	22.275 b	15.823 b	9.494 ab	2.936 a
ABC	45.645 d	35.524 c	21.746 b	18.718 b	14.604 c	4.833 ab
CD	58.439 e	54.382 e	35.018 d	25.732 c	20.235 d	9.717 d
BCD	56.983 e	43.741 d	32.349 c	24.562 c	18.466 d	9.408 cd
CON	46.853 d	42.632 d	31.961 c	23.545 c	18.254 d	9.725 d
CV%	3.3	8.3	5.2	9.1	14	21

TABLE 4.5: MEAN VALUES OF LEAF AREA DURATION (D) (cm² day)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (62-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	63591 a	19890 a	28216 a	24854 a	17341 a	21743 a
B	71563 ab	35173 b	52529 b	51687 b	41660 ab	61958 ab
C	72254 c	48668 bc	72711 b	72588 b	69296 b	116730 bc
D	69317 ab	47094 bc	104270 c	127214 c	131564 c	230291 d
AB	80183 c	50390 c	63127 b	64729 b	53798 b	56454 ab
ABC	98177 d	92082 d	138549 d	146549 c	132576 c	195158 cd
CD	95463 d	97987 d	173171 e	192842 d	190779 a	377125 e
BCD	103539 d	127289 e	221943 f	231857 e	229676 e	483490 f
CON	111340 e	137463 e	237621 f	252960 e	232626 e	436014 ef
CV%	6.2	13	12	13	15	25

TABLE 4.6: MEAN VALUES OF SPECIFIC LEAF AREA (SLA) ($\text{cm}^2 \text{g}^{-1}$)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	90.88 a	75.56 a	71.93 a	59.94 a	50.9 a	50.4 a
B	101.77 c	95.83 c	92.94 c	84.21 c	72.0 bc	53.2 ab
C	110.07 e	115.68 e	113.70 e	99.61 e	86.5 d	79.1 cd
D	110.01 e	137.02 h	161.35 h	140.59 h	145.6 f	134.8 f
AB	97.38 b	88.76 b	85.41 b	78.39 b	67.1 b	54.5 ab
ABC	99.95 bc	101.78 d	104.13 a	92.28 d	81.0 cd	67.2 bc
CD	114.17 f	130.33 g	137.99 g	125.45 g	118.2 e	103.3 f
BCD	108.47 de	121.46 f	125.95 f	117.30 f	115.0 e	100.2 e
CON	106.08 d	113.98 e	121.35 f	115.90 f	111.3 e	92.8 de
CV%	2.0	3.1	2.8	3.1	7.8	8.8

Except in period 3, the SLA of BCD plants did not differ significantly from that of CON plants. However the trend of higher SLA in BCD plants still remained until the final period.

4.4.1.8 Overall Growth Component Data

Highly significant differences among treatment means observed in the ANOVA of overall D, SLA, F and R suggest that they were greatly affected by defoliation treatments (Table 4.7). Low significant differences ($P < 0.05$) observed in ANOVA of overall E could be due to the very high CVs recorded. Examining the residual values show that this was due to very high variation in treatment A plants.

Plants receiving treatments BCD and CON recorded significantly higher overall D and R than those of the rest of treatments. The highest overall SLA and R were observed in treatment D plants. Treatment BCD plants recorded slightly higher overall R and E than those of CON plants. They were however not significantly different.

The lowest overall SLA, F and R were observed in both treatment A and B plants. Overall E was lowest in treatment A plants but it did not differ significantly from E values of treatments B, D and AB plants.

The negative values of overall R and E observed in treatment A plants indicate that they were actually losing their dry weight after defoliation treatments.

TABLE 4.7: MEAN VALUES OF OVERAL GROWTH COMPONENTS DATA

TREATMENTS	GROWTH COMPONENTS				
	D	SLA	F	R	E
A	32449 a	66.61 a	18.36 a	-8.40 a	-0.403 a
B	52428 ab	83.34 c	24.56 b	5.03 b	0.046 ab
C	76041 b	100.78 e	26.67 c	14.77 d	0.726 bc
D	118646 c	138.39 i	43.40 h	12.86 cd	0.431 a-c
AB	61447 b	78.58 b	24.59 b	11.42 c	0.305 a-c
ABC	133849 c	91.05 d	28.95 d	26.05 e	0.816 bc
CD	191262 d	121.57 h	38.95 g	27.35 e	0.764 bc
BCD	232965 e	114.72 g	35.98 f	37.20 f	1.096 c
CON	237816 e	110.23 f	33.86 e	35.80 f	0.950 c
CV%	13	2.1	2.7	8.5	102

4.4.2 Stem Data

4.4.2.1 Total Stem Dry Weight

Figures 4.7a and 4.7b show the time trend of stem dry matter accumulation. Total stem dry weight was found to be little affected by defoliation treatments. There were no significant differences observed at 72, 99 and 109 DAT (Table 4.8). Significant differences among treatment means in some of the treatments were observed at 79, 89 and 134 DAT.

4.4.2.2 Relative Growth Rate (R_S)

Plants receiving treatment A were observed to lose stem dry weight in P4, a response which was earlier than that of the control plant. The stems of plants receiving treatments CD and BCD were observed to continue their growth until final harvest (Table 4.9).

Significant differences amongst treatments observed in all periods suggest that the R of stems (R_S) was affected by defoliations.

4.4.2.3 Stem Length and Number of Node

Except at 89 and 134 DAT, the means of stem lengths were not significantly different among the treatments (Table 4.10). This result suggested that the defoliation effects were small and observed only at the two harvests mentioned above.

Defoliation treatments did not affect the number of nodes per plant. This is shown by the nonsignificant differences in means of node number at all harvests (Table 4.11).

4.4.2.4 Dry Weight of Stem From Different Sections

Nonsignificant differences among treatment means in Table 4.12, suggest that defoliation treatments did not affect

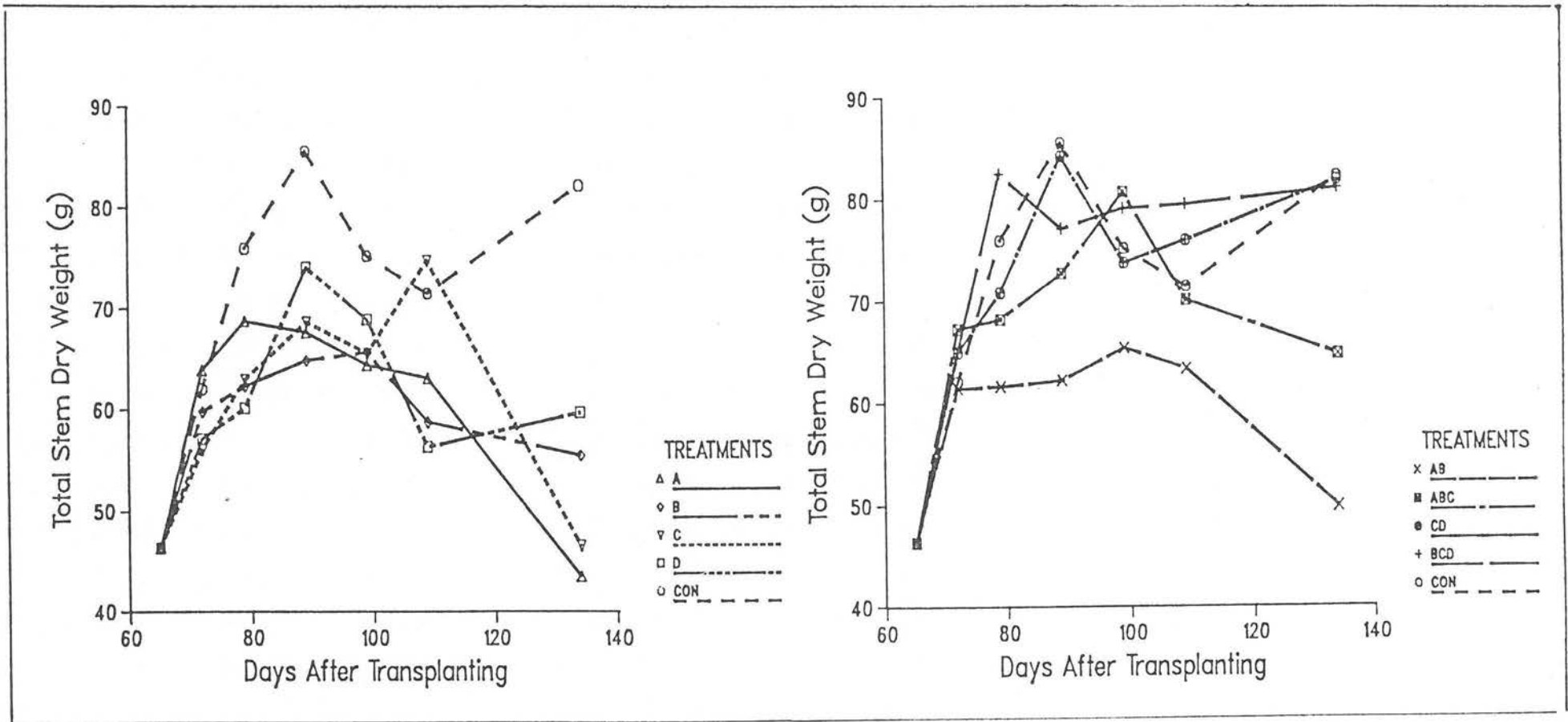


Figure 4.7: Effect of treatments on stem dry weight accumulation.

TABLE 4.8: MEAN VALUES OF TOTAL STEM DRY WEIGHT (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	63.92	68.96	67.58 a	64.32	63.02	43.45 a
B	59.79	62.30	64.83 a	65.57	58.70	55.42 a
C	56.05	62.94	68.59 a	65.47	74.67	46.50 a
D	57.13	60.13	74.02 ab	69.33	58.00	59.62 a
AB	61.41	61.58	62.19 a	65.35	63.31	51.48 a
ABC	67.23	68.19	72.71 ab	80.62	70.04	64.61 ab
CD	64.95	70.81	84.15 b	73.73	75.32	81.74 b
BCD	64.92	82.48	77.10 ab	79.05	79.38	80.94 b
CON	62.05	75.94	84.75 b	75.16	71.38	82.06 b
CV%	17	13	13	17	20	22

TABLE 4.9: MEAN VALUES OF R FOR TOTAL STEM DRY WEIGHT (R_S) ($\text{mg g}^{-1} \text{ day}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	46.24 f	10.86 e	-2.10 b	-5.03	-2.01 f	-14.94 b
B	36.68 c	5.92 c	3.91 d	1.05 d	-11.07 c	-2.30 d
C	27.46 a	16.61 g	8.52 f	-4.74 c	13.22 i	-19.01 a
D	30.18 b	7.33 d	20.74 i	-6.63 b	-17.85 a	1.10 e
AB	40.50 d	0.43 a	0.89 c	4.89 f	-3.14 e	-8.30 c
ABC	53.47 h	2.03 b	6.36 e	10.29 g	-14.07 b	-3.24 d
CD	48.53 g	12.36 f	17.23 h	-13.31 a	2.17 h	3.28 f
BCD	48.56 g	34.24 i	6.81 a	2.44 e	0.45 g	0.78 e
CON	41.99 e	28.90 h	10.93 g	-12.08 a	-0.14 d	5.59 g
CV%	28	36	72	36	113	90

TABLE 4.10: MEAN VALUES OF TOTAL LENGTH OF STEM (cm plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	364	454	436 ab	448	472	464 ab
B	369	415	464 ab	496	508	486 a-c
C	355	439	473 b	499	528	431 a
D	355	423	505 cd	528	612	567 b-d
AB	362	403	432 a	497	516	486 a-c
ABC	349	414	463 ab	466	500	484 a-c
CD	372	476	507 cd	522	596	611 cd
BCD	366	483	508 cd	535	573	651 d
CON	365	482	515 d	506	537	546 cd
CV%	8	9	5	10	12	15

TABLE 4.11: MEAN VALUES OF TOTAL NUMBER OF NODES PER PLANT

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	36.75	42.07	42.75	42.50	44.75	44.3
B	34.75	41.25	44.00	46.75	47.00	46.4
C	36.00	41.25	42.25	46.75	46.25	38.3
D	35.25	40.50	42.75	45.96	45.82	48.5
AB	35.25	38.50	43.75	47.75	44.50	46.6
ABC	35.25	40.25	43.50	46.50	44.75	42.0
CD	35.50	41.75	43.00	44.25	44.75	79.8
BCD	35.50	41.50	43.00	42.75	47.25	51.8
CON	34.50	41.25	42.61	44.75	45.25	48.8
CV%	4	5	5	8	7	15

TABLE 4.12: MEAN VALUES OF STEM DRY WEIGHT FROM SECTION A (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	12.12	10.15	11.02	8.65	9.38	9.06
B	9.80	58.66	9.18	8.21	7.94	6.42
C	8.87	8.77	9.21	6.79	8.85	6.91
D	7.35	7.62	9.70	8.11	7.10	6.16
AB	9.26	7.17	9.82	7.76	6.60	7.15
ABC	9.93	7.73	9.46	9.49	8.45	7.44
CD	8.47	9.88	10.71	7.95	8.31	8.90
BCD	12.11	12.75	11.52	10.37	9.98	9.46
CON	10.95	9.40	9.69	7.05	8.47	7.66
CV%	26	28	8	8	22	24

stem dry weights from Section A.

For stem dry weights from Section B (Table 4.13), significant differences were observed only at final harvest (134 DAT). The highest mean was observed in plants receiving treatment ABC. The same situation was found in stem dry weights Section C (Table 4.14) where a significant difference was observed only in the final harvest.

In Section D, significant differences among treatment means were observed in the third (89 DAT) and final harvests (134 DAT) (Table 4.15). The results suggest that stem dry weights from Section D was affected by defoliations in these periods.

4.4.3 Leaf Data

4.4.3.1 Total Leaf Dry Weight

The most obvious effect of defoliations was to reduce the total dry weight of most of the treated plants to values lower than those of CON plants (Table 4.16). These values however increased again at different rates depending on the treatments (Figure 4.8a and 4.8b)

Immediately after defoliations, plants receiving treatments A, B and D had significantly low leaf dry weights. The leaf dry weight of treatment A plants kept on reducing until 79 DAT and increased only a little at 89 DAT. It reduced again after 89 DAT to a minimum at 134 DAT. The leaf dry weights of plants receiving treatment B followed the same trend as those of treatment A, except that they gained a much higher dry weight at 89 DAT and this continued until final harvest. Treatment B plants had significantly higher leaf dry weights than those of treatment A plants at 89 and 109 DAT.

Significant differences among treatment means were observed at all harvests suggesting that the effect of defoliation was still present until final harvest.

TABLE 4.13: MEAN VALUES OF STEM DRY WEIGHT FROM SECTION B (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	16.95	14.28	13.58	13.36	11.82	9.23 a-c
B	13.61	11.83	10.94	11.19	11.13	9.54 a-d
C	13.22	12.60	13.11	12.00	10.70	7.55 a
D	11.75	11.12	12.83	10.74	8.63	8.35 ab
AB	14.35	10.64	9.73	12.70	9.73	9.55 a-d
ABC	14.09	11.10	12.44	14.53	11.58	12.99 d
CD	13.81	14.80	13.51	12.26	11.02	12.04 cd
BCD	16.95	13.26	14.56	11.30	13.41	11.41 b-d
CON	15.69	12.03	14.14	10.16	11.94	10.27 a-d
CV%	23	24	18	21	16	22

TABLE 4.14: MEAN VALUES OF STEM DRY WEIGHT FROM SECTION C (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	23.93	21.85	20.07	17.35	13.80	13.53 ab
B	21.34	15.72	19.51	16.55	17.05	13.73 ab
C	18.83	16.91	19.83	16.84	22.63	12.79 ab
D	12.19	18.45	17.56	15.46	12.12	11.90 a
AB	22.56	18.40	17.55	19.62	17.80	12.30 a
ABC	22.53	19.67	22.04	22.38	18.26	17.62 bc
CD	23.41	19.12	26.07	19.70	19.99	17.46 bc
BCD	23.23	25.35	20.38	22.77	18.62	19.61 c
CON	23.08	24.76	23.25	21.73	16.10	17.30 bc
CV%	17	21	5	19	24	20

TABLE 4.15: MEAN VALUES OF STEM DRY WEIGHT FROM SECTION D (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	10.93	22.7	22.9 a	25.0	28.0	11.6 a
B	15.04	26.1	25.2 ab	29.6	22.6	25.7 a-c
C	15.13	24.7	26.4 ab	29.8	32.5	19.2 ab
D	15.84	22.9	33.9 bc	35.0	30.1	33.2 b-d
AB	15.24	25.4	25.1 ab	25.3	29.2	20.8 ab
ABC	20.68	29.7	28.8 a-c	34.2	31.8	26.6 a-c
CD	19.36	27.0	33.9 bc	33.8	36.0	43.3 cd
BCD	12.63	31.1	30.6 a-c	34.6	37.4	40.5 cd
CON	12.32	29.8	37.7 c	36.2	34.9	46.8 d
CV%	3	28	21	28	34	37

TABLE 4.16: MEAN VALUES OF TOTAL LEAF DRY WEIGHT (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134*
A	40.97 a	32.80 a	44.87 a	33.67 a	28.25 a	5.11 a
B	55.20 a	49.69 ab	63.78 b	58.12 ab	55.89 b	23.96 ab
C	58.90 b	61.41 b	67.01 b	80.21 bc	79.45 b	35.97 ab
D	40.89 c	55.42 ab	74.00 b	109.14 c	78.13 b	50.56 bc
AB	88.51 b	73.79 b	74.17 b	91.42 bc	64.44 b	14.41 ab
ABC	138.54 cd	121.40 c	146.24 c	173.13 de	152.52 e	68.58 bc
CD	99.93 b	114.13 c	144.46 c	165.21 d	153.58 e	121.51 cd
BCD	131.07 c	165.47 d	188.34 d	207.57 ef	191.79 f	194.82 d
CON	158.02 d	184.73 d	212.32 e	228.41 f	189.73 f	185.22 d
CV%	16.1	16.1	11.3	20.3	14.1	23.1

* ANOVA was carried out on transformed data. The formula of transformation is $y = \sqrt[3]{x}$, where x = original data and y = transformed data.

