SOURCE-SINK RELATIONSHIPS IN THE CUCUMBER PLANT (*Cucumis sativus* L.)

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ABSTRACT

In an attempt to increase the sink strength of the fruit, two auxin transport inhibitors were sprayed on to the whole plant or applied to the fruit, four days after first anthesis. Application to the plant increased fruit set, reduced the dry weight of all the component organs, but had little effect on the partitioning of the dry weight. With application to the fruit chlorflurenol had little effect, but TIBA at 200 ppm reduced fruit set on the lower nodes where it was applied. This reduction in fruit set reduced fruit dry weight and partitioning to the fruit.

As neither of these growth substances increased sink strength it was decided to investigate source sink relationships by altering the source strength. With increasing degree of leaf removal total plant dry weight was reduced but the partitioning was little affected. However with the severest leaf removal treatment a greater proportion was partitioned into the stem and less into the fruit, but the proportion partitioned into the leaves was not altered.

Deleafing as a method of reducing source strength has been criticised due to its effect on the distribution of hormones. For this reason the effect of shading was investigated. The partitioning of the absolute growth on plants that had developed medium

sized fruit was not affected by up to 58% shading. However with an increase in shading from 58% to 70% the partitioning to the fruit was reduced. Below a critical level of assimilate supply the competitive ability of the vegetative organs seemed to be higher than the fruit.

As deleafing and shading reduced source strength the effect of increasing source strength by carbon dioxide enrichment was investigated. Enrichment was applied from first anthesis and increased the growth rate of the plant in the following five weeks. The partitioning was not different to the control plants in the first week following anthesis. However in week two the partitioning to the fruit was less with enrichment. There appeared to be an accumulation of assimilates in the leaves due to the mobilising ability of the growing regions being insufficient for the higher rate of assimilation. In week three and four the mobilising ability of the growing regions increased and there appeared to be a redistribution of stored assimilates as there was a loss of leaf and petiole dry weight. The accumulation of assimilates inhibited the NAR but following the redistribution of stored assimilates the NAR recovered. In the fifth week the partitioning was very similar with or without enrichment, and these partitioning figures were very similar to that obtained with the various shading treatments in the previous

experiment. It appears that once the plant develops several medium sized fruit it partitions about 70% of the absolute growth into the fruit, 23% into the leaves, 6% into the stem, and 1% into the roots, over a wide range of assimilation rates.

With higher rates of assimilation fruit set and fruit size increased. This cultivar has many potential fruit sites as it produces few male flowers and often several flowers per node. With greater rates of assimilation fruit set will increase and should be capable of utilising the greater supply. Therefore the plant appears to be source limited.

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INTRODUCTION

The regions of assimilate production (leaves) are generally separate from the regions of consumption (growing regions, fruit, storage organs). The regions of production and consumption are referred to as 'source' and 'sink' respectively. Source strength has been defined as the rate of assimilation per plant (Warren Wilson, 1972). The term sink strength is generally used to refer to the potential capacity of a sink to accumulate assimilates and mobilising ability to describe the resultant accumulation of dry matter by a sink within the competitive framework of a whole plant (Wareing and Patrick, 1975).

The mobilising ability of sinks influences the photosynthetic rate (Neales and Incoll, 1968), the partitioning of assimilates and therefore crop yield. Wareing and Patrick (1975) believe that one of the most promising ways of increasing crop yield is by altering the distribution of assimilates. The main factor responsible for the increase in fruit yield of peanuts during the course of varietal improvement has been the change in partitioning of assimilates between the vegetative and reproductive parts (Duncan, McCloud, McGraw and Boote, 1978).

Fisher (1978) increased the mobilising ability of tomato fruits by improving natural fruit set. The mobilising ability may also be altered by applying growth substances. There is little information in the literature on the effect of the fruit's mobilising ability, and

therefore partitioning of dry weight, on fruit yield in indeterminate crops. Also there is little information on the effect of source strength on the partitioning of dry weight.

The present study was designed to see if two auxin transport inhibitors could increase the mobilising ability of cucumber fruit, and to investigate the effect of altering source strength by various methods (deleafing, shading, carbon dioxide enrichment), on the partitioning of dry weight between the component organs and fruit yield.

CHAPTER ONE

REVIEW OF LITERATURE - THE CUCUMBER PLANT

1.1 The young cucumber plant

1.1.1 Contribution of cotyledons and leaves to growth.

Plant species whose cotyledons have a high expansion factor (e.g. cucumbers), have a less rapid and shorter initial weight loss at germination in contrast to the non-expanding type (e.g. peas, beans) (Lovell and Moore, 1970; Penny, Moore and Lovell, 1976a). The exponential dry weight increase of cucumber seedlings commences immediately after emergence, which contrasts with the decline in seedling dry weight for about ten days after emergence in hypogeal species such as peas and beans. These latter species have considerable quantities of dry matter in the seeds as carbohydrate reserves (Penny et al, 1976a).

Cucumber seedling development was inhibited by a reduction in the external supply of potassium, whereas with the french bean and blue lupin most of the potassium was found outside the cotyledons after fourteen days and this was not affected by the availability from the growing media. Species whose early growth is dependent on the distribution of reserves are insensitive to the external supply of potassium, but for species whose cotyledons have a primarily photosynthetic function, seedling growth is reduced by potassium deficiency (Penny et al, 1976a). A reduction in

the area of cucumber cotyledons or shading of both cotyledons substantially reduced growth (Penny, Moore and Lovell 1976b). Also inhibition of cotyledon photosynthesis, using DCMU (3(3,4-dichlorophenyl)-1,1-dimethylurea), after the first leaf had unfolded caused a reduction in the growth of the shoot, showing that at this age the photosynthates produced by the cotyledons still contribute to leaf development. Therefore at cotyledon expansion cucumber seedlings are very sensitive to environmental conditions which limit the rate of photosynthesis. Cotyledons during the first six days of expansion are more efficient, photosynthetic organs than foliage leaves (Newton, 1963).

Hopkinson (1964) studied the rate of photosynthesis of leaves on young cucumber plants during their life. The rate fell during its later life, partly as a result of shading by upper leaves and partly due to an independent age factor. The major contribution to growth came from leaves that were rapidly expanding. Expanding leaves between 25% and 75% of the final leaf area had the highest rate of photosynthesis per unit leaf area. The export of photosynthates declined rapidly just before the final leaf area was attained. The amount of phosphorus in each leaf reached a maximum at about 50% final leaf area and then there was a substantial loss from the leaf.

1.1.2 Factors influencing the growth of the young cucumber plant

1.1.2.1 Introduction

There have been very few detailed studies on the growth of the young plant as influenced by environmental factors (Milthorpe, 1959; Newton, 1965; Dennis, 1974). Many have studied the effects of various environmental factors on the final dry weight (Daunicht, 1965; Folster, 1974; Frydrych, 1976; Hardh, 1965; Krizek, Bailey, Klueter and Liu, 1974). The carry-over effects from propogation have also been studied. Generally any environmental factor, such as temperature, carbon dioxide enrichment and irradiance, which increases the growth of the young plant has been shown to increase early yield (Anon, 1969a,b; Bacher and Hallig, 1976; Dennis, 1974; Wilde, 1976), and sometimes total yield (Anon, 1969a,b; Dennis, 1975).

1.1.2.2 Temperature

Milthorpe (1959) investigated the growth of the young cucumber plant at various temperatures (12°, 18°, 24°, and 30° C). The cotyledons expanded for fourteen to sixteen days at all temperatures except at 12° C when the rate of expansion was extremely slow and terminated by the tenth day. At 12° C they were curled and brittle. The rate of expansion of the cotyledons was markedly influenced by temperature, with 24° C being the optimum. The maximum relative rate of expansion of the foliage leaf surface was at 24° C, declining slightly at 30° C, and the net assimilation rate varied in a similar manner. The rate of leaf production was the same at 24° and 30° C but less at 18° C.

However the rate of unfolding of leaves increased with temperature, with 30° C being the optimum. The rate of leaf production always exceeded the rate of unfolding, so a continually increasing number of leaves were contained in the terminal bud as the plant grew older (Atsmon and Galun, 1962; Milthorpe, 1959). The final size of individual leaves was similar at 18° and 24° C but much smaller at 30° C. At the higher temperature there was an element of self stability, the rate of unfolding of leaves was higher but the leaves did not expand as much (Milthorpe, 1959).

1.1.2.3 Photosynthetically active radiation (PAR)

Newton (1963) exposed young cucumber plants to various levels of irradiance and daylengths giving a range of total PAR. The amount of total PAR had a greater influence on leaf area and dry weight than changes in either of its components, intensity and duration. With a constant daily total PAR only small effects could be attributed to either length of photoperiod or irradiance.

High total PAR lead to a more rapid rate of unfolding of the first leaf. The time from unfolding of the cotyledons to unfolding of the first leaf was seven days at 15 cal. cm^{-2}, day^{-1} and four days over the range of 90 - 120 cal. cm^{-2} day^{-1}. Rates of leaf production and appearance were greatest with the highest amounts of PAR but the rates of expansion of individual leaves and their

maximum areas were greatest with intermediate amounts of PAR. The amount of PAR giving the maximum dry weight at any one age was higher than for leaf area (Newton, 1963). Krizek, Bailey, Klueter and Liu (1974) observed no change in plant leaf area with higher levels of irradiance but plant dry weight was greater. Dennis (1974) made successional sowings, once a month, and grew the plants in a greenhouse with half of the plants shaded. In all sowings leaf area was reduced by shading. The reduction in leaf area with the higher levels of PAR observed by Newton (1963) may have been due to a depletion of nutrients (Milthorpe and Newton, 1963).

1.1.2.4 Carbon dioxide

Many have observed increased growth with carbon dioxide (CO_2) enrichment of cucumbers (Daunicht, 1965, 1970; Hardh, 1965; Hopen and Ries, 1962; Krizek, Bailey, Kleuter and Liu, 1974; Newton, 1965; Wittwer and Robb, 1964). Hopen and Ries (1962) and Newton (1965) observed that the area of individual leaves was greater with enrichment. Hardh (1965) stated that a common feature of enriched plants was the well developed root system in comparison to non-enriched plants. Krizek et al (1974) considered the most striking feature of enrichment was the formation of precocious flower buds and extensive lateral shoots.

The largest benefits from enrichment have been

obtained at high levels of irradiance, (Hopen and Ries, 1962; Krizek et al, 1974; Wittwer and Robb, 1964). There is also an interaction between temperature, level of carbon dioxide and the level of irradiance. Temperatures, 20° and 30° C, had little influence on the relationship between the rate of photosynthesis and level of irradiance at normal carbon dioxide levels. However with enrichment light saturation occurred at a higher level of irradiance and photosynthesis was greater at 30° C than 20° C (Gaastra, 1962). At a low level of irradiance (6 klx) the optimum temperature for growth was not affected by the carbon dioxide level. However the growth was stimulated considerably more at the optimum temperature with enrichment, hence reducing the optimum temperature range. (Daunicht, 1970).

Klueter, Bailey, Bolton and Krizek (1973) studied the rate of photosynthesis of cucumber leaves at various temperatures and levels of irradiance. Using a 1000 parts per million (ppm) carbon dioxide, the optimum temperature for photosynthesis increased as the level of irradiance was increased.

A fluctuating temperature from 12° C at night to 30° C or 35° C by day promoted growth in comparison to a constant temperature of 19° C or 23° C, or with a smaller fluctuation of 18-24° C. This difference was less striking without enrichment (Hardh, 1965).

1.1.2.5 Root temperature

Results from several investigations tend to show that the optimum root temperature for the growth of the young cucumber plant is 25-35° C (Chermnykh, Chugunova and Kosobrukhov, 1975; Folster, 1974; Gohler, 1975). Folster (1974) using a nutrient solution, studied the influence of root temperature at different times of the year with two different air temperatures (20° and 25° C). In all cases growth was markedly reduced with a 16-17° C root temperature. With a 20° or 25° C air temperature the optimum root temperature during the winter months was 30° C, but there was little difference between 20°, 25° and 30° C. However during the spring and summer months 25° C was the optimum and growth was reduced with a root temperature of 30° C. This is similar to Chermnykh, Chugunova and Kosobrukhov's (1975) results, in which the optimum temperature was higher at lower levels of radiation.

1.1.2.6 Summary

The cotyledons of cucumbers are very efficient photosynthetic organs and the growth of seedlings is very sensitive to environmental conditions which limit the rate of photosynthesis. At higher temperatures the rate of unfolding of leaves is greater but the final size of the individual leaves is less. The optimum air temperature for growth of the young cucumber plant is at least 24° C, and the optimum root temperature is 25-30° C. The amount of total PAR had a greater influence on leaf area

and dry weight than either of its components, intensity and duration. Dry weight appears to be increased more than leaf area at higher levels of total PAR.

The photosynthetic rate is more sensitive to temperature with CO_2 enrichment. The growth and photosynthetic rate respond markedly to high levels of irradiance, optimum temperatures and CO_2 enrichment.

1.2 Sex expression

1.2.1 Types of sex expression

The following types of sex expression have been reported in cucumbers (Kubicki, 1969a-f).

a. androecious - bearing staminate flowers only.
b. monoecious - bearing staminate and pistillate flowers on the same plant.
c. gynoecious - bearing pistillate flowers only.
d. andromonoecious - bearing staminate and bisexual flowers.
e. gynomonoecious - bearing pistillate and bisexual flowers.
f. hermaphroditic - bearing bisexual flowers only.
g. trimonoecious - bearing staminate, pistillate and bisexual flowers.

Until the mid sixties almost all cultivars were of the monoecious type. An exception to this were the andromonoecious cultivars such as "Lemon" and its derivative, the Australian cultivar "Richmond Green Apple"

(Kubicki, 1974). Many of the greenhouse cultivars now grown are gynoecious.