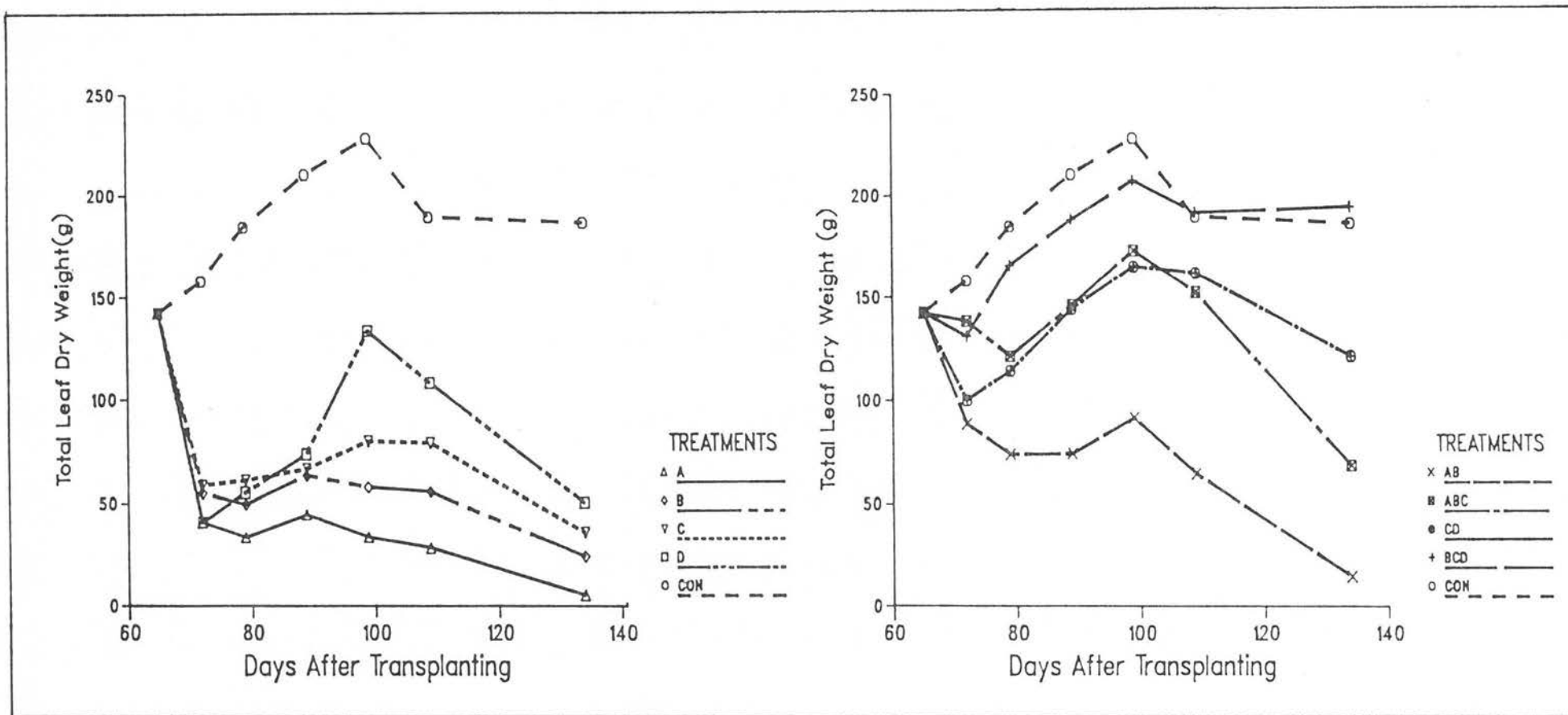


Figure 4.8: Effect of treatments on leaf dry weight accumulation.

4.4.3.2 Total Leaf Area

As expected, defoliation treatments brought the total leaf area of all treated plants to a level significantly lower than those of CON plants as shown at 72 DAT in Table 4.17. The general recovery trends of total leaf area were quite similar to those of total leaf dry weight (Figure 4.9a and 4.9b).

Leaf area of CON plants differed significantly from that of treatment BCD only at 71 and 89 DAT. The data show a general trend of reducing differences among treatment means. This is indicated by only three homogeneous subsets remaining at final harvest as compared to five such subsets at 72 DAT.

At the first two harvests (72 and 79 DAT), treatments ABC, CD, BCD, CON had total leaf areas significantly higher than those of other treatments. However at 89, 99 and 109 DAT, only plants receiving treatments CD, BCD and CON remained significantly higher.

At final harvest, the leaf area of plants receiving treatment D was in the same homogeneous subset as those of treatments CD, BCD and CON. It is also interesting to note that, even though not statistically different, the total leaf area of BCD plants was slightly higher than those of CON plants toward the end of growing season as shown at 109 and 134 DAT in Table 4.15.

4.4.3.3 Relative Growth Rate (R_L)

The mean R_L of all treated plants except treatments A and B, became negative in period 6. The mean R_L of treatments A and B plants became negative in period 5 (Table 4.18). The negative value of R_L indicates that the leaf dry weight was reducing. In period 6, treatments D and AB plants had the highest rate of dry weight reduction. The lowest rate was in treatments B and C plants.

Treatment D plants showed a higher leaf growth in periods

TABLE 4.17: MEAN VALUES OF TOTAL LEAF AREA* ($\text{cm}^2 \text{ plant}^{-1}$)

TREATMENTS	DAYS AFTER TRANSLANTING					
	72	79	89	99	109	134
A	3089 a	2490 a	3059 a	1911 a	1557 a	183 a
B	5368 ab	4683 ab	5823 b	4514 ab	3818 ab	1139 a
C	6707 bc	7198 bc	7344 b	7173 b	6686 b	2652 ab
D	4725 ab	8731 c	12124 c	12716 c	13620 c	4729 bc
AB	7830 c	6568 bc	6058 b	6888 b	3872 ab	645 a
ABC	12971 d	13338 d	14372 c	14938 c	11577 c	4036 ab
CD	12195 d	15801 d	19833 d	18735 d	18884 d	10142 c
BCD	14503 d	21866 e	22523 d	23348 e	22087 d	16592 c
CON	16732 e	22543 e	25603 e	25382 e	21143 d	13738 c
CV%	16.2	16.3	14.2	16.4	22.0	41.55

* ANOVA was carried out on transformed means. The formula of transformation is $y = \sqrt{x}$, where x = original data and y = transformed data.

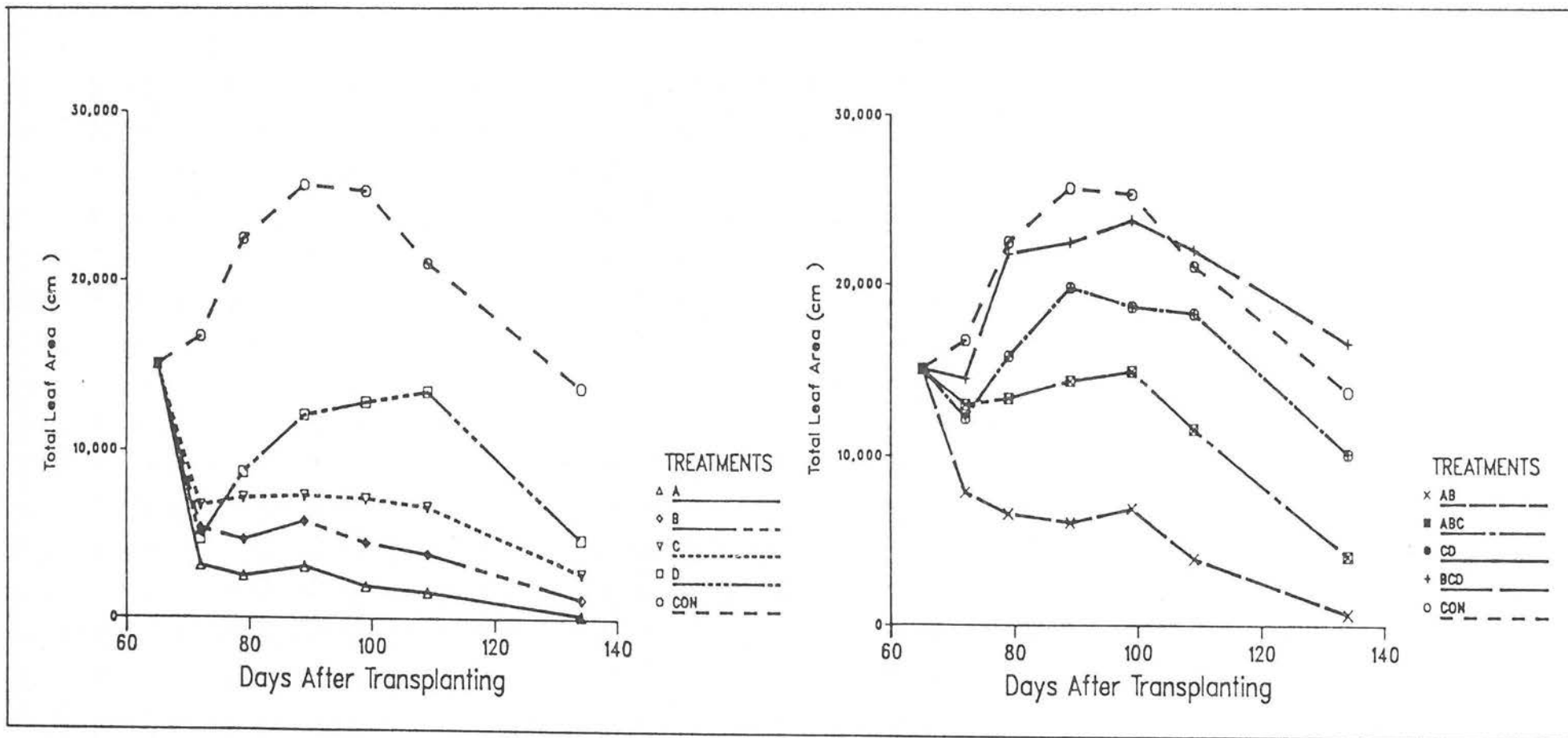


Figure 4.9: Effect of treatments on leaf area expansion.

TABLE 4.18: MEAN VALUES OF R FOR TOTAL LEAF DRY WEIGHT (R_L) ($\text{mg g}^{-1} \text{ day}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	-177.84 a	-29.23 a	31.95 g	-36.9 a	-13.38 bc	-41.9 ab
B	-135.13 b	-15.83 b	25.17 ef	-11.0 b	-2.43 d	-28.7 c
C	-125.78 c	5.38 c	8.75 b	17.2 c	-0.15 d	-34.0 bc
D	-178.14 a	42.93 f	29.10 fg	38.6 d	-33.15 a	-18.4 d
AB	-67.67 d	-26.33 a	0.48 a	20.3 c	-34.58 a	-44.5 a
ABC	-3.64 g	-18.99 b	18.64 d	16.7 c	-12.52 bc	-32.4 bc
CD	-50.33 e	18.85 d	23.60 e	13.2 c	-7.12 cd	-9.5 de
BCD	-11.56 f	33.23 e	12.95 c	9.6 c	-7.79 cd	0.6 f
CON	15.16 h	22.27 d	13.92 c	7.2 c	-18.47 b	-1.0 e
CV%	1.21	1.89	1.37	5.22	2.54	3.19

3, 4 and 5 before dropping suddenly in periods 6 and 7. The relative growth rate of treatment BCD plants was higher than that of CON plants in periods 3 and 7 and were not different significantly in periods 4 and 4.

4.4.3.4 Leaf Area Duration (D) from Different Sections

In Section A, there was a trend of higher D in treatment A than that of other treatments (Table 4.19). Except in period 4, this difference however was not big enough to show a significant difference statistically. In period 4, the mean of treatment A was significantly higher than that of treatment AB but not significantly different from those of treatments ABC and CON.

The D of sections B and C was not affected by defoliation treatments. This is showed by the nonsignificant differences amongst treatment means in all periods as shown in Table 4.21.

In Section D, significant differences were observed only in period 2 (Table 4.22). Nonsignificant differences amongst treatment means were observed in the rest of the periods. However, the trend of higher D for section D of treatment D and CD plants was still present until period 6.

4.4.3.5 Specific Leaf Area (SLA) From Different Sections

Generally, in Section A, leaf of CON plants had a higher SLA than those of other treatments. This is showed by the significant differences between treatment means in periods 2, 3, 4 and 6 (Table 4.23). The SLA of treatments AB and ABC plants was somewhere in between those of treatments A and CON. Period 7 was omitted from analysis due to a very large number of missing values.

In Section B, significant differences amongst treatment means were observed in periods 2 and 3. Nonsignificant differences were observed in the rest of the periods (Table 4.24). In the first two periods, CON and treatment BCD plants had a

TABLE 4.19: MEAN VALUES OF D FOR SECTION A (cm² day)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	19802	20131	28659 b	26751	19491	25237
AB	17202	15501	18130 a	17595	13793	11178
ABC	16831	15420	22091 ab	22301	17925	20513
CON	19229	17843	21738 ab	16416	11319	16232
CV%	15	25	18	35	54	52

TABLE 4.20: MEAN VALUES OF D FOR SECTION B (cm² day)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
B	35050	35173	52530	51687	41660	61958
AB	35090	34889	44997	47135	40005	45276
ABC	32950	32422	46553	49964	44304	64243
BCD	35568	39107	55016	52004	46588	80772
CON	36493	38757	53823	49854	39821	67483
CV%	11.5	16.8	15.5	13.2	14.2	33.1

TABLE 4.21: MEAN VALUES OF D FOR SECTION C (cm² day)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
C	44979	48668	72711	72588	69296	154269
ABC	42009	44239	69905	74285	70348	141863
CD	48207	54080	78927	72360	61499	106361
BCD	44625	50555	75532	71876	67829	141049
CON	42360	47742	72977	72223	63988	112529
CV%	8.3	11	7.8	11	13	19

TABLE 4.22: MEAN VALUES OF D FOR SECTION D (cm² day)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
D	22923 b	47094	104270	125427	130512	237244
CD	22365 b	43908	99244	120482	131889	263309
BCD	14742 a	37626	91395	107976	115260	261668
CON	14339 a	33956	86266	113486	116722	239752
CV%	17	22	15	16	20	26

TABLE 4.23: MEAN VALUES OF SLA FOR SECTION A ($\text{cm}^2 \text{g}^{-1}$)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
A	77.46 a	74.2 a	73.4 a	59.2	51.4 a	NA
AB	80.12 ab	77.6 ab	73.2 a	68.1	57.6 ab	NA
ABC	79.37 ab	82.8 b	85.6 b	74.7	62.6 ab	NA
CON	84.19 b	84.0 b	83.6 b	74.4	68.2 b	NA
CV%	4.1	6.3	6.2	13	14	

NA = Not available

TABLE 4.24: MEAN VALUES OF SLA FOR SECTION B ($\text{cm}^2 \text{g}^{-1}$)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
B	97.70 ab	95.7 ab	92.9	84.8	73.0	52.8
AB	94.62 a	92.7 a	90.3	83.6	70.7	44.9
ABC	94.84 a	98.7 ab	99.8	88.2	75.4	50.3
BCD	99.53 bc	102.4 bc	96.8	91.8	86.8	71.2
CON	102.26 c	108.5 c	105.8	96.1	84.0	61.4
CV%	2.9	5.7	9.2	9.3	13	34

significantly higher SLA than those of treatments B, AB and ABC.

In Section C, significant differences amongst treatment means were observed in periods 5 and 6 (Table 4.25). Period 7 was not included in the analysis for the same reason as in Section A. In periods 5 and 6, treatment C plants had a significantly lower SLA than those of treatments BCD and CON. Nonsignificant differences were observed amongst the means of treatment C, ABC and CD plants.

Defoliation treatments did not affect the SLA for Section D. This is illustrated by the nonsignificant differences amongst treatment means in all periods as shown in Table 4.26.

4.4.4 Flower Data

Nonsignificant differences at all harvests were observed in ANOVAs of male flower, female flower and total flower dry weights. Only the mean values of total flower dry weight are shown in Table 4.27. The results suggest that defoliation treatments did not influence flower dry weights.

4.4.5 Fruit Data

4.4.5.1 Total Fruit Dry Weight

ANOVA of total fruit dry weight revealed the presence of highly significant differences between treatment means at all harvests. These results suggest that fruit dry weight accumulations were greatly affected by defoliation treatments (Table 4.28). The time trends of dry weight accumulation of fruit in every treatment are shown in Figures 4.10a and 4.10b. Figure 4.10b shows that fruit from treatment BCD plants gained their dry weight at constantly high rates until final harvest (134 DAT).

The total fruit dry weights for each treatment at final harvest are shown in Figure 4.11. The figure clearly shows that,

TABLE 4.25: MEAN VALUES OF SLA FOR SECTION C ($\text{cm}^2 \text{g}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
C	118.8	115.4	113.2	99.5 a	87.1 a	NA
ABC	113.9	114.6	116.3	101.1 ab	90.5 a	NA
CD	120.6	119.7	115.6	101.6 ab	89.1 a	NA
BCD	120.2	123.6	120.9	113.6 bc	105.3 b	NA
CON	117.4	119.3	123.4	115.4 c	100.3 ab	NA
CV%	4.4	5.1	4.8	7.8	9.2	NA

TABLE 4.26: MEAN VALUES OF SLA FOR SECTION D ($\text{cm}^2 \text{g}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	2 (65-72)	3 (72-79)	4 (79-89)	5 (89-99)	6 (99-109)	7 (109-134)
D	139.02	138.4 ab	161.3	145.2	151.0	136.1
CD	145.72	147.0 b	162.9	146.0	137.5	125.0
BCD	141.52	143.8 ab	160.3	144.6	145.2	129.1
CON	138.89	133.4 b	150.9	150.3	150.9	132.1
CV%	2.8	4.5	8.3	8.8	13	12

TABLE 4.27: MEAN VALUES OF TOTAL FLOWER DRY WEIGHT (g plant^{-1})

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	6.81	5.15	2.90	1.165	0.277	0.41
B	7.55	4.99	2.73	1.145	0.127	0.59
C	5.90	4.97	2.81	1.420	0.163	0.00
D	6.46	4.48	4.44	1.388	0.528	0.06
AB	7.15	4.85	2.89	1.225	0.188	0.02
ABC	7.64	5.35	2.93	1.715	0.128	0.00
CD	5.83	3.70	2.77	1.032	0.459	0.32
BCD	6.64	3.51	2.80	1.497	0.500	0.63
CON	5.34	4.33	4.15	1.215	0.275	1.52
CV%	19	16	17	14	17	34

TABLE 4.28: MEAN VALUES OF TOTAL FRUIT DRY WEIGHT (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	36.0 ab	36.5 ab	82 a	63 a	79 a	101 a (8.83)*
B	23.8 ab	73.6 ab	139 a	157 ab	226 ab	190 ab (16.6)
C	66.3 b	87.1 ab	172 a	274 b	391 bc	410 bc (35.8)
D	7.6 a	17.5 a	75 a	186 ab	397 bc	517 cd (45.2)
AB	53.9 ab	111.1 bc	134 a	274 b	279 a-c	346 a-c (30.2)
ABC	71.1 b	181.3 cd	439 bc	541 cd	571 cd	703 de (61.5)
CD	38.4 ab	103.2 ab	336 b	488 c	705 de	841 e (73.5)
BCD	52.3 ab	249.1 d	429 bc	683 de	925 e	1488 g (130)
CON	132.0 c	264.4 d	500 c	773 e	898 e	1144 f (100)
CV%	56	45	27	30	36	27

* Value in the bracket shows the percentage of dry weight as compared to CON.

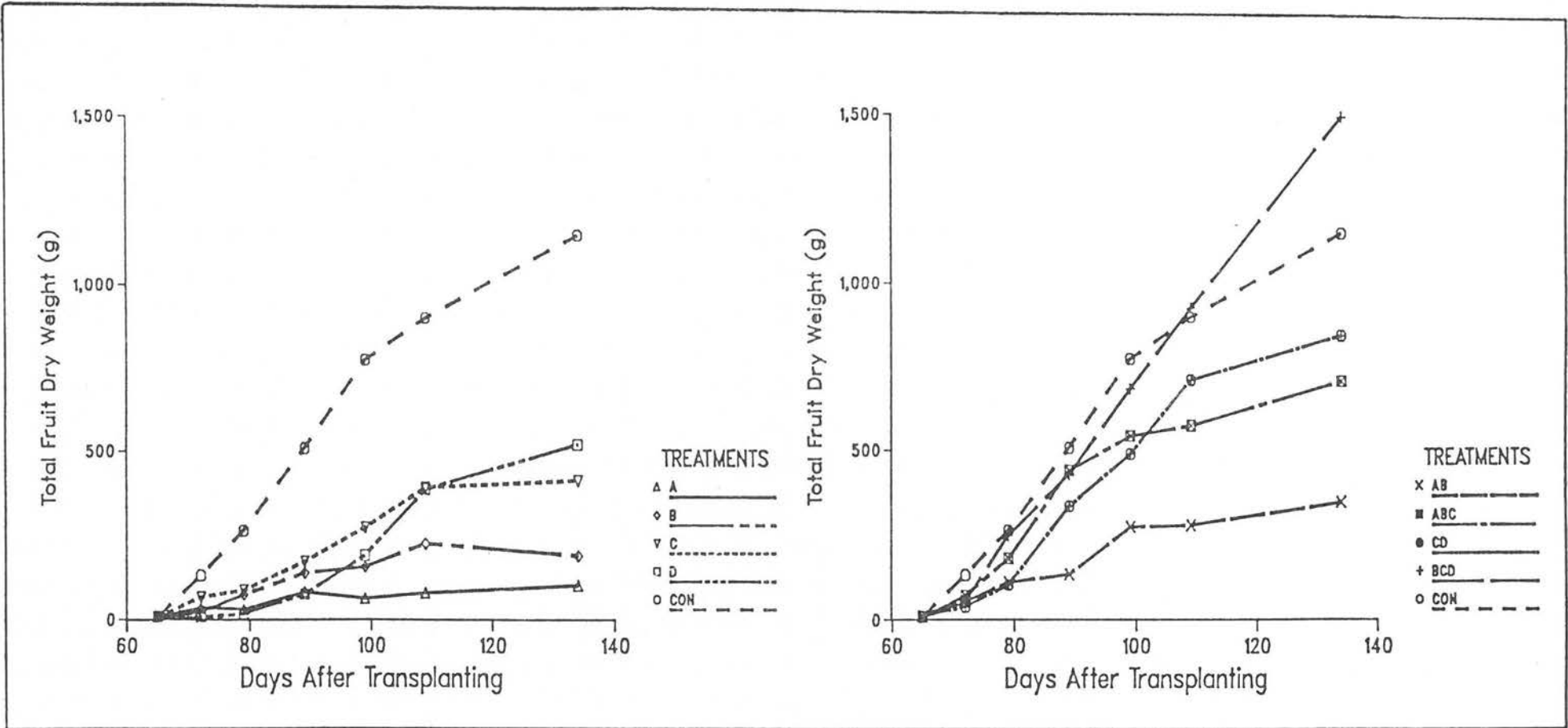


Figure 4.10: Effect of treatments on fruit dry weight accumulation.

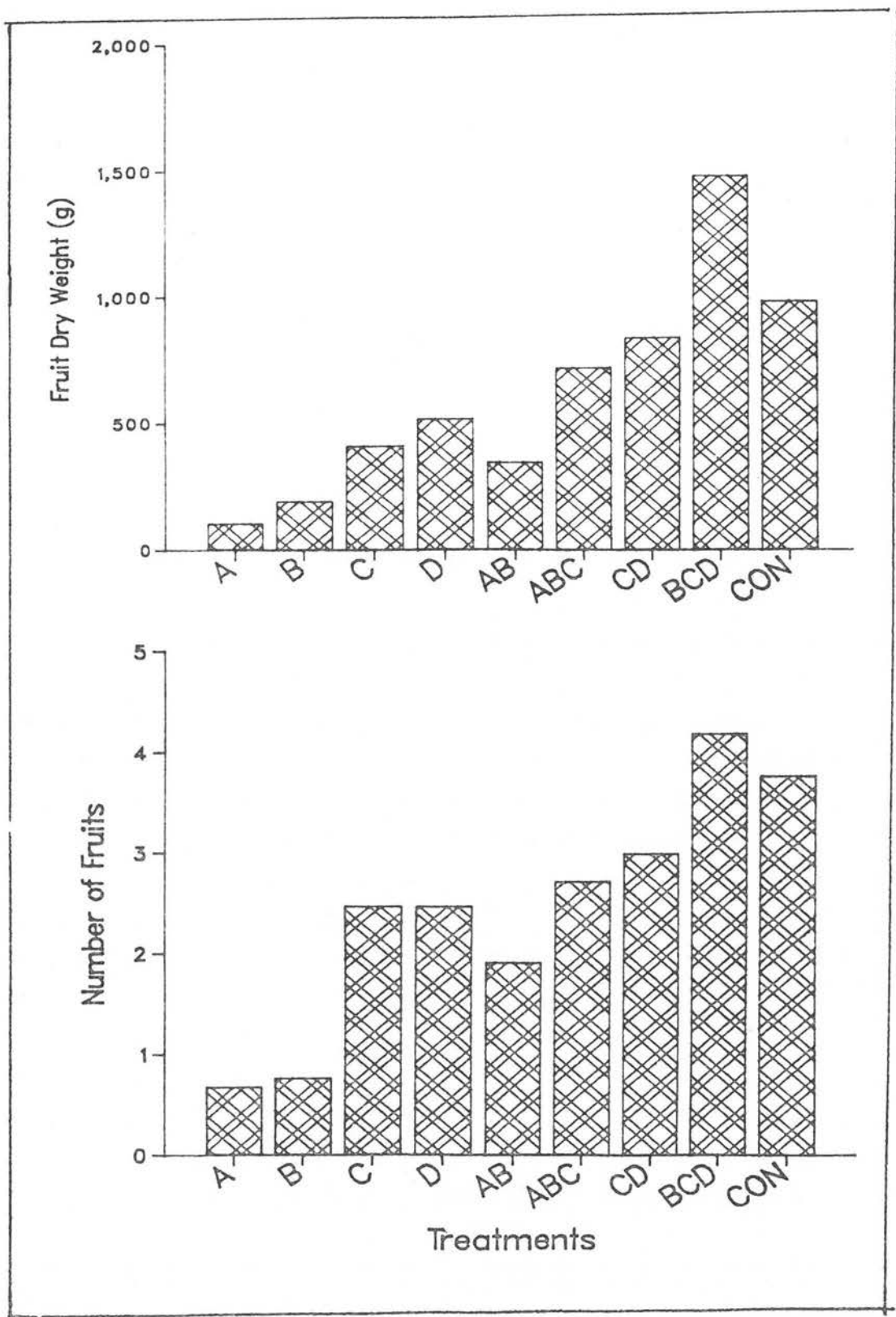


Figure 4.11: Effect of treatments on fruit dry weight per plant (top).

Figure 4.12: Effect of treatments on number of fruits per plant (bottom).

the fruits of treatment BCD plants gained the highest dry weight followed by those of CON, CD, ABC, D, C, AB, B and A plants. The fruit dry weight of treatment BCD plants was $1488 \text{ g plant}^{-1}$ and significantly higher than that of CON plants which was only $1144 \text{ g plant}^{-1}$.

4.4.5.2 Relative Growth Rate (R_F)

ANOVA of R_F for total fruit dry weight indicates highly significant differences amongst treatment means at all harvests (Table 4.29). This result suggests that the R_F of fruit dry weight was greatly affected by defoliation treatments. The R_F of fruit from all treated plants were significantly lower than those of CON plants in the first 8 days after treatments (P2). The total dry weight of fruit from treatment D plants was actually reduced in this period. This is shown by the negative value of R_F . The R_F of fruits from treatment A plants was fluctuating between positive and negative values suggesting that the total fruit dry weight was increasing or reducing with time.

Generally, R_F of total fruit dry weight was reduced with time at different rates depending on treatments. The fruit of treatment BCD plants was found to have quite high R_F values in all periods, being significantly higher than that of CON plants in the final period (P7).

4.4.5.3 Total Number of Fruits

ANOVA of total fruit number revealed the presence of highly significant differences among treatment means at all harvests (Table 4.30). F test values were increased with time showing that the differences between treatment means were increasing toward the end of the growing period. These results suggest that the total number of fruit per plant was greatly affected by the treatments and that the effect was greater with time.

Table 4.30 shows that the number of fruit of all treated plants except BCD was reduced with time as shown in successive

TABLE 4.29: MEAN VALUES OF R FOR FRUIT DRY WEIGHT (R_F) ($\text{mg g}^{-1} \text{ day}^{-1}$)

TREATMENTS	PERIODS (DAYS AFTER TRANSPLANTING)					
	P2 (65-72)	P3 (72-79)	P4 (79-89)	P5 (89-99)	P6 (99-109)	P7 (109-134)
A	248.2 c	-17.3 a	94.2 cd	-24.9 a	27.4 abc	11.62 c
B	181.7 b	169.5 cd	65.2 bc	12.2 b	34.9 bc	-6.12 a
C	339.8 d	36.8 a	69.5 bc	46.9 c	35.1 bc	2.21 b
D	-8.1 a	187.3 cd	132.0 e	93.1 e	76.0 d	10.85 c
AB	309.0 d	103.6 b	18.6 a	72.6 d	0.2 a	7.09 bc
ABC	349.4 e	134.3 bc	88.9 cd	20.9 b	5.0 ab	8.44 bc
CD	258.3 c	143.4 bc	119.2 de	37.5 c	36.7 c	7.12 bc
BCD	304.3 d	225.1 d	54.4 b	46.6 c	30.4 bc	19.04 d
CON	438.7 f	99.3 b	63.9 bc	43.5 c	14.9 abc	9.76 bc
CV%	8.6	34	26	26	64	62

TABLE 4.30: MEAN VALUES OF TOTAL NUMBER OF FRUITS PER PLANT*

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	2.75 ab	1.46 a	1.50 a	0.50 a	0.75 a	0.75 a
B	3.50 abc	1.25 a	1.75 a	1.75 b	2.00 ab	0.89 a
C	2.50 a	3.50 b	1.50 a	2.00 bc	2.75 b	2.50 bc
D	3.30 ab	2.75 ab	1.75 a	1.93 bc	2.59 b	2.50 bc
AB	5.41 c	2.50 ab	2.66 ab	2.00 bc	2.25 b	1.97 b
ABC	5.25 c	4.00 b	3.50 b	3.25 b-d	3.25 b	2.75 b-d
CD	4.50 bc	4.00 b	3.50 b	3.50 cd	1.75 ab	3.00 b-d
BCD	4.00 a-c	3.75 b	4.00 b	3.25 b-d	3.00 b	4.25 d
CON	4.00 a-c	4.25 b	3.58 b	4.50 d	3.00 b	4.00 cd
CV%	2.4	3.7	2.4	3.9	4.6	2.6

* ANOVA was carried out on transformed data. The formula of transformation is $y = \sqrt{x + 0.5}$, where x = original data and y = transformed data.

harvests. High levels of abortion occurred in plants receiving treatments A and B. Treatment D plants had their total fruit number reduced at 79, 89 and 99 DAT but increased again at 109 and 134 DAT. The number of fruit from treatment BCD plants was increased slightly at the final harvest. CON plants were found to have a constant fruit number at all harvests.

The total number of fruit at final harvest for every treatment is shown in Figure 4.12. The highest number recorded was 4.25 fruits plant⁻¹ produced by treatment BCD plants. They were not significantly different however from those of treatments ABC, CD and CON plants which averaged 2.75, 3.00 and 4.00 fruits plant⁻¹ respectively.

4.4.5.4 Fruit Dry Weight from Different Sections

As there was no fruit set in Section A, ANOVA was carried out only on the fruit dry weight data of Sections B, C and D. The original mean values of fruit from Sections B, C and D are shown in Tables 4.31, 4.32 and 4.33 respectively.

Highly significant differences among treatment means of fruit dry weight from Section B were observed only at 72 DAT. Nonsignificant differences were observed from the rest of the harvests. High CVs were also recorded at all harvests except 72 DAT (Table 4.31). These results suggest that defoliation treatments affected the fruit dry weight of Section B only at first harvest (72 DAT). However, the high CV recorded could be the reason for the nonsignificant differences observed among the treatment means from the rest of harvests. The mean values in Table 4.31 do show some treatment effects on the fruit dry weight at all harvests.

ANOVA of fruit dry weight from Section C revealed the presence of highly significant differences among treatment means at 79, 89, 99 and 134 DAT (Table 4.32). Nonsignificant differences were observed at 72 and 109 DAT. The very high CV recorded at these two harvests probably was the reason for

TABLE 4.31: MEAN VALUES OF FRUIT DRY WEIGHT FROM SECTION B* (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	32.7 a	19	67	63	27	77
B	8.1 a	52	51	0	72	114
C	54.1 a	24	117	143	97	33
D	2.3 a	4	0	56	23	69
AB	35.8 a	87	90	163	158	124
ABC	35.2 a	84	274	157	95	131
CD	14.0 a	46	112	81	106	270
BCD	31.0 a	75	49	0	190	131
CON	110.7 b	60	88	69	182	244
CV%	98	132	104	121	149	123

* ANOVA was carried out on transformed data except at 72 DAT. The formula of transformation is $y = \sqrt{x + 0.5}$, where x = original data and y = transformed data.

TABLE 4.32: MEAN VALUES OF FRUIT DRY WEIGHT FROM SECTION C* (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	3.2	18.5 a	14 ab	0 a	52	0 a
B	15.0	14.2 a	88 ab	102 a	122	45 ab
C	11.7	43.7 ab	56 ab	91 a	213	213 ab
D	4.1	4.5 a	0 a	3 a	0	0 a
AB	18.1	17.5 a	31 ab	109 a	100	147 ab
ABC	31.1	75.3 b	113 ab	332 bc	274	458 bc
CD	20.5	49.6 a	120 b	217 ab	323	459 bc
BCD	20.4	114.1 bc	337 c	447 c	307	1060 c
CON	20.2	180.3 c	313 c	468 c	318	347 bc
CV%	96	24	41	69	119	54

* ANOVA was carried out on transformed data except at 72 and 99 DAT. The formula of transformation is $y = \sqrt{x + 0.5}$, where x = original data and y = transformed data.