There are two groups of genes which determine the sex expression in cucumbers. The first group governs the intensity of femaleness from androecious to gynoecious, or from the andromonoecious to hermaphroditic sex expression. The second group governs the floral structure, therefore the formation of pistillate flowers in monoecious and gynoecious plants, or bisexual flowers in andromonoecious and hermaphroditic plants. In comparison with ovaries in pistillate flowers, those in bisexual flowers are shorter and do not thin down near the calyx (Kubicki, 1969f). Differences in the shape of ovaries between pistillate and bisexual flowers are maintained or sometimes enhanced in the fruits. Thus fruits derived from bisexual flowers are shorter, bulgy, sometimes circular and they carry "shoulders" which are the remainders of the corolla (Kubicki, 1969f). More recently a bisexual flower with normal ovaries, similar to those which normally occur in pistillate flowers has been found (Kubicki, 1974).

1.2.2 Sex differentiation of flowers

Atsmon and Galun (1960) studied the development of three types of flowers in the cucumber plant (staminate, pistillate and hermaphroditic). This was done by dissection of several successive buds on the main axis of monoecious plants (known to produce staminate flowers on the lower nodes), gynoecious and hermaphroditic plants.

They showed that all the three flower types passed through a bisexual stage. Unisexual flowers are formed by inhibition in development of the pistil or stamens, and with the development of both types of sex organs hermaphroditic flowers are produced. Similarly, observations by Kubicki (1969f) on the differentiation of floral buds in gynoecious, hermaphroditic, monoecious, trimonoecious and andromonoecious cucumber plants showed that the early buds were much alike.

Further evidence that shows that occurence of bisexual flowers in the early stages of development was obtained by applying growth substances to detached floral buds which were potentially staminate flowers (Galun, Jung, and Lang, 1962). Indolyl-3-acetic acid when applied to the detached floral buds induced them to develop into pistillate flowers.

1.2.3 Factors influencing sex expression

1.2.3.1 Introduction

Cucumbers, as with other cucurbits, show a tendency towards increasing feminisation with age. In acropetal order, monoecious cucumber cultivars may have a 'blind' phase, in which no flowers develop, then produce staminate flowers, followed by a phase of producing staminate and pistillate flowers, and finally some cultivars reach a phase of producing pistillate flowers only (Matsuo, 1968). This gradient is particularly striking along the main stem. With laterals the terminal phase is always reached much

sooner and some cucumber laterals are entirely pistillate (Shifriss and Galun, 1956). The length of certain zones can be widely changed down to 0% and up to 100% by (a) genetic manipulations; (b) environmental conditions, such as day length and temperature; (c) hormonal treatments.

Environmental factors and genotype interact in their influence on sex expression. A method to measure the influence of environmental factors on the sex expression is required. The ratio of staminate to pistillate flowers has been used (Whitaker, 1931; Hall, 1949). However this is not a good index of sex expression as cucurbits are indeterminate usually, and there is a tendency of increasing feminisation with age. Therefore with ontogeny the ratio of staminate to pistillate flowers will decrease. Another index is the ratio of staminate to pistillate flowers over a set number of nodes (Nitch et al, 1952; Matsuo, Uemoto and Fukushima, 1969). Shifriss and Galun (1956) with cucumber and Hopp (1962) with Cucurbita moschata, reported that as a cultivar characteristic the position of the first pistillate flower on the main stem, expressed as the number of nodes prior to this flower was quite constant under a given environment. Shifriss (1961) considered that this was a good index of sex tendency. Atsmon and Galun (1962) showed that the location of the first, second and third pistillate flower could all be reasonable indices of sex tendency but the location of the first pistillate flower would be more convenient to observe.

1.2.3.2 Environment

In cucurbits there is a gradual shifting from the production of staminate to the production of pistillate or hermaphroditic flowers with age. Environmental factors modify the length, but not the order. Sex tendency is greatly affected by temperature and day length. Short days and low temperatures individually increase the degree of feminisation, and their effect is additive (Nitch et al, 1952; Ito and Saito, 1960). However with one cultivar long days promoted female flower differentiation (Matsuo, 1968). Galun (1961), Shifriss, George and Quinones (1964) and Fukushima, Matsuo and Fujieda (1968) showed that lines with markedly different degrees of feminisation respond to day length and temperature. However two cultivars were insensitive to temperature and daylength. One of these, MSU 713-5 did not respond probably due to its high degree of feminisation.

The other cultivar, Improved Long Green, produced only staminate flowers on the first fifteen nodes and did not respond to daylength and temperature on these nodes. If the treatments were applied later, that is when closer to the change from the staminate phase to the mixed phase a response may have occurred. Besides these two cultivars the promotive effect of low temperature was observed in all the other cultivars, regardless of their origin. However the origin of the cultivars influenced the sensitivity to daylength. Cultivars from the North Chinese variety - complex and the European variety - complex were

temperature sensitive and daylength sensitive. Cultivars from the South Chinese variety - complex were sensitive to temperature and daylength.

With two cultivars the greatest response from a photoperiodic treatment was at the age of two to four expanded leaves (Matsuo et al, 1969). However these cultivars only produce staminate flowers on the lower nodes. Cultivars with a lower degree of feminisation may be more sensitive at a later stage. Very few daylength cycles appear to be necessary to affect the sex differentiation (Matsuo et al, 1969). Results by Matsuo and Fukushima (1970) showed that the sex differentiation in cucumbers is controlled by the phytochrome mechanism. With the long day cultivar 'Higanfushinari', light-breaks with red light of very low intensity induced more pistillate flower nodes in comparison to no interruption of the dark period. The increased pistillate flower differentiation with red light was reversed by subsequent far-red light.

There is disagreement in the literature about the effect of nitrogen level on sex expression. Tiedjens (1928) reported an increase in the proportion of pistillate flowers with higher levels of nitrogen but this is a poor index of sex expression due to the influence of nitrogen on the number of nodes produced. Ito and Saito (1960) reported that pistillate flower differentiation was promoted by low levels of nitrogen, while Atsmon and Galun (1962) found no difference.

Tarakanov (1971) claimed that with low levels of irradiance there is a shift towards staminate flower production. Shifriss, George and Quinones (1964) reported that a gynoecious cultivar differentiated staminate flower buds that did not reach anthesis on a few basal nodes, when crowded in flats. With carbon dioxide enrichment, Wittwer and Robb (1964) and Daunicht (1965) observed an increasing proportion of pistillate flowers in cucumbers. Tiedjens (1928) reported that the removal of pistillate flowers before fruit set occurred increased pistillate flower differentiation. Hopp (1962) also suggested that with Cucurbita moschata the maturing fruits may exercise an inhibitory effect on the production of pistillate flowers. These results suggest that decreased sink strength (fruit removal, see chapter 2) or increased source strength (carbon dioxide enrichment, higher levels of irradiance) may increase the number of flowers that become pistillate.

1.2.3.3 Growth substances

Exogenous application of auxin (Kubicki, 1965) and inhibitors of gibberellin biosynthesis (Halevy and Rudich, 1967) increase femaleness in monoceious cultivars. Application of gibberellin promotes the formation of staminate flowers in monoecious and gynoecious cultivars. (Peterson and Anhder, 1960). Determinations of endogenous growth substances indicate that strains with genetically strong female sex expression contain more auxin (Galun, Izhar and

Atsmon, 1965) and less gibberellin-like substances (Atsmon, Lang, and Light, 1968; Rudich, Halevy and Kedar, 1972b) than strains with strong male sex expression. Gibberellin content of the shoot apex falls with increasing age of the plant (Friedlander, Atsmon and Galun, 1977b). Thus it seems likely that the drop in endogenous gibberellin content plays a role in increasing female tendency.