TABLE 4.33: MEAN VALUES OF FRUIT DRY WEIGHT FROM SECTION D (g plant⁻¹)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	0.00	0.0	1 ab	0 a	0 a	24 a
B	0.63	7.5	0 a	55 ab	11 ab	31 a
C	0.87	19.5	0 a	40 a	64 a-c	164 ab
D	1.21	8.7	75 cd	127 bc	388 d	448 b
AB	0.00	6.1	12 a-c	2 a	7 ab	75 a
ABC	4.78	22.2	53 a-d	52 a	153 b-d	113 a
CD	3.98	7.5	104 d	190 c	269 cd	111 a
BCD	0.00	40.0	43 a-d	206 bc	306 cd	293 ab
CON	1.11	24.1	99 bcd	236 c	353 cd	553 b
CV%	58	57	68	59	39	61

nonsignificant differences observed. The results suggest that the dry weight accumulation of fruit from Section C was greatly affected by defoliation treatments. At final harvest (134 DAT) the fruit of treatment BCD plants recorded the highest dry weight. They were however not significantly different from those of treatments ABC, CD, BCD and CON. No fruit was found from section C of plants receiving treatments A and D.

Highly significant differences at four final harvests were observed in ANOVA of fruit dry weight from Section D (Table 4.33). The results again suggest that the defoliation treatments had exerted a great effect on the dry weight accumulation of fruit from Section D. At final harvest, while the highest fruit dry weight was recorded from CON plants, it was however not significantly different from those of treatments BCD, C and D plants.

The distribution of fruit dry weight on the plants at final harvest is shown in Figure 4.13 which shows that the CON plants had a higher fruit dry weight in Section D. Defoliation treatments had caused a change in this pattern. All treated plants had most of their fruit dry weight shifted to Section C, except plants receiving treatments A, B and D. Treatment D plants had more fruit dry weight in Section D similar CON plants but no fruit was found in Section C. Treatment A and B plants had more fruit dry weight in Section B.

4.4.5.5 Fruit Number from Different Sections

Nonsignificant differences among treatment means were observed at all harvests in ANOVA of fruit number of Section B (Table 4.34). This suggests that fruit number in Section B was not affected by defoliation treatments. The Table also shows that the number of fruit kept on reducing until final harvest in all treatments except treatment D and CD plants. Treatment D plants showed an increase in fruit number while treatment CD plants maintained the same number of fruit.

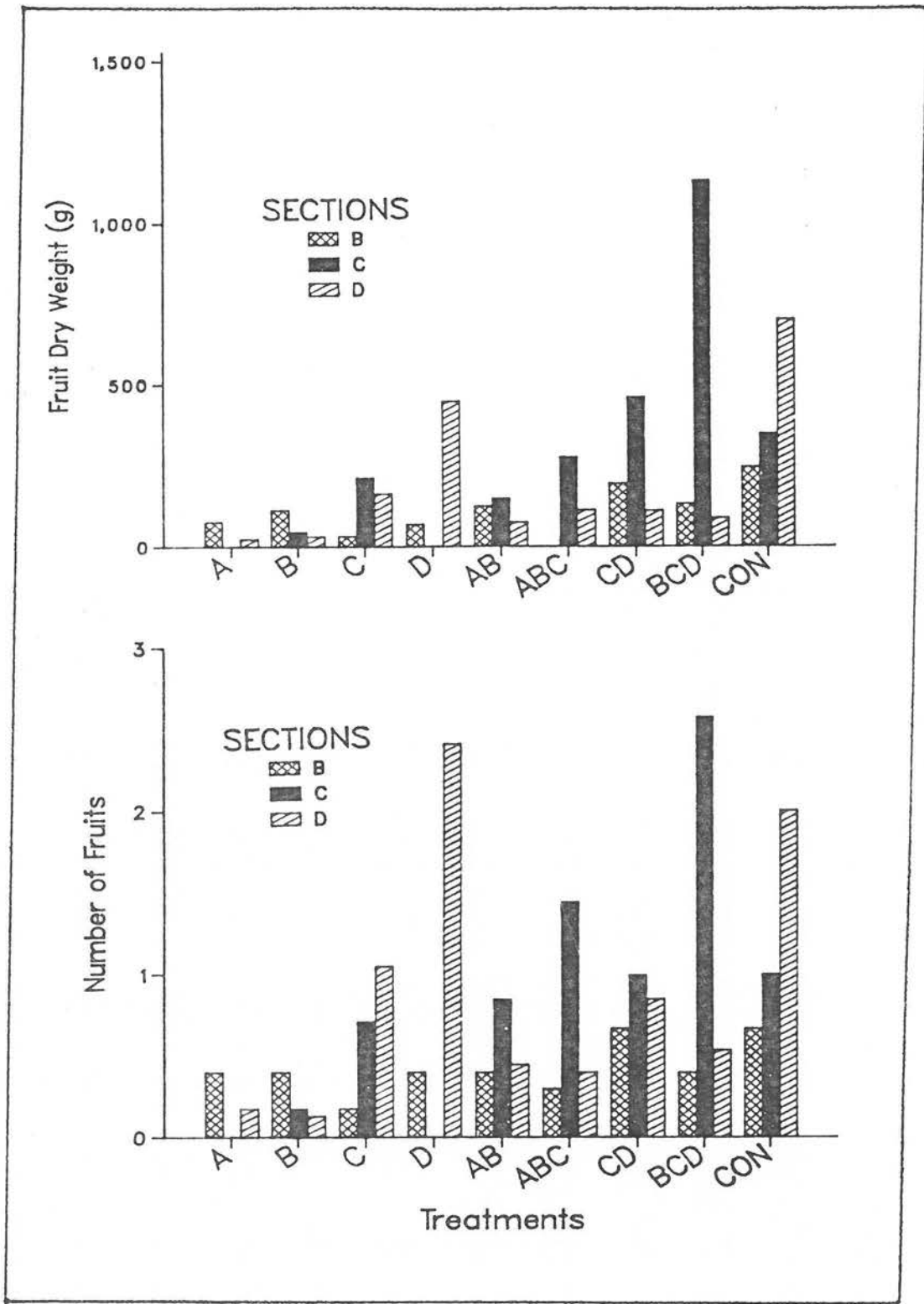


Figure 4.13: Effect of treatments on fruit dry weight per plant section (top).

Figure 4.14: Effect of treatments on number of fruits per plant section (bottom).

TABLE 4.34: MEAN VALUES OF NUMBER OF FRUITS FROM SECTION B*

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	1.00	0.32	0.750	0.500	0.250	0.50
B	1.00	0.50	0.250	0.000	0.500	0.50
C	0.75	1.00	0.500	0.750	0.500	0.25
D	0.25	0.25	0.000	0.354	0.365	0.50
AB	0.75	0.75	0.750	0.750	0.500	0.50
ABC	0.50	0.50	1.000	0.500	0.250	0.50
CD	0.75	0.25	0.500	0.500	0.250	0.75
BCD	1.25	0.50	0.250	0.000	0.500	0.50
CON	1.00	0.50	0.667	0.500	0.500	0.75
CV%	16	33	18	19	27	20

* ANOVA was carried out on transformed data. The formula of transformation is $y = \sqrt{x + 0.5}$, where x = original data and y = transformed data.

ANOVA of fruit number from Section C shows the presence of highly significant differences among treatment means at 79, 89, 99 and 134 DAT (Table 4.35). The results suggest that the number of fruit from Section C was greatly affected by defoliation treatments. At final harvest, treatment BCD plants had the highest fruit number and no fruit was found on treatment A and D plants. The Table reveals also that fruit abortion continued to occur with time in all treatments. The biggest number of fruit aborted was in treatment AB plants. Treatment BCD plants also experienced some fruit abortion until 109 DAT but increased again at final harvest due to the setting of new fruit in Section D.

Highly significant differences amongst treatment means at all harvests except at 79 DAT, were observed in ANOVA of fruit number from Section D (Table 4.36). This suggests that fruit number from Section C was greatly affected by defoliation treatments. In this section, fruit abortion occurred only in treatment ABC and CD plants while the plants receiving the rest of treatments had their fruit number increased at final harvests. The highest increase was in CON plants followed by treatment D plants.

The distribution of fruit number on the plants at final harvest is shown in Figure 4.14. Defoliation treatments caused a change in the distribution of fruit number on the plants, except in treatment C plants which were similar to those of CON plants. Treatments A and B plants had a higher fruit number in Section B. Treatment D plants although having a higher fruit number in Section D as did CON plants, had no fruit in Section C. Plants receiving the rest of the treatments had a similar pattern of fruit distribution in which highest fruit numbers were found in Section C, followed by sections D and B.

4.5 PARTITIONING OF DRY MATTER TO DIFFERENT ORGANS

Partitioning refers to the proportion of dry matter found in certain organs as compared to total dry matter. Data are

TABLE 4.35: MEAN VALUES OF NUMBER OF FRUITS FROM SECTION C*

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134**
A	1.75	1.02 abc	0.50 ab	0.00 a	0.50	0.00 a
B	2.50	0.50 ab	1.50 abc	1.00 abc	1.25	0.20 a
C	1.50	1.50 abc	1.00 ab	0.75 ab	1.50	0.80 ab
D	1.00	0.25 a	0.00 a	0.00 a	0.52	0.00 a
AB	3.25	0.75 abc	0.75 ab	1.00 abc	1.50	0.98 abc
ABC	3.50	2.50 c	1.00 ab	2.50 c	1.25	1.55 bc
CD	2.50	2.50 c	1.50 abc	1.50 bc	0.50	1.08 abc
BCD	2.75	2.00 bc	3.00 c	2.25 bc	1.00	2.64 c
CON	2.75	2.50 c	2.03 bc	2.50 c	1.00	1.00 abc
CV%	15	13	16	14	31	16

* ANOVA was carried out on transformed data. The formula of transformation is $y = \sqrt{(x + 0.5)}$ where x = original data and y = transformed data.

** due to the differences in the order of ranking between the original and transformed means, the retransformed means were presented.

TABLE 4.36: MEAN VALUES OF NUMBER OF FRUITS FROM SECTION D*

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	0.00 a	0.11	0.25 a	0.00 a	0.00 a	0.25 a
B	0.00 a	0.25	0.00 a	0.75 ab	0.25 ab	0.13 a
C	0.25 a	1.00	0.00 a	0.50 ab	0.75 abc	1.25 abc
D	0.25 a	2.25	1.75 b	1.59 b	1.71 bc	2.00 bc
AB	0.00 a	1.00	1.03 ab	0.25 a	0.25 ab	0.61 ab
ABC	1.25 b	1.00	1.50 b	0.25 a	1.75 c	0.50 ab
CD	1.25 b	1.25	1.25 b	1.50 b	1.00 abc	1.00 abc
BCD	0.00 a	1.25	0.75 ab	1.00 ab	1.50 bc	1.00 abc
CON	0.25 a	1.25	0.89 ab	1.50 b	1.50 bc	2.25 c
CV%	25	18	13	14	15	16

* ANOVA was carried out on transformed data. The formula of transformation is $y = \sqrt{(x + 0.5)}$ where x = original means and y = transformed data.

presented as percentages of total dry weight. The organs considered here are leaves, stems, flowers and fruits.

4.5.1 Leaves

ANOVA of dry matter fractions of leaves showed the presence of highly significant differences among treatment means in the first two (72 and 79 DAT) and final harvests (134 DAT) (Table 4.37). AT 89 DAT, significant differences were observed ($P < 0.05$). Nonsignificant differences were recorded at 99 and 109 DAT.

4.5.2 Stems

Highly significant differences among treatment means were observed at all harvests in the ANOVA of percentage partitioning to stem (Table 4.38). Significant differences are particularly high at the first four harvests and were lower in the last two harvests (109 and 134 DAT).

Treatment A plants were found to have constantly higher proportions of dry matter found in stems at all harvests except at 72 DAT. On the other hand, treatment BCD and CON plants had the least proportion of dry matter found in their stems.

In general, even though there was a trend of recovery in the dry matter partitioning to stems it was still far from complete. At final harvest, treatment A and B plants had 36.7 and 34.1% of dry matter partitioned to stems respectively as compared to less than 8% in the treatments ABC, C, BCD and CON plants.

4.5.3 Flowers

Significant differences among treatment means were observed only in the first three harvests in ANOVA of percentage dry matter partitioning to flowers (Table 4.39). Nonsignificant differences were observed in the later harvests (99, 109 and 134 DAT).

TABLE 4.37: MEAN VALUES OF DRY MATTER PARTITIONINGS TO LEAVES (%)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	28.09 a	22.95 a	23.05 a	21.23	16.35	1.20 a
B	37.90 bc	26.45 ab	23.86 a	20.94	16.84	8.24 b-d
C	31.75 ab	28.54 a-c	22.73 a	19.91	14.59	5.76 a-c
D	36.72 a-c	40.63 d	33.04 b	29.89	14.73	8.37 b-d
AB	42.18 cd	29.48 a-c	27.72 ab	21.17	15.92	3.02 ab
ABC	50.05 de	32.85 b-d	22.76 a	22.55	23.05	6.97 a-d
CD	47.91 de	40.41 d	25.47 a	22.96	17.04	11.57 cd
BCD	51.71 e	33.16 b-d	27.16 ab	21.27	16.01	11.27 cd
CON	44.34 c-e	35.94 cd	26.32 a	21.26	16.94	13.26 d
CV%	14	17	15	30	27	51

TABLE 4.38: MEAN VALUES OF DRY MATTER PARTITIONINGS TO STEMS* (%)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	44.9 cd	49.70 e	34.80 c	52.7 c	44.5 b	36.7 b
B	40.7 c	33.65 d	24.55 b	24.5 b	17.9 a	35.1 b
C	30.4 b	29.29 cd	23.42 b	16.3 ab	13.8 a	10.1 a
D	51.4 d	43.88 e	32.77 c	17.9 ab	10.3 a	9.7 a
AB	29.1 b	24.91 bc	24.39 b	15.5 ab	16.1 a	13.2 a
ABC	24.7 ab	18.90 ab	11.35 a	10.7 ab	10.3 a	8.1 a
CD	31.2 b	25.15 bc	14.90 a	10.4 ab	7.4 a	7.9 a
BCD	25.6 ab	16.51 a	11.11 a	8.2 a	6.6 a	4.6 a
CON	17.4 a	14.81 a	10.76 a	7.0 a	6.2 a	5.9 a
CV%	19	17	24	30	34	46

* ANOVA was carried out on transformed data at 99, 109 and 134 DAT. The formula of transformation is $y = \arcsin x$, where x = original data and y = transformed data.

TABLE 4.39: MEAN VALUES OF DRY MATTER PARTITIONING TO FLOWERS* (%)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	4.60 cd	3.70 d	1.468 de	1.015	0.228	0.509
B	5.20 d	2.79 cd	1.023 bc	0.459	0.032	0.161
C	3.33 bc	2.26 b-d	0.932 a-d	0.394	0.030	0.000
D	5.83 d	3.25 d	1.891 e	0.346	0.093	0.009
AB	3.61 bc	1.94 bc	1.138 c-e	0.298	0.047	0.004
ABC	2.77 b	1.54 a-c	0.464 ab	0.236	0.020	0.000
CD	2.79 b	1.31 ab	0.485 ab	0.143	0.037	0.030
BCD	2.63 b	0.71 a	0.40 ¹¹ a	0.157	0.042	0.037
CON	1.52 a	0.84 a	0.586 a-c	0.112	0.021	0.114
CV%	12	16	14	18	7	21

* ANOVA was carried out on transformed data. The formula of transformation is $y = \sqrt{x + 0.5}$ where x = original data and y = transformed data.

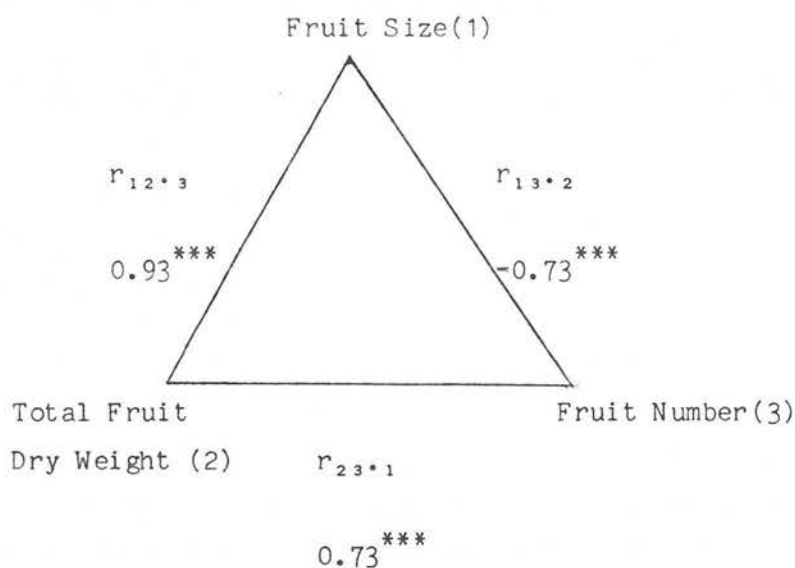
4.5.4 Fruits

ANOVA of the fraction of dry matter found in fruits revealed the presence of highly significant differences among treatment means at 79, 89 and 99 DAT. Significant differences at 5% level were detected at 72 and 109 DAT (Table 4.40). Nonsignificant differences were observed at final harvest.