Ethylene and 2-chloroethyl phosphonic acid, an ethylene releasing compound, promote femaleness (Rudich, Halevy and Kedar, 1969; Augustine, Baker and Sell, 1973). Thus the effect of ethylene is similar to auxin. Exogenous application of auxin increases ethylene production (Shannon and De La Guardia, 1969). Sex expression in the cucumber has been correlated with endogenous ethylene production. Gynoecious sex types produce more ethylene than monoecious plants (Rudich, Halevy and Kedar, 1972b). Plants grown under short days, which promotes femaleness, evolved more ethylene than plants grown under long day conditions (Rudich, Halevy and Kedar, 1972a). 2-chloroethyl phosphonic acid treatment reduced gibberellin activity, and increased the abscisic acid (ABA) content of cucumber leaves. ABA was at higher levels in gynoecious plants than monoecious plants (Rudich, Halevy and Kedar, 1972b). ABA promoted pistillate flower differentiation in gynoecious plants (Friedlander, Atsmon and Galun, 1977a; Rudich and Halevy, 1974), and staminate flower differentiation in monecious plants (Friedlander, Atsmon and Galun 1977c). The involvement of ABA in the sex

regulation appears to be a little more complicated. In conclusion it appears that four phytohormones (ethylene, auxin, gibberellin and ABA), may participate in the regulation of sex expression in the cucumber plant.

1.2.4 Summary

There are many types of sex expression that have been recorded in cucumbers, but until the mid sixties most cultivars were of the monoecious type. Gynoecious sex expression offers the possibility of preventing pollination and allowing the development of parthenocarpic fruit. With age there is an increasing degree of feminisation. Environmental conditions modify the length of each phase but not the order. Low temperature and short days increase the degree of feminisation, and the effect of each is additive. Levels of endogenous growth substances can be related to the sex expression. The application of exogenous growth substances can alter the sex expression.

1.3 Fruit Set

1.3.1 Fertilised fruit

Without the development of parthenocarpic fruit, pollination is required for fruit set and growth. Honey bees appear to be the main pollinator of cucumbers (Mann, 1953). For cucumber production Steinhauer (1974), and Seyman, Barnett, Thorp and Stranger (1969) recommend one colony of honeybees per acre. Seyman et al's (1969)

results show that the number and weight of fruit were higher near the hive than a distance from it. Increasing the number of colonies decreased the percentage of second grade fruit. When only a portion of the ovules have been fertilised, the fruit tissue immediately adjacent to the seed enlarges to a greater extent than the rest of the fruit tissue, and results in irregularly shaped fruit (Denna, 1973). Bees must touch the stigmas of pistillate flowers many times for the cucumber fruit to be of normal size. With only one visit a few pollen grains are left on the stigma, and so only a few ovules develop resulting in a misshapen fruit (Stout, 1979).

Denna (1973) found that the production of seeded fruit had a stronger inhibitory effect on growth than parthenocarpic fruit. Vegetative growth and fruit growth (fresh and dry weight) were all reduced with the development of seeded fruit on parthenocarpic cultivars. On non-parthenocarpic cultivars seeded fruit reduced the total plant dry weight in comparison with no fruit. One monoecious, non-parthenocarpic cultivar produced significantly more fresh and dry weight of fruit and vine growth than a gynoecious cultivar but this was associated with the delay in achieving fruit saturation due to the relative scarcity of female flowers during early growth. It appeared that early fruit and seed development inhibited vine growth and hence leaf production, which in turn reduced total dry matter production. The inhibitory effect on vine growth

was greater when the fruit contained seed than when it did not.

1.3.2 Parthenocarpic fruit

1.3.2.1 Introduction

Parthenocarpic fruit contain seedlike structures, some reaching the size of normal seeds, with fully developed seed coats but lacking embryos and endosperm. The seed cavity is completely filled with nucellar tissue (Nitch, 1952).

Parthenocarpic slicing cucumber cultivars have been grown for a long time in greenhouses. This avoids the necessity of having pollinating insects in the greenhouse. The long cucumber cultivars produce mishapen fruit when pollinated so pollination in greenhouses is prevented by screening to exclude the pollinating insects, or the male flowers are removed, or all-female cultivars are grown. Pike and Peterson (1969) considered that parthenocarpic, gynoecious pickling cucumbers will be advantageous for mechanical harvesting because of greater fruiting capacity, slower fruit maturity and the elimination of the need for pollinating insects. Parthenocarpic fruit have a slower fruit maturity and if combined with small fruit size this would allow for a single harvest regime for picking cucumbers (Denna, 1973). The development of the gynoecious cucumber line MSU 713-5 by Peterson (1960) and the discovery by Peterson and Anhder (1960) of a procedure for maintaining such lines by inducing staminate flowers with

gibberellic acid, has made it possible to utilise parthenocarpy by combining it with gynoecious sex expression. More recently the development of hermaphroditic pollen parents permits the production of gynoecious hybrids when crossed with gynoecious seed parents (Baker and Dean, 1978).

1.3.2.2 Inheritance of parthenocarpy

Parthenocarpy in the cucumber is characterised by an incomplete dominant gene P. Heterozygous Pp plants produce fruits later and generally fewer in number than the homozygous PP genotype (Pike and Peterson, 1969). Pike and Peterson (1969) stated that the homozygous pp plants do not produce parthenocarpic fruits, but Rudich, Baker and Sell's (1977) data shows that genetically non-parthenocarpic cultivars can set parthenocarpic fruit on older plants. Rudich, Baker and Sell (1977) with several cucumber cultivars observed that parthenocarpic fruit set was associated with intensity of femaleness. Strong femaleness resulted in earlier fruiting and greater numbers of parthenocarpic fruit. The association is not surprising when one looks at the four stages of flowering and fruiting proposed by Nitch et al (1952).

1.3.2.3 Influence of environment on parthenocarpic fruit set

Parthenocarpy in cucumber is subjected to the effect

of various environmental factors. Nitch et al (1952) found that low night temperatures and short daylength enhanced parthenocarpy in the cucumber, as also observed for Cucurbita pepo (Rylski, 1974). Rudich et al (1977) studied the influence of daylength and temperature on the production of parthenocarpic fruit on genetically parthenocarpic and non-parthenocarpic cucumber cultivars. Night temperature appeared to be more important than photoperiod. Differences in parthenocarpic fruiting between lines were greatest under high temperatures and long days. Parthenocarpic fruit has also been shown to develop on peppers (Rylski, 1973) and tomatoes (Osborne and Went, 1953) at low temperatures.

1.3.2.4 Growth substances

Nitch et al (1952) and Homan (1964) suggest that high auxin levels in the ovary are most likely responsible for parthenocarpy. The auxins, (Elassar, Rudich, Palevitch and Kedar, 1974) and auxin transport inhibitors (Beyer and Quebedeaux, 1972) are the most effective growth substances to induce parthenocarpy. The effect of photoperiod on parthenocarpy can also be explained as an auxin effect. Rudich, Halevy and Kedar (1972a) demonstrated that short photoperiods increased auxin activity, which may account for increased parthenocarpy. Also higher endogenous auxin activity in the ovaries of genetically parthenocarpic than non-parthenocarpic lines has been observed (Rudich et al, 1972b).