4.6 CORRELATIONS AND REGRESSIONS DATA

4.6.1 Partial Correlation

Partial correlation coefficients (r_p) involving total fruit dry weight, fruit size (average dry weight per fruit) and fruit number were calculated. The partial correlation coefficients for each pair of variables when the third variable was held constant are shown in the Table 4.41. Initially, r_p overall, involving all treatments was computed. The result indicates that total fruit dry weight was highly correlated with both fruit size and fruit number as follows:



High and positive correlations between total fruit dry weight and fruit size ($r_{12 \cdot 3}$), fruit dry weight and fruit number

TABLE 4.40: MEAN VALUES OF DRY MATTER PARTITIONINGS TO FRUITS (%)

TREATMENTS	DAYS AFTER TRANSPLANTING					
	72	79	89	99	109	134
A	22.4 a-d	23.6 ab	40.7 ab	25.0 a	38.9 a	56.8
B	16.2 ab	37.1 bc	50.6 b-d	54.1 b	65.2 b	56.5
C	34.5 cd	39.9 c	52.9 b-e	63.4 b	71.5 b	84.1
D	6.1 a	12.2 a	32.3 a	51.8 b	78.8 b	81.9
AB	25.1 b-d	43.7 c	46.7 bc	63.1 b	68.0 b	83.8
ABC	22.4 a-c	46.7 c	65.4 e	66.5 b	66.6 b	84.9
CD	18.1 a-d	33.1 ab	59.1 c-e	66.5 b	75.6 b	80.5
BCD	20.1 a-d	49.6 c	61.3 de	70.3 b	77.4 b	94.1
CON	36.7 d	48.4 c	62.3 de	71.6 b	76.8 b	80.7
CV%	46	27	16	21	18	22

Table 4.41 Partial correlation coefficients between total fruit dry weight and fruit size ($r_{12.3}$), total total fruit dry weight and fruit number ($r_{23.1}$) and between fruit number and fruit size ($r_{13.2}$)

PARTIAL CORRELATION COEFFICIENTS (r_p)			
	12.3	13.2	23.1
SECTIONS			
B	0.978 ***	-0.620 ***	0.593 ***
C	0.872 ***	-0.636 ***	0.590 ***
D	0.890 ***	-0.641 ***	0.727 ***
TREATMENTS			
A	0.978 ***	-0.533 **	0.430 *
B	0.846 ***	-0.702 ***	0.500 **
C	0.903 ***	-0.826 ***	0.742 ***
D	0.956 ***	-0.529 **	0.513 **
AB	0.648 ***	-0.742 ***	0.351 ns
ABC	0.859 ***	-0.792 ***	0.654 ***
CD	0.939 ***	-0.639 ***	0.474 *
BCD	0.959 ***	-0.758 ***	0.713 ***
CON	0.942 ***	-0.857 ***	0.805 ***

Significant

* 5%

** 1%

*** 0.1%

showed that the high total fruit dry weight was due to increases in both fruit number and fruit size. However, fruit size contributed more than fruit number since $r_{12 \cdot 3}$ was higher than $r_{23 \cdot 1}$.

The overall pattern of relationships was still quite similar when calculated on both Section and treatment basis (Table 4.41) with positive values of $r_{12 \cdot 3}$ and $r_{23 \cdot 1}$ and negative values of $r_{13 \cdot 2}$. In treatment AB plants however, $r_{23 \cdot 1}$ was not significant suggesting that only fruit size contributed to total fruit dry weight.

4.6.2 Regression Analysis

In order to establish an overall relationship between total dry matter accumulation and total leaf area duration (D), total plant dry weight and fruit dry weight from final harvest were regressed with total D as the independent variable. Total D is the summation of all D from six periods.

The regression lines are shown in Figure 4.15. The equations of the lines are as follows:

$$Y_t = -23.4 + 10.3X; \quad R^2 = 0.91^{***}$$

$$Y_f = -42.1 + 8.97X; \quad R^2 = 0.82^{***}$$

where Y_t and Y_f represent the total plant dry weight and total fruit dry weight in g respectively and X represents total D in square meters. Very high R squared values for both regressions suggest that the dry weight accumulation was highly influenced by total D. In the t-test of regression slopes, calculated-t was found to be 2.67. Since tabulated-t at $p < 0.05$ is 2.00, the slopes were significantly different which indicate that total plant dry weight and total fruit dry weight had different regression lines when regressed against total D.

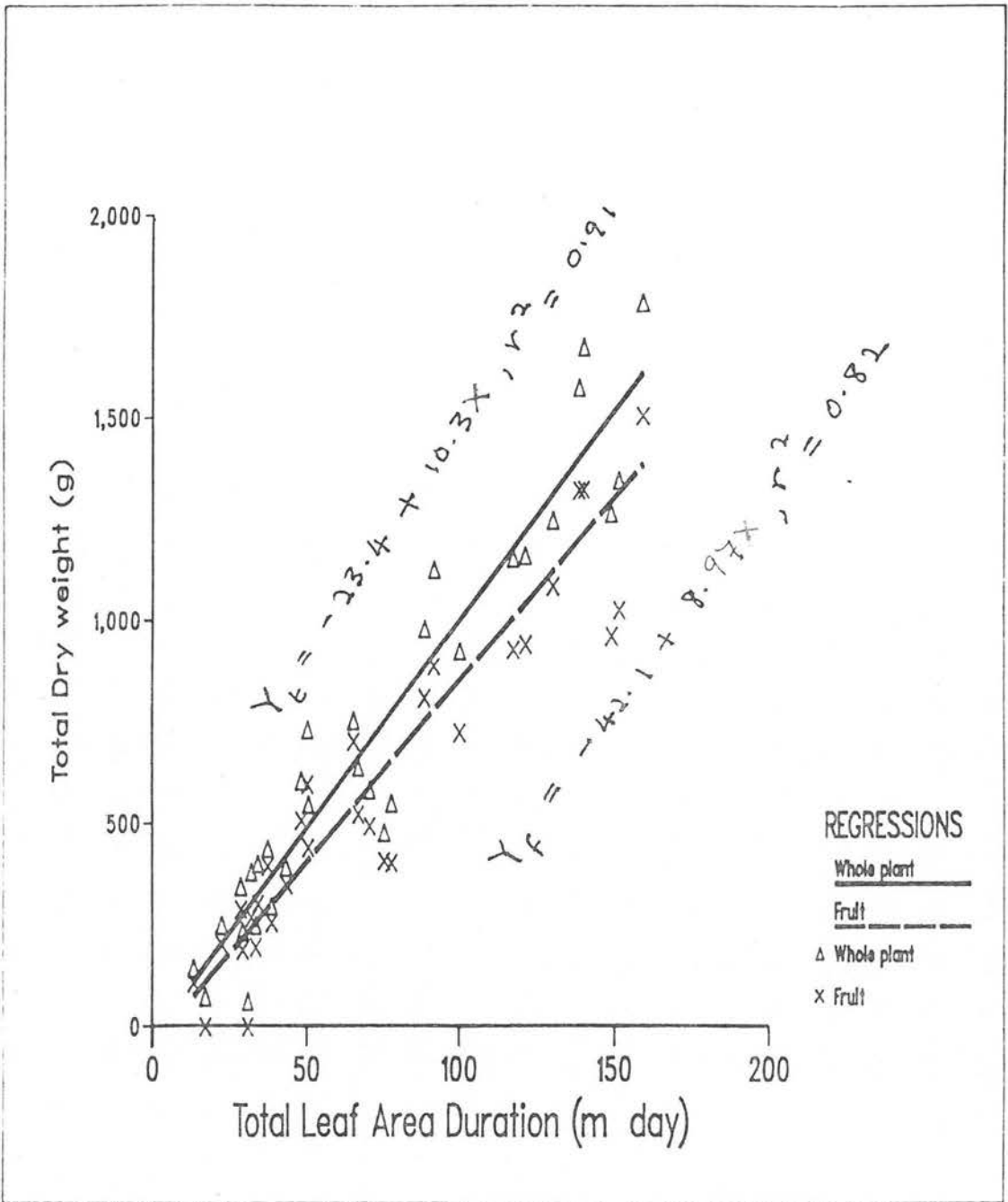


Figure 4.15: Linear regressions of total plant dry weight (Y_t) and fruit dry weight (Y_f) with total leaf area duration (D).

5 DISCUSSION

5.1 INTRODUCTION

In this chapter, discussions on the growth and development, partitioning of dry matter and relationships between dry matter accumulation and leaf area duration will be sequentially presented. It is necessary to note here that all the computations of growth components were carried out using the above ground dry matter only, since root sampling was not included in this experiment. This is important because increases in partitioning of dry matter to root may cause a reduction in top growth. Growth components computed using these data only, without taking into consideration the root dry weight, will give apparent reductions in both E and R which are not true.

Depending on the plant species (Gales 1979), partitioning of dry matter to root can be substantial in situations such as water stress (Passioura 1981) and nutrient deficiency (Rufy et al 1984). Nutrients supplied in this experiment should be enough for the season. The approximate weight of nutrients removed by the crop are 55:50:75 kg ha of N:P:K respectively at a planting density of about 5000 plants per ha (Ministry of Agriculture and Fisheries 1983). The rate of fertilizer used in this experiment was 120:100:100 kg per ha of N:P:K respectively at 4761 plants per ha.

5.2 PLANT GROWTH AND DEVELOPMENT

5.2.1 The Control Plants

Even though the total dry matter accumulation curve of CON plants shows no sign of a sudden change of total dry weight (Figure 4.1), the \log_e curve which represents the plant growth rate shows a sudden drop after 90 DAT, before increasing again after 110 DAT. A slight drop was observed also at about 60 DAT. These reductions were more apparent on the R curve (Figure 4.2a).

A big drop in R values was observed between 57 to 65 DAT and 99 to 109 DAT. When the components of R i.e. E and F were plotted against time, the factor that contributed to these reductions was apparent. Two big drops which were within the periods similar to R were observed in E values (Figure 4.2b) whereas no such drop occurred in F values. The reduction in R therefore, was due mainly to a reduction in E rather than F. Since E is a physiological parameter which may be affected partly by environment factors (Thorne 1960), the weather data during the experimental period were examined. As shown in Appendix 1a, the total precipitation was very low in weeks 9 and 15 which was coincidental with the periods of low R values. Therefore it is most likely that the plants had experienced water stress in both periods. Incidentally, daily bright sunshine hours were also low in both periods (Appendix 1c). Water stress and light intensity have been reported to affect the rate of photosynthesis. Caemmerer and Farquhar (1984) working with Phaseolus vulgaris found that the CO₂ assimilation rate was markedly reduced when grown under a low light-regime. The same result was also observed when plants experienced water stress. The reduction in E observed in this experiment therefore could be due mainly to either water stress or low light or both. If water stress was the sole factor, partitioning of dry matter to root must not be discounted.

It is important to establish the fact that the CON plants had experienced an apparent reduction in E values in these two periods. The first dry period was prior to defoliations and therefore will have the same effect on all plants. The plants may have responded differently in the second period since it occurred after defoliation treatments.

5.2.2 Leaf Growth

Obviously, the leaf is the plant organ which is affected most, since the treatments involved defoliations. The immediate effects of treatments on the total leaf dry weight accumulation and leaf area expansion were reflected in the harvest following the defoliations which was at 72 DAT in Table 4.16 and 4.17

respectively. Except that of treatments A and B, the leaf dry weight and the leaf area of plants receiving other treatments increased again after defoliations.

The leaf growth after defoliations depends largely on the age of leaves left on the plants. Treatment A plants which had a block of the oldest leaves, was observed to have the lowest leaf growth in terms both of leaf area and leaf dry weight. On the other hand, treatment D plants having a block of youngest leaves after defoliations showed the biggest leaf growth among the one leaf block plants (treatments A, B, C and D) (Figure 4.8 and 4.9). This effect of leaf age was reflected also in those plants having more than one block of leaves (treatments AB, ABC, CD, and BCD). Similar results were found by Alderfer and Eagles (1976) who observed that partial defoliation promoted leaf expansion in leaves that had not fully expanded before the treatments. Similarly, Hodgkinson (1974) observed differential effects of partial defoliation in Medicago sativa leaves of different ages.

Toward the end of the growing period (from 109 DAT onward), treatment BCD plants showed a trend of having higher leaf dry weights and leaf areas than those of CON plants (Table 4.16 and 4.17). The reason for this is much more complicated to explain. It seems that defoliation of the basal leaf block (treatment BCD plants) delayed the leaf senescence of the remaining leaves which was reflected in their leaf area duration (Table 4.5) and leaf dry weight (Figure 4.8) in the final period (P7). Work by Yoshioka and Takahashi (1983) on "Netted Melon" using ^{14}C -tracer showed that leaves at the base of the stem supplied most of their assimilates to the root system, if there was no fruit set at the lower node number. In plants having fruit set at the lower node, competition for assimilates from the base leaves between fruit and roots was observed and resulted in stunted plant growth due to poor root growth. In the work reported here defoliation of leaf in Section A (base leaves) had caused abortion of fruits from section B (Table 4.31 and 4.34). This probably resulted in more assimilates from section B leaves being translocated to the root system. In the CON plants, high number of fruits in Section B

(Table 4.34, Figure 4.14) probably had created an intense competition for assimilates from Section A and B leaves between fruits and root system which resulted much poor root growth in CON plants. Data of Yoshioka and Takahashi (1983) showed that in plants with fruits at the lower node, only 6% of base leaf assimilates were found in the roots. Furthermore, leaves at Section A on CON plants were old and their E values probably lower than those recorded in treatment A plants (Figure 4.5) since they were not alone. Therefore, prolonged and better leaf growth toward the end of the growing period as observed in treatment BCD plants could be due to a better root system possessed by the plants. This argument however cannot be proved in this study since root sampling was not included.

Another possible explanation of the prolonged leaf area duration during the last period was probably the way the plant responded to defoliations. Studies by Thrower (1967), Woolhouse (1967) and Alderfer (1974) showed that partial defoliation of a plant delays the senescence of remaining leaves. The reason for this has been associated with changes in water status and nutrients (Pate *et al* 1979, Preiss 1982) or hormone levels (Patrick and Wareing 1976, Yu and Yang 1980, Porter 1981, Tietz *et al* 1981).

The effect of defoliation on the SLA was found to depend also mainly on the age of leaves left on the plants after defoliation. Plants with older leaves tend to have lower SLA than those with younger ones (Table 4.6). Thus treatments A, B, AB, ABC plants had a lower SLA than those of treatments C, D, CD, BCD and CON plants. Similar results were observed when SLA was computed as the average of six periods (Table 4.7). In other words, older leaves responded to defoliations by increasing their dry weight while younger leaves, increased their leaf area.

Field observations also showed that the leaf of defoliated plants tend to be darker-green in colour than that of CON plants. Among the treated plants, the colour was darker on the older leaves. This observation was similar to those reported by

Alderfer and Eagles (1976), and Carmi and Koller (1979) who studied Phaseolus vulgaris leaves.

5.2.3 Stem Growth

5.2.3.1 Dry weight

Compared to other plant organs, stem growth was found to be the least affected by defoliations. The differences in the total stem dry weight was observed only at 89 and 134 DAT (Table 4.8). This was due to the differences in R_g (Table 4.9) which resulted in stems of different treatments reaching different maximum levels since all of them arrived at this point at about the same time (between 89 and 99 DAT). After this point, the stems of all treatments seem to lose their dry weights which continued until 109 DAT (Figure 4.7). Beyond this point, the stems of treatments D, CD, BCD and CON plants increased again while those of other treatments kept on reducing till final harvest. Data from the section basis showed that, the increase in stem dry weight was due to an improvement in dry matter accumulation of Section D stem (Table 4.12, 4.13, 4.14 and 4.15). The stem dry weight of Sections A, B and C of all treatments kept on reducing even in the final period (P7). The loss of stem dry weight was probably due to the retranslocation of dry matter from the stem to active growing fruits. Studies on potato (Moorby 1970), Jerusalem Artichoke (Helianthus tuberosus) (Incoll and Neales 1970) and wheat (Rawson and Evan 1971, Rawson and Hofstra 1969) have shown that, remobilization and retranslocation of carbohydrate from the stem helped to maintain the high growth rate in tubers or grains during the period of low photosynthesis.

The period in which stems lost their dry weight was during dry weather (Appendix 1a) and low daily bright sunshine hours (Appendix 1c). This unfavourable weather probably caused a reduction in the rate of photosynthesis reflected in the observed E values in the corresponding periods (Figure 4.5). The increase in the dry weight of Section D stems which was observed in P7 in some of treatments was probably due to high E recorded in this

period.

5.2.3.2 Stem Length and Number of Nodes per plant

Only the total length of the stem was found to be affected by defoliations. No effect of treatments was observed in the number of nodes per plant until at final harvest (134 DAT) (Table 4.10 and 4.11). Even the effect on stem length was very small and was observed only at 89 and 134 DAT. The results suggest that the differences in stem length were due to differences in internode length and not number of nodes. These results are in agreement with that reported by Wilkerson et al (1984) who found that defoliations reduced the stem weight to length ratio of peanuts.

5.2.4 Flower Development

Field observations showed that the flower buds which later developed into male flowers could be clearly seen at three weeks after transplanting. Only male flowers developed in Section A of the stem while the other stem sections had only female flowers. Female flowers were observed to develop at almost each node of the Section B, C and D stems. The first male flower was opened four days earlier than the first female flower which was on February the third 1984 (45 DAT).

The male, female and total flower dry weight was not affected by defoliations. All treatments showed a similar trend of higher total dry weight early in the growing period, reducing progressively when plants were getting older (Table 4.27). This was because at the time of defoliation treatments being carried out, all flowers had already differentiated into different sexes. Female flowers can be clearly differentiated from male flowers through their swollen ovaries, which are absent in male flowers. In Cucurbita maxima and Cucurbita pepo, the majority of the flowers was observed to differentiate either male or female within 40 DAT (Hume 1980, Hume and Lovell 1983).

5.2.5 Fruit Growth

5.2.5.1 Total Fruit Dry Weight

The final yield was greatly affected by defoliation treatments. Except in treatment BCD plants, all other treatments produced less yield as compared to CON plants (Table 4.28). Even in BCD plants, the fruit dry weight became higher than that of CON plants only after 109 DAT (Figure 4.10). This occurred mainly because the R_F in the treatment BCD plants was higher in the last 25 days before harvest (P7) (Table 4.29).

Partial correlation analysis shows that the higher total fruit dry weight was contributed both by the increase in fruit size and fruit number (Table 4.41). However, when these two factors were compared, fruit size was found to be the more dominant factor. In another words, fruit size varied more than fruit number.

Fruit size was found to be negatively correlated with fruit number which shows that fruit size was decreasing as fruit number increased. The above trend was similar when considered both on a Section and a treatment basis. There was however, one exception in treatment AB where fruit number did not contribute to the total fruit dry weight. This was due to the very low fruit number found in this treatment (Table 4.30).

The overall relationship between the total fruit dry weight accumulation of all treatments and D can be significantly ($P < 0.001$) explained by the linear regression $Y_F = -42.1 + 8.97X$ where Y_F is the total fruit dry weight in g and X is the leaf area duration in square meters. The R^2 of the line is 0.82

5.2.5.2 Fruit Abortion

Fruit abortion refers to the premature shedding or abscission of fruit from the plant. It is a common phenomenon and has been reported for a number of plant species including apples

(Luckwill 1953), beans (Tamas et al 1979) and cotton (Davis and Addicott 1972, Lipe and Morgan 1972). Both environment and internal factors influence the rate of fruit abortion (Addicott and Lyon 1973). Environment factors such as mineral deficiencies, drought and low light have long been known as factors responsible for shedding of flowers and fruits (Gartner 1844). Recent work suggests that the process of abscission is hormonally mediated (Heindl and Brun 1983, Huff and Dybing 1980), and is related to the availability of assimilates (Hardman and Brun 1971; Schou, Jeffers and Streeter 1978; Streeter and Jeffers 1979).

In the work reported here, fruit abortion seems to occur in all treatments including the CON plants. However, the effect of defoliations on the level of abortion was very clear (Table 4.30). Plants having only one block of leaf left (treatments A, B, C and D) suffered most, with fruit number at final harvest ranging between 0.75 to 2.50 fruits per plant. Even treatment AB plants, which had two blocks of leaf, still suffered very high levels of fruit abortion with only 1.97 fruits per plant recorded at final harvest. The majority of fruit abortion was found to occur in the first 14 days after treatments.

Among the plants with one block of leaf, treatment A plants suffered the greatest fruit abortion, followed by treatments B, C and D plants in decreasing order. Leaf on Sections A, B, C and D represent the age groups from older to younger respectively. Since old leaf is usually associated with low E values and young newly matured leaf associated with high E values (Hopkinson 1964, 1966), the availability of assimilates could be the major factor that influences fruit abortion. In Cucurbita pepo, young leaf started to export assimilates when about 35% expanded and the entire leaf blade began to export at 45% expanded (Turgeon and Webb 1973). The above arguments are supported by the trend of E values in plant of treatments A, B, C and D (Figure 4.5).

This association of fruit abortion level with the proportion of young leaf on the plants was reflected also in those plants with more than one block of leaf (Treatments AB, ABC, CD,

BCD and CON). The trend was less fruit aborted in the plants with a higher proportion of young leaf and vice versa.

Abortion of fruit in CON plants could be due to too many fruit being set and the available assimilates not enough to support the subsequent fruit growth and development. This was associated probably with the high level of pollinating agents (bees) available in the experiment plots (about 60,000 working bees) (Plate 2).

5.2.5.3 Distribution of Fruit Dry Weight and Fruit Number on the Plants

The distribution of fruit dry weight and fruit number on the plants at final harvest was affected by defoliation treatments. Distance from source (leaf) to sink (growing fruit) seems to be the dominant factor that influences this distribution. This is especially clear in the treatments with one block of leaf on the plant. Plants with leaf on Section A (treatment A) and B (treatment B), had more fruit dry weight in Section B, whereas plants with leaf in Section C (treatment C) and D (treatment D) had more fruit dry weight in Section C and D respectively (Figure 4.13). Treatment A plants had more fruit on Section B because there were no female flowers developed in Section A. Fruit abortion was the major factor that reduced the fruit number in stem Sections without leaf (Table 4.34, 4.35 and 4.36). These results were in agreement with the trend of stronger movement of assimilates toward the closest sink which has been observed in most plants (Wardlaw 1968).

There was no fruit found in Section C of treatment A and D plants (Figure 4.13). This was again due to complete fruit abortion which occurred earlier (Table 4.35). The reason for this is not clear. It could be due to intense competition for assimilates which occurred immediately after defoliations. In treatment A plants, the available assimilate was enough probably to support only the fast growing fruit in Section B which is closer to source, resulting in complete abortion of fruit from

Section C. Fruit in Section D developed very much later (after 109 DAT) (Table 4.36).

A similar situation had occurred probably in treatment D plants. Abrupt reduction in supply of assimilates immediately after defoliation created an intense competition for assimilates between fruit in Sections B and C. At the time of treatments being carried out, fruits in Section B were much bigger and older than fruits in Section C (Table 4.31, 4.32, 4.34, 4.35). Studies have shown that bigger and older fruit represent stronger sink strengths (Rawson and Hofstra 1969) so facilitating assimilates supply from a distance source (Wolswinkel 1984). Therefore most assimilates will go to fruits in Section B resulting in abortion of fruits in Section C. Although fruits in Section D were also small and newly set, they had the advantage of being the closest to source (Wardlaw 1968) and therefore would probably still get enough assimilates.

In the plants with more than one block of leaf, the plants of all treatments except those of CON plants, produced more yield in Section C. CON plants produced more fruit dry weight and fruit number in Section D. The reason for this is also not clear. The pattern of distribution shows that all treatments which had leaf in Section C, tended to have more yield in Section C except in CON plants. Figure 4.5 shows that leaves from Section C have a very high E when they were alone on the plants. Although this value probably is lower in the presence of other blocks of leaf, the trend is still there probably. Studies have shown that defoliation will increase the photosynthetic capacity of the remaining leaf (Neales et al 1971, Thorne and Koller 1974, Peet and Kramer 1981, Caemmerer and Farquhar 1984). If this is true, Section C leaf must have supplied the majority of assimilates needed for fruit growth, which in turn benefited the closest sink. In this case, the closest sinks were the fruits in Section C. This explains why fruit in Section C grew better than fruit in other Sections.

In the presence of all other blocks of leaf as in CON plants, the E values of Section C leaf probably are lower and this represents the normal situation when there is no defoliation. In this situation, the leaf of Section D is probably the the major supplier of assimilates which resulted in more yield produced in section D.

5.2.6 Whole Plant Growth

Discussions in the earlier Sections show that the growth of Cucurbita moschata Dunchesne, cultivar Butternut Waltham, the plant under study was greatly affected by defoliations (Table 4.1). The plants responded differently depending on the age of leaves left on the plants after defoliations. The growth of treatment A plants which had a block of oldest leaves was reduced most, with only 150.38 g of total dry matter per plant recorded at final harvest. This value was equivalent to about 11% of total dry matter recorded from CON plants. Growth was improving as the age of leaves left on the plants was getting younger, as shown in treatments B, C and D plants. Total dry weights, recorded at final harvest from treatments B, C and D plants were 269.72, 492.77 and 627.23 g per plant respectively. These correspond to 19%, 35% and 44% of CON plants respectively.

The effect of leaf age on the plant growth can be explained through leaf photosynthetic activity after defoliations. As has been discussed in the earlier Sections (section 5.2.2), younger leaves grew better (Table 4.18, Figure 4.9) and had higher E values (Table 4.2, Figure 4.4) than older leaves. This resulted in higher R values (Table 4.3, Figure 4.4) in those plants with higher proportions of young leaves left on the plants after defoliations.

Similar explanations can be applied to those plants with more than one block of leaves. Treatment AB plants which had the oldest blocks of leaves produced only 410.43 g per plant of total dry matter at final harvest. This corresponds to 29% of dry matter recorded from CON plants, which was lower than those of

treatments C and D plants. Better plant growth was observed in plants with a greater proportion of younger leaves. Total dry weights recorded from treatments ABC, CD, BCD plants were 835.78, 1044.32 and 1763.97 g per plant and correspond to 59%, 74% and 125% of CON plants respectively. CON plants produced 1413.23 g per plant of total dry matter at final harvest.

It was also evident that, D and E in the later periods (P6 and P7) can influence the final total dry weight of the plants. Treatment BCD plants were observed to have a similar total dry weight as CON plants from 79 to 109 DAT. High E and D values recorded in these two periods helped to maintain a constantly high R (Table 4.3, Figure 4.4) in treatment BCD plants during P6 and P7. As a result, a constantly high dry matter accumulation was maintained in treatment BCD plants until final harvest (Figure 4.3). Thus, the 25% extra dry matter recorded in treatment BCD plants was accumulated mainly in the P7.

The overall total dry matter accumulation was found to be linearly related ($R^2 = 0.91$, significant at $P < 0.001$) to the total D. The formula for the regression line is $Y_t = -23.4 + 10.3X$, where Y_t is the total plant dry weight in g and X is leaf area duration in square meters.

5.3 PARTITIONING OF DRY MATTER BETWEEN ORGANS

Partitioning of dry matter which is calculated as the fraction of dry matter found in plant organs was greatly altered by treatments (Table 4.37, 4.38, 4.39 and 4.40). This result was not unexpected because the treatments employed in this experiment involved removing some of the leaves from the plants. The main concern here was how each plant organ responded to this defoliation.

In general, all treated plants showed a trend of "recovery" which resulted in the proportion of dry matter found in each organ similar to that of CON plants. Partitioning of dry matter to

leaves became similar in all treatments at 99 and 109 DAT (Table 4.37). They became different again at final harvest (134 DAT) due to the senescence of Section A leaves. Recovery in partitioning to stems was not completed even until final harvest. The stems of treatment A and B plants had a higher percentage of dry matter than the stem of plants receiving other treatments (Table 4.38). This was due to the high stability observed in stem dry weight (Table 4.8) and to the differences in the dry weight loss due to retranslocation (Section 5.2.3). Partitioning to flowers became similar to that of CON plants at 99 DAT (Table 4.39) while in fruit, this was observed only at final harvest (Table 4.40). There was a trend of higher partitioning of dry matter into the fruit of treatment BCD plants which was due to high E and D during P7 (Table 4.5, Figure 4.5).

6 CONCLUSIONS

1. Removal of a basal leaf block (treatment BCD) significantly increased the total plant dry weight and yield by 25% and 30% respectively, as compared to the CON plants. Removal of one or more block of leaves from other parts of the stem, all caused reductions in the total plant dry weight and yield. Higher growth and yield in the treatment BCD plants were due to the high D and E in the last period (P7). Reductions in growth and yield in the other treatments were due mainly to continuing low total leaf area present on the plants after defoliation.

2. Variations both in the fruit size (dry weight per fruit) and fruit number per plant were found to contribute to the variation in yield. However, when these two factors were compared, fruit size was the more dominant factor.

3. The pattern of fruit distributions on the plant was influenced strongly by the position of leaves. Stem sections with leaves present had bigger fruits as well being more numerous. Fruit abortion was higher in the stem sections without leaves.

4. The pattern of flower development was not affected by defoliation. This was due to the differentiation of flowers into different sexes long before defoliation.

5. Stem was the plant organ found to be the least affected by defoliations. Defoliation however caused the total stem dry weight to reach different levels. A higher maximum was achieved by those plants with more leaf area and a greater proportion of younger leaves (treatments D, CD, ABC, BCD and CON). The dry weight loss after this maximum was however higher in plants with less total leaf area and a greater proportion of older leaf (treatments A, B, C, and AB).

6. The plants exhibited a very stable pattern of dry matter partitioning between its organs. The partitioning between

organ in treated plants became similar to that of CON plants toward the end of growing period. Partitioning of dry matter to fruits was found to be greater towards the end of growing period irrespective of the pattern of defoliations. Thus, treatment BCD plants showed a trend of higher dry matter being partitioned to fruits compared to other treatments because their D and E values were high during the last period.

7. The overall plant growth and development was linearly related to the total leaf area duration after defoliation.

8. The results suggest that, a correct pattern of defoliation at a suitable time can improve the growth and yield of an annual crop. Similar responses may or may not occur in water melon plants. This can be confirmed only by carrying out a similar experiment under Malaysian condition and using water melon plants.

7. REFERENCES

- ADDICOTT, F.T. and LYON, J.L. (1973). Physiological ecology of abscission. pp. 85-117. In Sheeding of plant parts. Edited by Kozlowkiski T.T. New York: Academic Press.
- ALDERFER, R.G. (1974). Photosynthesis in developing plant canopies. pp. 227-8. In Perspectives in Biophysic Ecology. Edited by D.M. Gates. New York: Springer-verlag.
- ALDERFER, R.G. and EAGLES, C.F. (1976). The effect of partial defoliation on the growth and photosynthetic efficiency of bean leaves. Bot. Gaz. 137: 351-55.
- ALTUS, D.P. and CANNY, M.J. (1982). Loading of assimilates in wheat leaves. I The specialization of vein types for separate activities. Aust. J. Plant Physiol., 9: 571-81.
- ANDERSON, R. and CRONSHAW, J. (1970). Sieve pore-plate in tobacco and bean. Planta 91: 173-80.
- BAILEY, L.H. (1944). Manual of Cultivated Plants. New York: The Macmillan Company. 851p.
- BEHNKE, H.D. (1971). The contents of sieve plate pores in Aristolochia. J. Ultrastructure Res. 36: 493-98.
- BIDDULP, O., and CORRY, R. (1960). Demonstration of two translocation mechanism in studies of bidirectional movement. Plant Physiol. 35: 689-95.
- BIELESKI, R.L. (1962). The Physiology of Sugarcane V. Kinetics of Sugar Accumulation. Aust. J. Biol. Sci. 15: 429-44.

- BLACKMAN, V.H. (1919). The compound interest law and plant growth. Ann. Bot. 33: 353-60.
- BLISS, C.I. (1967). Statistic in Biology Vol. 1. New York: McGraw-hill. 560 p.
- BRIGGS, G.E., KIDD, F. and WEST, C. (1920a). A quantitative analysis of plant growth. Part I. Ann. Appl. Biol 7: 103-23.
- BRIGGS, G.E., KIDD, F. and WEST, C. (1920b). A quantitative analysis of plant growth. Part II. Ann. Appl. Biol 7: 202-23.
- CAEMMERER, S. VON and FARQUHAR, G.D. (1984). Effect of partial defoliations, changes of irradiance during growth, short-term water stress and growth at enhanced $p(\text{CO}_2)$ on the photosynthetic capacity of leaves of Phaseolus vulgaris L. Planta 160: 320-29.
- CAMERON-MILLS, V. and DUFFUS, C.M. (1979). Sucrose transport in isolated immature barley embryos. Ann. Bot. 43, 559-69.
- CANNY, M.J. (1962). The mechanism of translocation. Ann. Bot. 26: 603-17.
- CANNY, M.J. (1973). Phloem Translocation. Cambridge: Cambridge University Press. 301 p.
- CANNY, M.J. (1975). Mass transfer. pp. 139-53. In Transport in Plants. I. Phloem Transport. Edited by M.H. Zimmerman and J.A. Milburn. Berlin: Springer.
- CANNY, M.J. (1984). Translocation of nutrients and hormones. pp. 277-96. In Advanced Plant Physiology. Edited by M.B. Wilkins. London: Pitman Publishing Limited.

- CANNY, M.J. and PHILLIPS, O.M. (1963). Quantitative aspect of a theory of translocation. Ann. Bot. 27: 379-402.
- CARMI, A. and KOLLER, D. (1979). Regulation of photosynthetic activity in the primary leaves of bean (Phaseolus vulgaris L.) by materials moving in the water conducting system. Plant. Physiol. 64: 285-88.
- CAUSTON, D.R. (1977). Plant growth analysis: a biological application of calculus. pp. 205-17. In A Biologist's Mathematics. London: Edward Arnold.
- CAUSTON, D.R. and VENUS, J.C. (1981). The Biometric of Plant Growth. London: Arnold. 62 p.
- CHIN, C.K. and WESTON, G.D. (1975). Sucrose absorption and synthesis by excised Lycopersion esculentum roots. Phytochemistry 14: 69-70.
- CHRISTY, A.L. and FERRIEF, J.M. (1973). A Mathematical Treatment of Munch's Pressure-flow Hypothesis of Phloem Translocation. Plant Physiol. 52: 531-8.
- COOK, M.G. and EVANS, L.T. (1978). Effect of relative size and distance of competing sinks on the distribution of photosynthetic assimilates in wheat. Aust. J. Plant Physiol., 5: 495-509.
- CRAFTS, A.S. (1932). Phloem Anatomy, Exudation, and Transport of Organic Nutrients in cucurbits. Plant Physiol. 7: 183-225.
- CRAFTS, A.S. and CRISP, C.E. (1971). Phloem Transport In Plants: Freeman, San Francisco.