Auxin transport inhibitors induce parthenocarpic fruit development on genetically non-parthenocarpic cultivars when pollination is prevented (Robinson, Cantliffe and Shanon, 1971) and also improves fruit set of open pollinated plants in the field (Cantliffe and Phatak, 1975). Auxin transport inhibitors which have been shown to induce parthenocarpic fruit development in cucumbers are chlorflurenol (Robinson et al, 1971; Beyer and Quebedeaux, 1972), DPX 1840 (Beyer and Quebedeaux 1972, 1974), Naptalan (Beyer and Quebedeaux 1972, 1974), TIBA (Cantliffe, 1972a and b; Beyer and Quebedeaux, 1972), and daminozide (Pigott, 1976).

Mechanical harvesting of pickling cucumbers brought about the need for cultivars and cultural methods which maximise yield in a single harvest. At the high populations used for pickling cucumbers, non-parthenocarpic cultivars generally have no more than one fruit per plant at any one time (Cantliffe, 1972). Seed development in the fruit appears to restrict further fruit set (McCollum, 1934). The auxin transport inhibitors appear to show some promise in increasing the number of fruit on each plant. They also increase the concentration of fruit production and increase yield particularly in the valuable small size grades (Cantliffe and Phatak, 1975; Dean, 1978).

When chlorflurenol was applied to plants whose flowers had been pollinated, about 80% of the fruit contained seed. The number of seed in these fruit was reduced even on ovaries that had been fertilised five days before application

(Cantliffe, 1974, 1977). The reduction in seed numbers may have overcome the inhibitory effect of seed on fruit set. Fruit set with chlorflurenol application to non-parthenocarpic cultivars was increased when combined with pollination (Cantliffe, 1974, 1977). The optimum concentration for fruit set in cucumbers with chlorflurenol and TIBA is 50-100 ppm (Cantliffe, Robinson and Bastdorff, 1972; Cantliffe, Robinson and Shannon, 1972). At these concentrations fruit set occurred on flowers that had reached anthesis about three days before spraying. Parthenocarpic fruits developed from flowers opening as many as eight days after treatment with 1 ppm and mainly from flowers at anthesis at the time of application with 10-40 ppm. The number of flowers thathave reached anthesis at the time of application influences the number of fruit that set (Dean, 1978; Palevitch, Pressman and Rudich, 1972).

Dean (1978) compared the response to chlorflurenol application on four gynoecious cultivars with varying degrees of genetic parthenocarpy. The degree of genetic parthenocarpy contributed positively to the effect of chlorflurenol on increasing fruit set per plant and total yield. Dean (1978) considered the combination of gynoecious sex expression, parthenocarpic fruit set and chlorflurenol is necessary to maximise the yield of little pickles.

The morphactins, including chlorflurenol, have a relatively low mammalian toxicity. In contrast to

several other synthetic growth regulators, such as TIBA, B-995, Amo 1619 and M.H., morphactins are rapidly metabolised in plants and rapidly degraded in the soil by microbes, and so there are no residue problems (Schneider, 1970).

1.3.2.5 Summary

The seed development in pollinated fruit inhibits further fruit set to a greater extent than parthenocarpic fruit set. Gynoecious, parthenocarpic cultivars offer a way of increasing fruit set for mechanical harvesting of pickling cucumbers. Auxin and auxin transport inhibitors are the most effective growth substances to induce parthenocarpy. The auxin transport inhibitor, chlorflurenol, increases fruit set with open pollination and decreases the number of seed in the fruit. With pickling cultivars chlorflurenol has a greater effect on fruit set of genetically strong parthenocarpic cultivars than weak or non-parthenocarpic cultivars.

1.4 Mature Plant

Developing cucumber fruits inhibit growth and development of other parts of the plant (Denna, 1973; De Stigter, 1969; Matsuzaki and Hayase, 1963).

Competition between the fruit and vegetative growth has been observed with a range of crops (Leonard, 1962; Fisher, 1977), including the cucumber plant. Loomis and Crandall (1977) found that the rate of increase in leaf area of

fruiting and non-fruiting plants coincided until early fruit development. Then the rate of increase became less for the fruiting plants. With the retention of fruit on the main stem of a glasshouse cultivar, the fruit yield was higher in the first month of harvesting but the growth of laterals was reduced, in comparison to removal of the main stem fruit. The fruit yield was less in the second month with the retention of fruit in comparison to removal of fruit on the main stem (Anon, 1969).

It has been customary to grow cucumbers with large quantities of nitrogen and water to produce a succulent plant with high quality fruit. The cucumber plant is tolerant of excess nitrogen in contrast to the tomato plant which produces soft vegetative growth and poor fruit set with excess nitrogen. With increasing nitrogen, Matsuzaki and Hayase (1963) found that the number of harvested fruits increased, but the mean weight showed little difference (fruits were harvested ten days after pollination). There was a highly significant positive correlation between vegetative growth and fruit growth. The rate of fruit set and the number of flowers reaching anthesis were both dependent on the vegetative vigour of the plants. The nodal zone where flowers aborted occurred at the time when total weight of developing fruits on lower nodes was maximum. When the fruits were harvested flowering and fruit set increased again. Matsuzaki and Hayase (1963) attributed the lack of fruit set, causing the peaks in fruit development, to competition for nutrients. However this may have

been due to a competition for assimilates, as with lower levels of nitrogen, leaf growth was reduced, which would consequently reduce the production of assimilates.

It appears that a fertilised cucumber ovary can stay in a resting stage for a long period without losing the capacity to resume normal growth (De Stigter, 1969; McCollum, 1934). On removal of the larger fruit the smaller fruit resumes growth (De Stigter, 1969). If left on the plant they remain inhibitory until they begin to yellow and the seed coats harden. This competition between the fruit may be due to competition for assimilates or some growth factor. The cucumber plant appears to possess a regulatory mechanism that limits the proportion of the dry weight that can be devoted to fruit and seed production. Seed dry weight accumulated at the expense of fruit rather than vine dry weight when parthenocarpic fruit development was compared with fertilised fruits. The presence of fruit was observed to have an inhibitory effect on the vine growth that was greater when the fruit contained seed than when it did not (Denna, 1973).

When many fruits are developing the growth of the roots stop and part of the existing roots turn brown or die (Van der Post, 1968). De Stigter (1969) observed the growth of individual roots after pollination of flowers. Three to four days after pollination root growth began to decrease, and this decline continued until root growth stopped completely. Harvesting of the fruit resulted in a gradual recovery of root growth. When root growth was

studied with and without fruit, fluctuations in root number were greatest with fruit, however without fruit the decline in root growth showed similar fluctuations but started later and were less pronounced (Van der Post, 1968). A comparison between the cucumber, tomato and pepper plants showed that the cucumber plant grows much faster and the fluctuations in root growth were greater.