- CROMPTON, H.J., LLOYD-JONES, C.P. and HILL-COTTINGHAM, D.G. (1981). Translocation of labelled assimilates following photosynthesis of $^{14}\text{CO}_2$ by field bean, Vicia faba. Physiol. Plant. 51: 189-94.
- CRONSHAW, J. (1975). P-protein. pp. 79-115. In Phloem Transport. Edited by Aronoff, S., Daninty J., Gorham P.R., Srivastara L.M. and Swanson, C.A. New York-London: Plenum Press.
- CRONSHAW, J. (1981). Phloem structure and function. Ann. Rev. Plant Physiol. 32: 465-84.
- CRONSHAW, J., and ANDERSON, R. (1969). Sieve plate pores of Nicotiana. J. Ultrastructure Res. 27: 134-48.
- CRONSHAW, J. GILDER, J. and D. STONE. (1973). Fine Structural Studies of P-proteins in Cucurbita: Cucumis, and Nicotiana. J. Ultrastruct. Res. 45: 192-205.
- DANIEL, C. (1959). Use of half-normal plots in interpreting factorial two-level experiments. Technometrics 1: 311-41.
- DAVIS, L.A. and ADDICOTT, F.T. (1972). Abscisic acid: correlations with abscission and with development in the cotton fruit. Plant. Physiol. 49: 644-48.
- DEMSEY, G.P., BULLIVANT, S. and BIELESKI, R.L. (1975). The distribution of P-protein in mature sieve elements of celery. Planta 126: 47-59.
- DE MARIA, M.E., and THAINE, R. (1974). Strands in sieve tubes in longitudinal cryostat section of Cucurbita pepo stems. J. Exp. Bot. 25: 871-75.

- DIXON, H.H. and GIBBON, M.W. (1932). Bast sap in plants.
Nature (Lond.) 130: 661-62.
- DUNCAN, D.B. (1955). Multiple range and multiple F test.
Biometrics 11: 1-42.
- ESAU, K. (1969). The phloem. In Encyclopedia of Plant Anatomy.
Vol. V/2 Edited by Zimmerman, W. Ozenda, P., and Wulff,
H.D. Berlin-Stuttgart: Gebruder Borntraeger.
- EVANS, G.C. (1972). The Quantitative Analysis of Plant Growth.
Vol. 1. London: Blackwell Scientific Publications.
734 p.
- EVANS, G.C. and HUGHES, A.P. (1961). Plant growth and the aerial
environment. I. Effect of artificial shading on
Impatiens parviflora. New Phyto. 60: 150-80.
- EVANS, L.T., WARDLAW, I.F. and FISHER, R.A. (1975). Wheat. pp.
101-150. In Crop Physiology - some case histories.
Edited by L.T. Evans. Cambridge: Cambridge University
Press.
- EVERT, R.F., BORNMAN, C.H., BUTLER, V. and GILILAND, M.G. (1973).
Structure and development of the sieve-wall protoplast
in leaf vein of Welwitschia. Protoplasma 76: 1-21.
- EVERT, R.R., ESCHRICH, W. and EICHORN, S.E. (1973). P-protein
distribution in nature sieve elements of Cucurbita
maxima. Planta 109: 193-200.
- FELKER, F.C. and SHANNON, J.C. (1980). Movement of ¹⁴C-labelled
assimilates into kernel of Zea mays L. Planta Physiol.
65: 864-70.

- FELLOW, R.J. and GEIGER, D.R. (1974). Structural and physiological changes in sugar beet leaves during sink to source conversion. Plant Physiol. 54: 877-85.
- FENSOM, D.S. (1957). The bio-electric potentials of plants and their functional significance I An electro-kinetic theory of transport. Can. J. Bot. 35: 573-82.
- FENSOM, D.S. (1972). A theory of translocation in phloem of Heracleum by contractile protein microfibrillar material. Can. J. Bot. 50: 479-97.
- FENSOM, D.S. (1975). Other possible mechanisms. pp. 354-65. In Transport in Plants I. Phloem Transport. Edited by M.H. Zimmermann and J.A. Milburn. New York: Springer-Verlag.
- FENSOM, E.S. (1981). Problems Arising From A Munch-type Pressure Flow Mechanism of Sugar Transport in Phloem. Can. J. Bot. 59: 425-32.
- FISHER, D. (1975). Structure of Functional Soybean Sieve Elements. Plant Physiol. 56: 55-60.
- FISHER, R.A. (1921). Some remarks on the methods formulated in a recent article on "the quantitative analysis of plant growth". Ann. Appl. Biol. 7: 367-72.
- FONDY, B.R. and GEIGER, D.R. (1977). Sugar Selectivity and Other Characteristic of Phloem Loading in Beta vulgaris L. Plant Physiol 59: 953-60.
- FRANCE, J. and THORNELLY, H.J.M. (1984). Mathematical Models in Agriculture. Butterworth. 352 p.

- GALES, K. (1979). Effect of water supply on partitioning of dry matter between roots and shoots in Lolium perenne. J. App. Eco. 16: 863-877.
- GALLANGER, J.N., BISCO, P.V. and SCOTT, R.K. (1975). Barley its environment. V. Stability of grain weight. J. App. Eco. 12: 3129-36.
- GAMALEI, YU.V. and PAKHOMOVA, M.V. (1980). Distribution of Plasmodesmata and Parenchyma Transport of Assimilates in Leaf of Several Dicots. Fiziol. Rast. 28: 901-12.
- GARTNER, C.F. (1844). quoted in Sexton, R. and Woolhouse, H.W. (1984). Senescence and abscission. pp. 469-97. In Advanced Plants Physiology. Edited by Wilkins, M.B. London: Pitman Publishing Ltd.
- GAYLER, K.R. and GLASZIOU, K.T. (1972). Sugar Accumulation In Sugarcane. Plant Physiol. 49: 563-68.
- GEIGER, D.R. (1975). Phloem loading. pp. 395-431. In Transport in Plants. I. Encyclopedia of Plant Physiology New series vol. I. Edited by M.H. Zimmerman and J.A. Milburn. New York: Springer-Verlag.
- GEIGER, D.R. (1979). Control of Partitioning and Export of Carbon in leaves of Higher Plants. Bot. Gaz. 140: 241-48.
- GEIGER, D.R. and FONDY, B.R. (1980). Response of Phloem Loading and Export to Rapid Changes in Sink Demand. Ber. Disch. Bot. Ges. 93: 177-86.
- GIEGER, D.R., GIAQUINTA, R.T., SOVONICK, S.A. and FELLOW, R.J. (1983). Solute Distribution in Sugar Beet Leaves in Relation to Phloem Loading and Translocation. Plant Physiol. 52: 585-89.

- GIAQUINTA, R.T. (1977). Sucrose hydrolysis in relation to phloem translocation in Beta vulgaris. Plant Physiol. 60: 339-343.
- GIAQUINTA, R.T. (1983). Phloem Loading of Sucrose. Ann. Rev. Plant Physiol. 34: 347-87.
- GIFFORD, R.M. and EVANS, L.T. (1981). Photosynthesis, Carbon Partitioning and Yield. Ann. Rev. Plant Physiol. 32: 485-509.
- GLASZIOU, K.T. and GAYLER, K.R. (1972). Storage of Sugars in the Stalk of Sugarcane. Biol. Rev. 38: 471-488.
- GOMEZ, K.A. and GOMEZ, A.A. (1984). Statistical Procedures for Agriculture Research. 2nd. ed. New York: John Wiley. 680 p.
- GREGORY, F.G. (1926). The effect of climatic conditions on the growth of barley. Ann. Bot. 40: 1-26.
- HAMPSON, S.E., LOOMIS, R.S. and RAINS, D.E. (1978a). Characteristic of Sugar Uptake in Hypocotyls of Cotton. Plant Physiol. 62: 846-50.
- HAMPSON, S.E., LOOMIS, R.S. and RAINS, D.W. (1978b). Regulation of Sugar Uptake in Hypocotyls of Cotton. Plant Physiol. 62: 851-55.
- HARDMAN, L.L. and BRUN, W.A. (1971). Effect of atmospheric carbon dioxide enrichment at different developmental stages on growth and yield components of soybeans. Crop Sci. 11: 886-888.
- HART, J.B. and SABNIS, D.D. (1973). Chlochlorogenic acid-binding protein from Phloem and Xylem of A Higher Plant. Planta 109: 147-52.

- HEINDL, J.C. and BRUN, W.A. (1983). Light and shade effect on abscission and ^{14}C -assimilate partitioning among reproductive structure in soybean. Plant Physiol. 73: 434-39.
- HO, L.C. and BAKER, D.A. (1982). Regulation of Loading and unloading in Long Distance Transport Systems. Plant Physiol. 56: 225-30.
- HODGKINSON, K.C. (1974). Influence of partial defoliation on photosynthesis, photorespiration and transpiration by lucerne leaves of different ages. Aust. J. Plant Physiol. 1: 561-78.
- HOLL, W. (1975). Radial transport in rays. pp. 432-48. In Transport in Plants I. Phloem Transport. Edited by M.H. Zimmermann and J.A. Milburn. New York: Springer-Verlag.
- HOPKINSON, J.M. (1964). Studies on the expansion of the leaf surface, IV. The carbon and phosphorus economy of a leaf. J. Exp. Bot. 15: 125-37.
- HOPKINSON, J.M. (1966). Studies on the expansion of the leaf surface. VI. Senescence and usefulness of old leaves. J. Exp. Bot. 15: 762-70.
- HUFF, A. and DYBING, G.D. (1980). Factors affecting of flowers in soybean [(Glucine max L.) Merrill]. J. Exp. Bot. 31:
- HUME, R.J. (1980). Responses of Cucurbita pepo and Cucurbita maxima to ethrel. Thesis, p.H.D., University of Auckland. 161 p.
- HUME, R.J. and LOVELL, P.H. (1983). The control of sex expression in cucurbits by Ethepon. Ann. Bot. 52: 689-95.

- HUNT, R. (1978). Plant Growth Analysis. The Institute of biology's studies in biology no. 96. London: Edward Arnold (Publishers) Limited. 67 p.
- HUNT, R. (1982). Plant Growth Curves. London: Arnold. 256 p.
- ILKER, R. and CURRIER, H.B. (1974). Heavy Micromyosin Complexing Filaments in the Phloem of Vicia faba and Xylosma congestum. Planta 120: 311-16.
- INCOLL, L.D. and NEALES, T.F. (1970). The stem as a temporary sink before tuberization in Helianthus tuberosus L. J. Exp. Bot. 21: 469-76.
- JANNER, C.F. (1968). Synthesis of starch in detached ears of wheat. Aust. J. Biol. Sci. 21: 597-608.
- JANNER, C.F. (1974). An Investigation of the Association between Hydrolysis of Sucrose and Its Absorption by Grains of Wheat. Aust. J. Plant. Physiol. 1: 319-29.
- JOHNSON, R.P.C. (1968). Microfilaments in pores between freeze-etched sieve elements. Planta 81: 314-32.
- JOHNSON, R.P.C. (1973). Filaments but no membranous transcellular strands in sieve elements. Planta (Berl.) 81: 314-32.
- JOHNSON, R.P.C. (1973). Filaments but no membranous transcellular strands in sieve pore in freeze-etched translocating phloem. Nature 244: 464-66.
- JOHNSON, R.P.C. (1978). The microscopy of P-protein filaments in freeze-etched sieve tube pores. Planta 143: 191-205.
- KLEINIG, H., DORR, I., WEBER, C. and KOLLMAN, R. (1971). Filamentous proteins from plant sieve tubes. Nature (London) New Biol. 229: 152-153.

- KOLLMANN, R. DORR, I. and KLEINIG, H. (1970). Protein Filament-Structural Components of the Phloem exudate I. Observations with Cucurbita and Nicotiana. Planta 95: 86-94.
- KOMOR, E. (1977). Sucrose uptake by cotyledons of Ricinus communis L.: Characteristics, Mechanism, and Regulation. Planta 137: 119-31.
- KRIEDEMANN, P. and BEEVERS, H. (1967). Sugar uptake and translocation in the castor bean seedling I. Characteristic of transfer in intact and excised seedlings. Plant Physiol. 42: 161-73.
- KURSANOV, A.L. and BROVCHENKO, M.I. (1970). Sugars in the Free Space of Leaf Plates: Their origin and possible involvement in transport. Can. J. Bot. 48: 1243-50.
- LANG, A. (1973). A working model of a sieve tubes. J. Exp. Bot. 24: 896-904.
- LEOPOLD, A.C. and KRIEDMAN, P.E. (1975). Plant Growth and Development. 2nd. Ed. New York: Mc Graw-hill Book Comp. pp. 41-76.
- LIPE, J.A. and MORGAN, P.W. (1972). Ethylene role in fruit abscission and dehiscence processes. Plant Physiol. 50: 759-64.
- LOOMIS, R.S., RABBINGE, R. and NG, E. (1979). Explanatory models in crop physiology. Ann. Rev. Plant Physiol. 30: 339-67.
- LUCKWILL, L.C. (1953). Studies of fruit development in relation to plant hormones. I. J. hort. Sci. 28: 14-24.

- LUSH, W.M. (1976). Leaf structure and translocation of dry matter in a C³ and C⁴ Grass. Planta 130: 235-44.
- MAC ROBBIE, E.A.C. (1971). Phloem translocation, facts and mechanism: a comparative survey. Biol. Rev. 46: 429-81.
- MAC ROBBIE, E.A.C. (1975a). Activated Mass Flow: Surface Flow. pp. 585-600. In Phloem Transport. Edited by Aronoff, S., Dainty, J., Gorham, R.P. Srivastara, L.M. and C.A. Swanson. New York: Plenum Press.
- MAC ROBBIE, E.A.C. (1975b). Mechanisms, Comparative Behavior. pp. 601-609. In Phloem Transport. Edited by Aronoff, S., Dainty, J., Gorham, R.P., Srivastara, L.M. and C.A. Swanson. New York: Plenum Press.
- MADORE, M. and WEBB, J. (1981). Leaf free space analysis and vein loading in Cucurbita pepo. Can. J. Bot. 59: 2550-57.
- MAKUNGA, O.H.D., PEARMAN, I., THOMAS, S.M. and THORNE, G.N. (1978). Distribution of photosynthate produced before and after anthesis in tall and semi-dwarf winter wheat, as affected by nitrogen fertilizer. Ann. App. Biol. 88: 429-37.
- MARSHALL, C. and SAGAR, G.R. (1978). Transport in phloem. p. 254-93. In Plant Structure, Function and Adaptation. Edited by Hall, M.A. Hong Kong: The Macmillan Press Ltd.
- MASON, T.G. and MASKELL, E.J. (1928a). Studies on the Transport of Carbohydrate in the Cotton Plant I. Ann. Bot. 42: 189-253.

- MASON, T.G. and MASKELL, E.J. (1928b). Studies on the Transport of Carbohydrate in the Cotton Plant II. Ann. Bot. 42: 571-636.
- MCARTHUR, J.A., HESKETH, J.D., and BAKER, D.N. (1975). Cotton. pp. 297-325. In Crop Physiology. Edited by L.T. Evans. London: Cambridge University Press.
- MELARAGNO, J.E. and WALSH, M.A. (1976). Ultrastructure features of developing sieve elements in Lenina minor L. - the Protoplast. Amer. J. Bot. 63: 1145-57.
- MERSEY, B. and MCCULLY, M.E. (1978). Monitoring the course of fixation of plant cells. J. Microsc. (Oxford) 114: 49-76.
- MILBURN, J.A. (1974). Phloem transport in Ricinus: Concentration gradients between source and sink. Planta (Berl.) 117: 303-19.
- MINISTRY OF AGRICULTURE AND FISHERIES. (1980). Horticulture produces and practices. Aglink: HPP 262.
- MISHRA, U. and SPANNER, D.C. (1970). The fine structure of sieve tubes of Salix caprea L. and its relation to the electrostatic theory. Planta 90: 43-56.
- MOORBY, J. (1970). The production, storage, and translocation of carbohydrates in developing Potato Plants. Ann. Bot. 34: 297-308.
- MOORBY, J. (1981). Transport System in Plants. London and New York: Longman. 169 p.
- MURMANIS, L. and EVERT, R.F. (1966). Some Aspects of Sieve Cell Ultrastructure in Pinus strobus. Amer. J. Bot. 53: 1065-78.

- NEALES, T.F., TREHARNE, K.J., and WAREING, P.F. (1971). A relationship between net photosynthesis, diffusive resistance, and carboxylating enzyme activity in bean leaves. pp. 89-96. In Photosynthesis and Photorespiration. Edited by Hatch, M., Osmond, D.C., and Slatyer, R.O. New York: Wiley.
- NIE, N.H., HULL, C.H., JENKINS, J.G., STEINBRENNER, K. and BENT, D.H. (1975). SPSS: Statistical Package for the Social Science. 2nd. ed. New York: MacGraw-Hill. 678 p.
- PALEVITZ, B.A. and HEPLER, P.K. (1975). Is P-protein Actin-like? - Not Yet. Planta 125: 261-71.
- PARTHASARATHY, M.V. (1975). Structural considerations in phloem transport. pp. 3-33. In Encyclopedia of Plant Physiology. Edited by M.H. Zimmerman and J.H. Milburn. Berlin: Springer-verlag.
- PASSIOURA, J.B. (1981). Water collection by roots. pp. 39-53. In The Physiology and Biochemistry of Drought Resistance in Plants. Edited by Paleg, L.G. and Aspinall, D. Sydney: Academic Press.
- PATE, J.S. (1980). Transport and partitioning of nitrogenous solutes. Ann. Rev. Plant Physiol. 31: 313-40.
- PATE, J.S., ATKINS, C.A., HAMEL, K., McNEK, D.L. and LAYZELL, P.B. (1979). Transport of organic solutes in phloem and xylem of a nodulated legum. Plant Physiol. 63: 1082-88.
- PATRICK, J.W., and WAREING, P.F. (1976). Auxin-promoted transport of metabolites in stem of Phaseolus vulgaris L. J. Exp. Bot. 27: 969-82.