CHAPTER TWO

REVIEW OF LITERATURE - SOURCE - SINK RELATIONSHIPS

2.1 Terminology

2.1.1 Sink Strength

In this discussion the terms 'source' and 'sink' are used in relation to assimilates only. These terms are frequently used when describing plant growth although they are used in many different ways, which can lead to confusion. Warren Wilson (1972) described three criteria which are used for defining source and sink:

a. Transport - "Sources are regions that export assimilates, while sinks import them".

b. Morphology - "Because mature leaves tend to be associated with production and export of assimilates, whereas other parts (roots, meristems, fruits and storage organs during their accumulation phase) tend to be associated with import and utilization of assimilates, the terms source and sink are applied to particular parts of the plant".

c. Metabolism - "Sources produce assimilates by photosynthesis or by mobilization of stored materials, while sinks utilize assimilates in respiration and growth".

Warren Wilson (1972) suggested that sources and sinks

should be defined in terms of losses and gains from a particular plant part, as this would allow measurement. He defined the terms as follows:

Source strength = source size x source activity,

i.e. rate of assimilation per plant = leaf area per plant x rate of assimilation per unit leaf area.

Sink strength = sink size x sink activity,

i.e. absolute growth rate = dry weight x relative growth size.

According to this definition if sink strength was measured with plants grown under different environmental conditions which mainly affected the rate of photosynthesis (e.g. CO_2 level, level of radiation) the calculated values would be different. For this reason Watson (1971) defined sink strength as the rate of growth of the useful plant parts when the supply of photosynthate is in excess (i.e. when a small change in the supply does not affect the rate of growth). Watson (1971) introduced another term, sink capacity, which he defined as the integral of sink strength over the period of intake of photosynthate. This is equivalent to the potential yield of the useful plant parts. Warren Wilson's (1972) formulae describe what has happened and as such are a reasonable explanation. However they do not explain the mechanism by which a sink competes for assimilates.

Wareing and Patrick (1975) criticised Warren Wilson's definitions for two reasons. Firstly dry matter data does not account for respiratory losses of assimilates

imported into sinks. This loss varies considerably according to the sink, especially between storage versus growth. Secondly, they felt 'implicit in this definition of sink activity is the assumption that assimilate uptake is non-limited by supply and unaffected by neighbouring sinks'. Generally the dry matter accumulation is an indication of the competitive ability of a sink relative to other sinks. For this reason they introduced the term 'mobilizing ability' to describe the accumulation of dry matter by a sink within the competitive framework of a whole plant. Barnes (1979) used the term mobilizing ability and defined it as follows:

mobilizing ability = sink size x relative sink activity

where relative sink activity is the activity as defined by Warren Wilson, but "with the condition that the total strength of other sink regions and the total rate of assimilate uptake are not fixed standard values".

Evans (1975) also criticised Warren Wilson's (1972) definitions. Sinks may have a high priority in obtaining assimilates even though according to this definition they have a small sink strength. He gave an example of a grass with a shoot apex dry weight of only a few micrograms and a low relative growth rate, yet even with stresses placed on the plant it continues to receive a stable supply of assimilates. Another reason he criticised this definition is that sinks of equal activity do not receive assimilates in proportion to their relative size, but the distribution is heavily biased towards the larger sink

(Peel and Ho, 1970; Cook and Evans, 1976).

Although these terms have been defined in traditional growth analysis measures and so amenable to experimental measurement, few workers have measured them. However the terms sink strength and sink capacity are frequently used in the literature. Generally only the dry weight is measured at some point in time and if greater than the control, this treatment is referred to as having a greater sink strength or sink capacity, when the plants are grown in the same environment (Hardman and Brun, 1971; Fischer and Wilson, 1975; Fisher, 1978). Sink demand or assimilate demand is another term occasionally used in the literature, especially with altered plants. With removal of some leaves from a plant the sink strength according to Warren Wilson's (1972) or Watson's (1971) definition will be reduced or the same. However the remaining leaves have to supply the same number of sinks, and therefore the demand for assimilates per leaf is greater (Thorne and Koller, 1974).

2.1.2 Sink or source limitation

Frequently the terms sink limitation and source limitation are used in the literature to describe what is limiting yield. The net production and net consumption (growth and storage) of assimilates within the whole plant must be in balance. Accordingly Wareing and Patrick (1975) proposed that when the actual rate of assimilate production is less than the potential maximum rate of

consumption, the rate of assimilate accumulation is determined by the rate of production (source limitation). When the potential rate of production is greater than the actual rate of consumption, then the rate of assimilate accumulation is determined by the rate of consumption (sink limitation). Nevertheless because of complex interactions between source and sink, both can, at least to some extent, be simultaneously limiting growth.

This model assumes that the movement of assimilates between sink and source is not limited by the capacity of the phloem for translocation. This generally appears to be valid (Wardlaw and Moncur, 1976), but there are some reports of the vascular system restricting transport of assimilates from source to sink (Jenner, 1974). This restriction would be indistinguishable from the 'sink-limited' situation in the above proposed model. Most of the evidence for the path not limiting translocation involves the demonstration of spare translocation capacity. However this does not imply that no control is exerted by the path. Lang (1978) imposed mild temperature changes upon the source, path and sink regions and monitored the translocation rate. He concluded that the translocation rate is under the control of source, path and sink regions of the plant.

2.2 Sink strength and the photosynthetic rate

2.2.1 Effect on the photosynthetic rate

Often leaves operate below their maximum potential

photosynthetic rate due to the inability of sinks to utilise the assimilates. Increasing or decreasing the sink strength or altering the ratio of sources to sinks, and therefore altering the demand for assimilates from the leaves has frequently been shown to alter the photosynthetic rate. Partial defoliation or shading some of the leaves increases the rate of photosynthesis of the remaining leaves (Wareing, Khalifa and Treharne, 1968; Neales, Treharne and Wareing, 1971; Thorne and Koller, 1974; Kriedmann, Loveys, Possingham and Satch, 1976). The commonest method that has been used to alter the sink demand is to remove the fruit or seeds (King, Wardlaw and Evans, 1967; Neales and Incoll, 1968; Hansen, 1970; Kriedemann et al, 1976; Hall and Milthorpe, 1978). Other methods that have been used to alter sink demand include control of the sink temperature, control of the degree of pollination and grafting a larger sink on to the plant. Cooling sugar beet roots markedly reduced the rate of net photosynthesis (Habeshaw, 1973). Reciprocal grafts between tops and roots of sugar beet and spinach beet roots showed that grafted plants with sugar beet roots had a greater net assimilation rate (NAR) irrespective of the type of top (Thorne and Evans, 1964).

The influence of the removal of sinks on the rate of photosynthesis appears to depend on whether other sinks on the plant can utilise the extra assimilates. Removal of potato tubers from plants low in nitrogen halved the NAR, but for plants with a higher nitrogen level the NAR was

reduced by only 21%. At the higher nitrogen level new leaves and buds grew, that is, other sinks developed (Nosberger and Humphries, 1965).

There is a substantial amount of evidence showing that the rate of net photosynthesis of a leaf is influenced by manipulations that vary the ratio of sources to sinks. However in a few cases increases in the net photosynthetic rate coincide closely with changes in sink demand produced by anthesis, fruit development or the development of other sinks. Following anthesis, the decline in the rate of net photosynthesis of individual leaves was reversed in pepper plants (Hall and Brady, 1977). Changes in net photosynthesis of pea leaflets were found to reflect closely the pattern of assimilate demand of subtended fruit during development. Photosynthesis of leaflets subtending a developing fruit had two peaks in photosynthesis corresponding with periods of higher dry weight accumulation in the fruit (Flinn, 1974). Also following tuberisation of potatoes the rate of net photosynthesis increased (Moorby, 1968).

Light saturation occurs at a higher level of irradiance with a lower source-sink ratio (Neales et al, 1971; Kriedemann et al, 1976; Hall and Brady, 1977). Experimental manipulations that alter the sink demand appear to affect the rate of net photosynthesis only after a period of days. (Wareing et al, 1968; Thorne and Koller, 1974; Geiger, 1976; Hall and Milthorpe, 1978). Thorne and Koller (1974) increased sink demand by shading

all but one leaf on plants. After two days the rate of net photosynthesis increased, reaching a maximum rate on day eight. The work by King et al (1967) is an exception to this as they observed a change three to fifteen hours after application of treatment. So far no explanation has been given for this.

2.2.2 Control mechanism

With greater sink demand the rate of export of photosynthates from a leaf is increased (Khan and Sagar, 1969; Thorne and Koller, 1974; Moorby and Jarman, 1975). Many investigators have proposed that assimilate accumulation in the source leaf may influence the rate of photosynthesis. A negative correlation between the net photosynthetic rate and leaf carbohydrate level has been observed by many, but there is as yet no proof that the two are causally associated (Neales and Incoll, 1968). Most of the earlier workers proposed a feedback control of photosynthesis by accumulated soluble sugars (Moss, 1962; Burt, 1964; Neales and Incoll, 1968). In recent work by Thorne and Koller (1974), Nafziger and Koller (1976) and Hall and Milthorpe (1978), a negative correlation between soluble sugar levels and the rate of photosynthesis has not been observed, but a negative correlation has been observed with starch levels (Chatterton, Carlson, Hungerford and Lee, 1972; Upmeyer and Koller, 1973; Thorne and Koller, 1974; Nafziger and Koller, 1976).

Most of the evidence for the product inhibition

hypothesis has come from experiments in which the source-sink balance was altered by removal of leaves or sinks, so as to alter the leaf carbohydrate level. However this may have also altered the hormonal balance within the plant (Wareing, Khalifa and Treharne, 1968). Certain hormones are known to affect the rate of photosynthesis (Treharne, Stoddard, Pughe, Parenjothy and Wareing, 1970). However there is some evidence from unaltered plants. Warren Wilson (1966) reported that growing plants at lower temperatures, the rate of photosynthesis decreased while the sugar content in the leaves greatly increased. Similarly a cold night prevented the breakdown and translocation of chloroplast starch, and the rate of photosynthesis was reduced the following day (Chatterton et al, 1972).

Nafziger and Koller (1976) altered the leaf starch concentration by controlling the CO_2 level for twelve hours. This had no affect on the soluble sugar concentration. Following this treatment they observed a strong negative correlation between the net photosynthetic rate and starch concentration.

Although many have observed a negative correlation between leaf carbohydrate level and the photosynthetic rate, many have criticised the idea of a direct feedback system in controlling the net photosynthetic rate (Neales and Incoll, 1968; Geiger, 1976; Hall and Milthorpe, 1978). Changes in net photosynthesis have been associated with changes in either leaf resistance or

residual resistance or both. When the source-sink balance has been altered some workers have observed most of the changes in leaf resistance with little or no change in residual resistance (Gifford and Marshall, 1973; Rawson, Gifford and Bremner, 1976); others have recorded the opposite (Neales, Treharne and Wareing, 1971; Hodgkinson, 1974; Nafziger and Koller, 1976); while others have found a change in both (Loveys and Kriedemann, 1974; Hall and Milthorpe, 1978). Several workers (Loveys and Kriedemann, 1974; Thorne and Koller, 1974; Nafziger and Koller, 1976) have observed a positive correlation between the residual resistance and starch concentration. It has been suggested that the rate of net photosynthesis is reduced with starch accumulation due to the starch causing a greater impedance to intracellular CO_2 transport (Nafziger and Koller, 1976).

Also included in the residual resistance is the carboxylation resistance. Positive correlations between net photosynthesis and the activities of ribulose -1,5-diphosphate (RuDP) carboxyglase or phosphoenolphrurate (PEP) carboxylase has been observed following an alteration of the source-sink balance (Wareing et al, 1968; Meidner, 1969; Neales et al, 1971; Thorne and Koller, 1974; Hall and Brady, 1977). The activity of these enzymes and net photosynthesis has been shown to be stimulated by the application of growth substances (Wareing et al, 1968; Treharne et al, 1970). Wareing et al, (1968) proposed that partial defoliation leads to increased

photosynthetic rates by increasing the supply of endogenous cytokinins, produced in the roots, to the remaining leaves which in turn leads to increased carboxylating enzymes. Thorne and Koller (1974) shaded some of the leaves and observed an increase in RuDP carboxylase activity in the source leaf. They suggested that this may have been caused by a change in hormone distribution. There is disagreement in the literature about the relative significance of the carboxylation resistance as the rate-determining process in photosynthesis (Chartier, Chartier and Catsky, 1970).

Loveys and Kriedemann (1974) proposed that the combined action of phaseic acid and abscisic acid exerts a fine control over photosynthesis. Following fruit removal the stomatal resistance increased and the abscisic acid and phaseic acid level rose. This was not due to a reduced leaf water potential. They suggest that this may represent a mechanism for regulating photosynthesis in response to developing organs and other sites of growth. More recently other workers have come to similar conclusions (Woolley, pers. comm.).

There is probably as much evidence for as against the hypothesis that photosynthesis is inhibited by the accumulation of assimilates (Geiger, 1976). However it is generally accepted that the source-sink balance influences the leaf and/or residual resistances. These resistances may be affected by hormones.

2.3 Source or sink limitation

2.3.1 Change with selection

For crops in which the economic yield is only a portion of the plant (storage organs, seeds or fruits), the most important determinant of economic yield is often not total crop photosynthesis, but the way in which assimilates are distributed within the plant.

With increased sink capacity of wheat the proportion of the assimilates partitioned to the grain during grain filling has increased. With the primitive wheats, during grain filling assimilates were partitioned between the roots, stem, tillers and the grain. However in the modern cultivars, at this stage nearly all assimilates are partitioned to the grain (Evans, 1975). With domestication of wild plants, the economically useful parts have been greatly increased in size or number by selection (Watson, 1971). In the early stages of domestication the sink capacity was probably limiting yield. The components of storage capacity can easly be observed and subject to selection, whereas photosynthesis cannot. Storage capacity and yield will tend to increase together with selection until they reach a limit set by the photosynthetic capacity. Further progress will then require both photosynthetic and storage capacity to be increased. For the environments they are adapted to, the modern cultivars of our major crops are likely to have their photosynthetic capacity and storage capacity fairly closely balanced (Evans, 1975).