- PATRICK, J.W. and MACDONALD, R. (1980). Pathways of Carbon Transport Within Developing Ovules of Phaseolus vulgaris L. Aust. J. Plant Physiol. 7: 671-84.
- PEEL, A.J. and HO, L.C. (1970). Colony size of Tuberolachnus salignus (Gmelin) in relation to mass transport of ^{14}C -labelled assimilates from the leaves in willow. Physiol. plant., 23: 1033-38.
- PEET, M.M. and KRAMER, P.J. (1981). Effect of decreasing source/sink ratio in soybeans on photosynthesis, photorespiration, transpiration and yield. Plant Cell Environ. 3: 201-266.
- PORTER, N.G. (1981). The directional control of sucrose and asparagine transport in lupin by abscisic acid. Physiol. Plant. 53: 279-84.
- PREISS, J. (1982). Regulation of biosynthesis and degradation of starch. Ann. Plant Physiol. 33: 431-54.
- RAWSON, H.M. and EVANS, L.T. (1971). The contribution of stem reserves to grain development in a range of wheat cultivars of different height. Aust. J. Agric. Res. 22: 851-63.
- RAWSON, H.M. and HOFSTRA, G. (1969). Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of the wheat plants. Aust. J. Biol. Sci. 321-31.
- RICHARDS, F.J. (1959). A flexible growth function for empirical use. J. exp. Bot. 10: 290-300.
- RICHARDS, F.J. (1969). The quantitative analysis of growth. pp. 3-76. In Plant Physiology VA. Edited by F.C. Steward. New York: Academic Press.

- RUFTY, T.W. JR., RAPER, C.D. JR., and HUBER, S.C. (1984).
Alteration in internal partitioning of carbon in
soybean plants in response to nitrogen stress. Can.
J. Bot.: 501-8.
- SABNIS, D.D. and HART, J.W. (1973). P-protein in Sieve
Elements. I Ultrastructure After Treatment With
Vinblastine and Colchicine. Planta 109: 127-133.
- SABNIS, D.D. and HART, J.W. (1974). Studies On the possible
Occurance of Actomyosin-like Proteins in Phloem.
Planta 118: 271-81.
- SABNIS, D.D. and HART, J.W. (1978). The Isolation and Some
Properties of a Lectin (haemagglutinin) from Cucurbita
Phloem Exudate. Planta 142: 97-101.
- SABNIS, D.D. and HART, J.W. (1979). Heterogeneity in Phloem
Protein Complements From Different Species. Planta 145:
459-460.
- SCHMITZ, K. and SRIVASTARA, L.M. (1974). Fine Structure and
Development of Sieve Tube in Laminaria groenlandica
Rosenv. Cytobiol. 10: 66-87.
- SCHOU, J.B., JEFFER, D.L., and STREETER, J.G. (1978). Effect of
reflections, black boards or shades applied at different
development stages on growth and yield components of
soybeans. Crop Sci. 18: 29-34.
- SHIH, C.Y. and CURRIER, H.B. (1969). Fine structure of phloem
cells in relation to translocation in the cotton
seedling. Ame. J. Bot. 56: 464-72.
- SIDDIQUI, A.W. and SPANNER, D.C. (1970). The state of pores in
the functioning sieve plates. Planta 91: 81-89.

- SOVONICK, S.A., GEIGER, D.R. and FELLOWS, R.J. (1974). Evidence For Active Phloem Loading in the Minor Veins of Sugar Beet. Plant Physiol. 54: 886-91.
- SPANNER, D.C. (1958). The translocation of sugar in sieve tubes. J. Exp. Bot. 9: 332-42.
- SPANNER, D.C. (1970). The electroosmotic theory of phloem transport in the light of recent measurements on Heracleum phloem. J. Exp. Bot. 21: 325-34.
- SPANNER, D.C. (1978). Sieve-plate Pores, Open or Occluded? A Critical review. Plant, Cell and Environment 1: 7-20.
- SPANNER, D.C. (1979). The electroosmosis theory of phloem transport: a final restatement. Plant, Cell and Environment. 2: 107-21.
- STACEY, D.L. (1983). The effect of artificial defoliation on the yield of tomato plants and its relevance to pest damage. J. Hort. Sci. 58: 117-20.
- STEEL, R.G.D. and TORRIE, J.H. (1960). Principles and Procedures of Statistics. New York: McGraw-Hill. 481 p.
- STEEL, R.G.D. and TORRIE, G.H. (1980). Principles and Procedures of Statistics: A Biometrical Approach. 2nd. Ed. Tokyo: McGraw-Hill Kongakusha. 634 p.
- STREET, H.E. and OPIK, H. (1976). The Physiology of Flowering Plants. 2nd. Ed. London: William Clowes and Sons Ltd. pp. 88-110.
- STREETER, J.G. and JEFFER, D.L. (1979). Distribution of total non-structural carbohydrates in soybean plants having increased reproductive load. Crop Sci. 19: 729-34.

- SZYNKIER, K. (1974). The effect of removing of supply or sink organs on the distribution of assimilates in two varieties of garden pea, Pisum sativum L. Acta Agric. Scand. 24: 7-12.
- TAMAS, I.A., WALLACE, D.H., LUDFORD, P.M. and OZBUN, J.L. (1979). Effect of older fruits on the abortion and abscisic acid concentration of younger fruits in Phaseolus vulgaris L. Plant Physiol. 64: 620-22.
- THAINE, R. (1961). Transcellular strands and particle movement in mature sieve tubes. Nature, Lond. 192: 772-3.
- THOMPSON, R.G., FENSOM, D.S., ANDERSON, R., DROUIN, R. and LEIPER, W. (1979). Translocation of ^{11}C From Leaves of Helianthus, Heracleum: Nymphoides: Ipomea: Trapaeolum, Zea: Fraxinus: Ulmus: Picea and Pinus; Comparative Shapes and Some Fine Structure Profile. Can. J. Bot. 57: 845-63.
- THORNE, G.N. (1960). Variation with age and net assimilation rate and other growth attributes of sugar-beet, potato, and barley in a controlled environment. Ann. Bot. 24: 356-71.
- THORNE, J.H. and KOLLER, H.R. (1974). Influence of assimilate demand on photosynthesis, diffusive resistance, translocation, and carbohydrate levels of soybean leaves. Plant Physiol 54: 201-7.
- THORNE, J.H. (1980). Kinetic of ^{14}C -photosynthate uptake by developing soybean fruit. Plant Physiol. 65: 975-79.
- THORNE, J.H. (1981). Morphology and Ultrastructure of Maternal Seed Tissue of Soybean in Relation to Import of Photosynthate. Plant Physiol. 67: 1016-25.

- THROWER, S.L. (1967). The pattern of translocation during ageing. Soc. Exp. Biol. Symp. 21: 483-506.
- TIETZ, A., LUDEWIG, M., DINGKUHN, M. and DORFFLING, K. (1981). Effect of abscisic acid on the transport of assimilates in barley. Planta 152: 557-61.
- TRIP, P. and GORHAM, P.R. (1968). Bidirectional translocation of sugars in sieve tubes of squash plants. Plant Physiol., Lancaster 43: 877-82.
- TROUGHTON, J.H. and SAMPSON, F.B. (1973). Plants - A Scanning Electron microscope Survey. Sydney: John Wiley and Sons, Australia Pty. Ltd. 155 p.
- TROUGHTON, J.H. and CURRIE, J.B. (1977). Relations between light level, sucrose concentration, and translocation of ^{11}C in Zea mays Leaves. Plant Physiol. 59: 808-20.
- TURGEON, R. and WEBB, J.A. (1973). Leaf Development and Phloem Transport in Curcubita pepo: Transition From Import to Export. Planta 113: 179-91.
- TURGEON, R. and WEBB, J.A. (1976). Leaf Development and Phloem Transport in Cucurbita pepo: Maturation of the Minor Veins. Planta. 113: 129-69.
- TURGEON, R., WEBB, J.A. and EVERT, R.F. (1975). Ultrastructure of Minor Veins in Cucurbita pepo Leaves. Protoplasma 83: 217-32.
- WARDLAW, I.F. (1968). The control and pattern of movement of carbohydrates in plants. Bot. Rev. 34: 79-105.

- WATSON, D.J. (1947). Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties and within and between years. Ann. Bot. N.S. 11: 41-76.
- WATSON, D.J. (1952). The physiological basis of variation in yield. Adv. Agron. 4: 101-45.
- WHEATHERLEY, P.E. and JOHNSON, R.P.C. (1968). The form and function of the sieve tube: a problem in reconciliation. Int. Rev. Cytol. 24: 149-92.
- WHITEHEAD, F.H. and MYERSCOUGH, P.J. (1962). Growth analysis of plants. The ratio of mean relative growth rate to mean relative rate of leaf area increase. New Phytol. 61: 314-21.
- WILKERSON, C.G., JONES, J.W. and POE, S.L. (1984). Effect of defoliation on the peanut plant growth. Crop Sci. 24: 526-31.
- WILLIAMSON, R.E. (1972). An Investigation of Contractile Protein Hypothesis of Phloem Translocation. Planta 106: 149-57.
- WOLSWINKEL, P. (1975). The Active Role of the Host (Ficia faba) In the Transfer of Nutrient Elements From the Phloem to the Parasite (Cuscuta species): Metabolically Controlled K^+ and Mg^{++} Release To the Free Space. Acta Bot. Neerl. 24: 211-224.
- WOLSWINKEL, P. (1979). Transport of assimilates and mineral elements at the site of attachment of Cuscuta. The role of phloem unloading in the parasitic relationship. pp. 154-64. In Proceeding of the Second Symposium on Parasitic Weeds. Edited by L.J. Musselman, A.D. Worsham and R.E. Eplee. Raleigh: North Carolina State University.

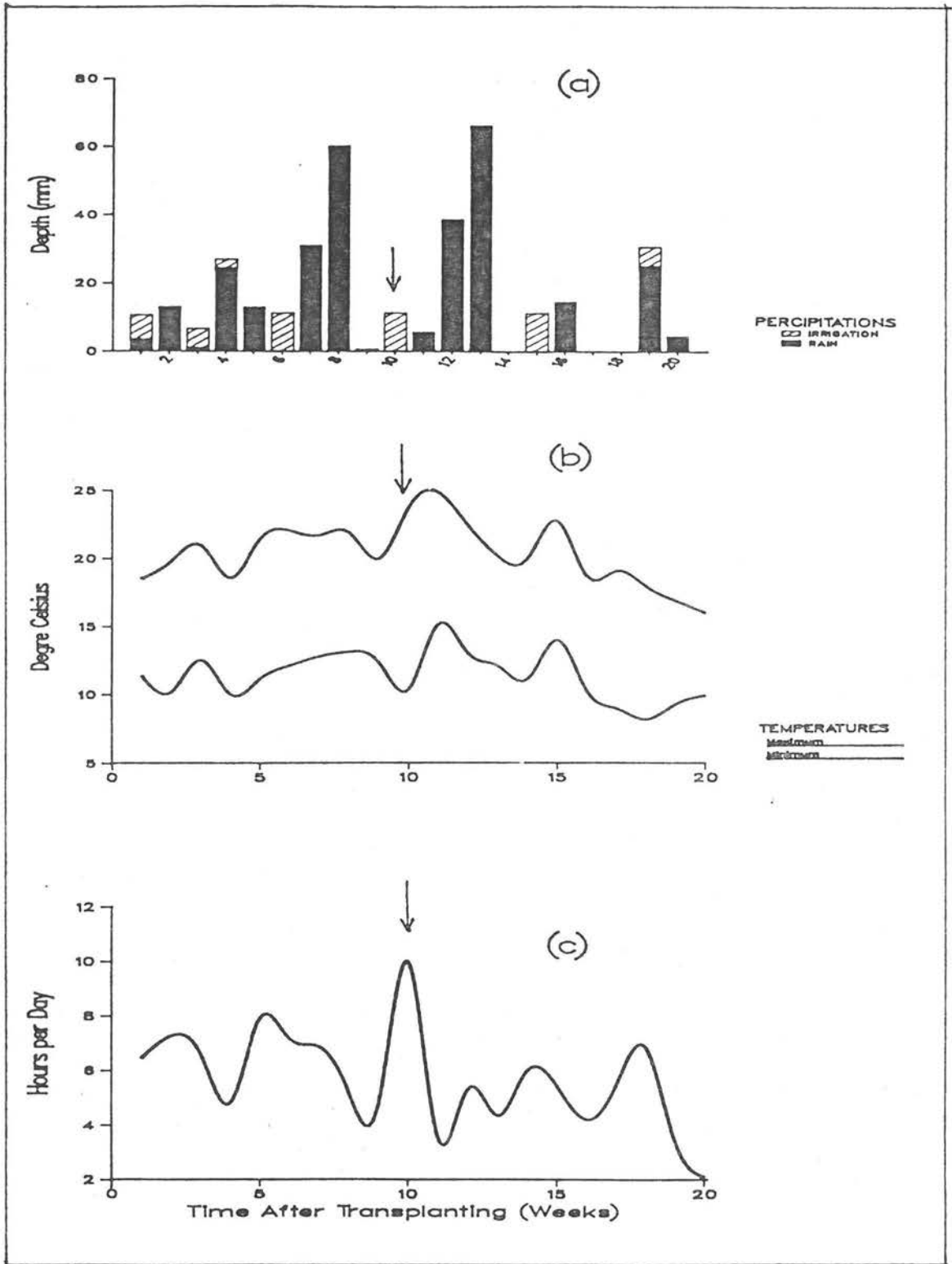
- WOLSWINKEL, P. (1974a). Complete Inhibition of Setting and Growth of Fruits of Vicia faba L., Resulting From the Draining of the Phloem System by Cuscuta sp. Acta Bot. Neerl. 23: 48-60.
- WOLSWINKEL, P. (1974b). Enhanced Rate of ^{14}C -solute Release to the Free Space by the Phloem of Vicia faba stems Parasitized by Cuscuta. Acta Bot. Neerl. 23: 177-88.
- WOLSWINKEL, P. (1978). Phloem Unloading in Stem Parts of Parasitized by Cuscuta: The Release of ^{14}C and K^+ to the Free Space at 0°C and 24°C . Physiol. Plant 42: 167-72.
- WOLSWINKEL, P. (1982). Is Enhanced Phloem Unloading in Plants Parasitized by Cuscuta Restricted to the Site of Attachment? Ann. Bot. 50: 863-67.
- WOLSWINKEL, P. (1984). Phloem Unloading and "Sink Strength". The Parallel Between the Site of Attachment of Cuscuta and Developing Legume Seeds. Plant Growth Regulation 2: 209-17.
- WOLSWINKEL, P., and AMMERLAAN, A. (1983a). Phloem Unloading in Developing Seeds of Vicia faba L. The Effect of Several Inhibitors on the Release of Sucrose and Amino Acids by the Seed Coat. Planta 158: 205-215.
- WOLSWINKEL, P. and AMMERLAAN, A. (1983b). Sucrose and Hexose Release by Excised Stem Segments of Vicia faba L. The Sucrose Specific Stimulating Influence of Cuscuta on Sugar Release and the Activity of Invertase. J. Exp. Bot. 34: 1516-27.

- WOLSWINKEL, P., AMMERLAAN, A. and KUYVENHOVEN, H. (1983).
Effect of KCN and P-chloromercuribenzenesulfonic Acid
on the Release of Sucrose and 2-amino (1-¹⁴C)
isobutyric Acid by the Seed Coat of Pisum sativum.
Plant Physiol. 59: 375-86.
- WOLSWINKEL, P., AMMERLAAN, A. and PETERS, H.F.C. (1984). Phloem
Unloading of Amino Acids at the Site of Attachment of
Cuscuta europea. Plant Physiol. 75: 13-20.
- WOOLHOUSE, H.W. (1967). The nature of senescence in plants.
Soc. Exp. Biol. Symp. 2: 179-213.
- YAMAGUCHI, M. (1983). World Vegetables. Connecticut: The AVI
Publishing Company, Inc. 415 p.
- YISHIOKA, H. and TAKAHASHI, K. (1983). Studies on the
translocation and accumulation of photosynthates in
fruit vegetables. VI Source-sink relationship in
"netted melon" plants with respect to the number and
position fruit-bearing structures. Bulletin Vegetables
and Ornamental Crops Research Station AII Ministry of
Agricultural and Forestry, Japan.
- YU, Y.-B., and YAANG, S.F. DATE (1980). Biosynthesis of wound
ethylene. Plant Physiol. 66: 281-85.
- ZIEGLER, H. (1975). Nature of Transported Substances. pp. 59-100.
In. Encyclopedia of Plant Physiology. I Transport in
Plants. Edited by Zimmermann, M.H. and Milburn, J.A.
Berlin: Springer-verlage.
- ZIMMERMANN, M.H. (1958). Translocation of Organic Substances in
Trees. III. Plant Physiol. 33: 213-17.

ZIMMERMANN, M.H. (1969). Translocation of nutrients. pp. 383-417.
In Physiology of Plant Growth and Development. Edited
by Wilkins, M.B. London: McGraw-Hill.

ZIMMERMANN, M.H. (1957a). Translocation of Organic Substances in
Trees I. Plant Physiol. 32: 288-91.

ZIMMERMANN, M.H. (1957b). Translocation of Organic Substances
in Trees II. Plant Physiol. 32: 399-404.



Appendix 1: Total percipitation (a), maximum and minimum tempratures (b) and bright sunshine hours (c) during the experimental period: Small arrow shows approximate time of treatments.