The storage capacity of a grain crop depends on the

yield components (number of ears per unit area, spikelets per ear, grains per spikelet and on grain size). Selection for these characters has not invariably lead to the yield increases expected. An increase in one component may be compensated by a reduction in the others (Hsu and Walton, 1971). Smocek (1969) showed that the biggest advances could be expected if the flag leaf area was used in combination with the components of yield as a selection criteria. An increase in storage capacity without an increase in assimilate supply would lead to more unfilled grains, whereas more assimilate without more storage capacity would result in little gain in yield. A progressive increase in potential yield of wheat of about one per cent per annum, has come from small increases in source and sink (Bingham, 1971).

2.3.2 Identifying limitation

To identify whether source or sink strength is limiting yield, one approach is to alter one of the processes independently of the other and measure the effect on yield. As just one approach limits the conclusion that can be drawn Fischer and Wilson (1975) and Fisher (1977) altered both separately. Photosynthesis may be both increased (CO_2 enrichment) and decreased (shading, leaf removal), but usually sink strength can only be reduced. However Fisher (1977) increased sink strength on tomato plants by increasing the degree of pollination.

Reductions in yield of the economic sink following

shading or reduction in leaf area does not necessarily imply that at full light or leaf area yield was source-limited, only that it was so when photosynthesis was reduced. Increase in yield with CO_2 enrichment implies that yield is source-limited at normal CO_2 levels. No yield reduction following shading or reduction in leaf area implies a sink-limitation, except where partial defoliation leaves sufficient leaf area for full light interception (Evans, 1975).

For a greenhouse tomato plant, the removal of one truss on a plant with ten trusses resulted in a reduction in yield from one to nine per cent depending on the position of the truss (Slack and Calvert, 1977). The removal of the lower trusses resulted in the greatest reduction in yield, whereas removal of the middle trusses resulted in little reduction. During the early stages of fruit development on the tomato plant sink appears to be limiting. Fisher (1977) increased fruit yield of young unstopped greenhouse tomato plants with CO_2 enrichment and by increasing sink strength with a truss vibrator. The two responses were additive. At this stage of development the tomato plant appears to be source and sink-limited.

Carbon dioxide enrichment during pod filling of soybeans caused a slight increase in pod numbers and a marked increase in pod weight and seed yield (Hardman and Brun, 1971). They concluded that the yield of soybeans was limited by the supply of assimilates during pod filling. Fischer and Wilson (1975) observed an increase in the grain

size of soybean up to a certain grain size with increased assimilate supply during grain filling. After this there was only a small increase in grain size with increased assimilate supply. They concluded that the supply of assimilates was the limiting factor at the lower level, but of decreasing importance as the grain size approached the maximum. There is an upper limit to such improvement, beyond which further increase will depend on changes in sink numbers.

Gifford, Bremner and Jones (1973) devised a method to determine to what degree grain yield is limited by the production of assimilates during grain growth (source-limited). They considered a culm or an area of crop during grain filling. If the net assimilation is altered during this period by a small amount (ΔA) by a treatment which primarily effects the rate of photo-synthesis, then the uptake of assimilation into the grain may be altered by (ΔU). The degree of source limitation was defined as

$$S = \frac{\Delta U}{\Delta A}$$

This method places the degree of source limitation on a 0 to 1 scale. When S = 1 all of the extra assimilate is taken up by the grain and therefore the plant is source-limited, and when S = 0 the extra assimilate has no influence on grain growth, therefore sink-limited. As neither ΔU or ΔA are easily measured they approximated the estimate of S by using dry weight data. U is replaced by

the amount of grain growth and A by the increase in total crop dry weight. It is not essential to know the dry weights at the time of applying the treatments, as the slope of the plot of final grain yield against final total plant dry weight will estimate S. This method is similar to the method used by Fischer and Wilson (1975).

Allison and Watson (1966) have shown that when the grain sink is removed by preventing pollination in maize, the dry matter that would have passed to the grain, accumulates in the stem and husks. They also found that when the source of assimilates is restricted by removing leaves, stem weight decreases as previously stored dry matter moves to the grain. The accumulation of mobilizable carbohydrate during the growth of the economic sink suggests that the sink capacity is limiting yield. With maize the rate of grain filling is faster in hybrids than in inbreds, whereas inbreds have a higher sugar content in their stems, suggesting that the rate of storage is more limiting to yield than is the rate of photosynthesis (Johnson and Tanner, 1972). Due to the dry weight distribution of some maize cultivars and the accumulation of sugars in stems during grain filling, Goldsworthy (1974) concluded that for these cultivars the sink capacity was limiting yield.

2.4 Summary

Usually the regions of assimilate production (leaves) are separate from the regions of consumption (growing

regions or storage organs). These regions of production and consumption are referred to as source and sink respectively. Usually with a reduction in the source-sink ratio of whole plants the net photosynthetic rate of the remaining leaves increases. Increasing sink strength by some means (e.g. sink temperature, grafting on a larger sink), has also been shown to increase the photosynthetic rate. Increasing the source-sink ratio or reducing sink strength usually reduces the photosynthetic rate.

Many have observed a negative correlation between soluble sugars or starch levels in the leaf and the photosynthetic rate, and it has been suggested that the build-up of these carbohydrates directly inhibits photosynthesis. However the product inhibition hypothesis has been criticised. The changes in net photosynthesis have been associated with changes in leaf and/or residual resistances, and RuDP or PEP carboxylase activity. The changes in resistances may be affected by hormones.

One approach to identify whether source or sink is limiting yield is to alter one of the processes independently of the other and measure the effect on yield. Altering just sink or source limits the conclusion that can be drawn, but altering both separately gives information on the limitation of source and sink. Frequently with an increase in the rate of photosynthesis, by increasing the level of radiation or with CO_2 enrichment, or by increasing the source-sink ratio, the growth of the remaining sinks is increased indicating a source-limited situation. If

increased sink-strength increases the growth of the sink this indicates a sink limitation. The accumulation of mobilizable carbohydrate during the growth of the economic sink suggests that sink is limiting.

Source-sink relationships is an important topic as sink strength influences the rate of photosynthesis, the partitioning of assimilates and therefore crop yield.

CHAPTER THREE

THE EFFECT OF TWO AUXIN TRANSPORT INHIBITORS ON GROWTH AND DEVELOPMENT

3.1 Introduction

The rate of photosynthesis (source) can be varied by increasing or decreasing the PAR or carbon dioxide supply, but in most source-sink relationship studies sink strength has only been reduced, not increased (2.3.2). Habeshaw (1973) and Fisher (1978) increased sink strength by increasing the sink temperature of sugar beet plants and by improving natural fruit set on tomato plants, respectively.

Auxin transport inhibitors have been shown to increase fruit set in a range of crops, including cucumbers (Cantliffe, 1972). They are thought to induce parthenocarpy by blocking the natural outward flow of auxin from the ovary, resulting in an accumulation of auxin within the ovary, sufficient to trigger parthenocarpy (Beyer and Quebedeaux, 1974). With parthenocarpic cultivars only a proportion of the flowers set fruit and fruit set on genetically strong parthenocarpic cultivars has been increased with auxin transport inhibitors (Dean, 1978).

This experiment was designed to examine the possibility of increasing sink strength by using two auxin transport inhibitors to increase fruit set and growth, on a long parthenocarpic cucumber cultivar.

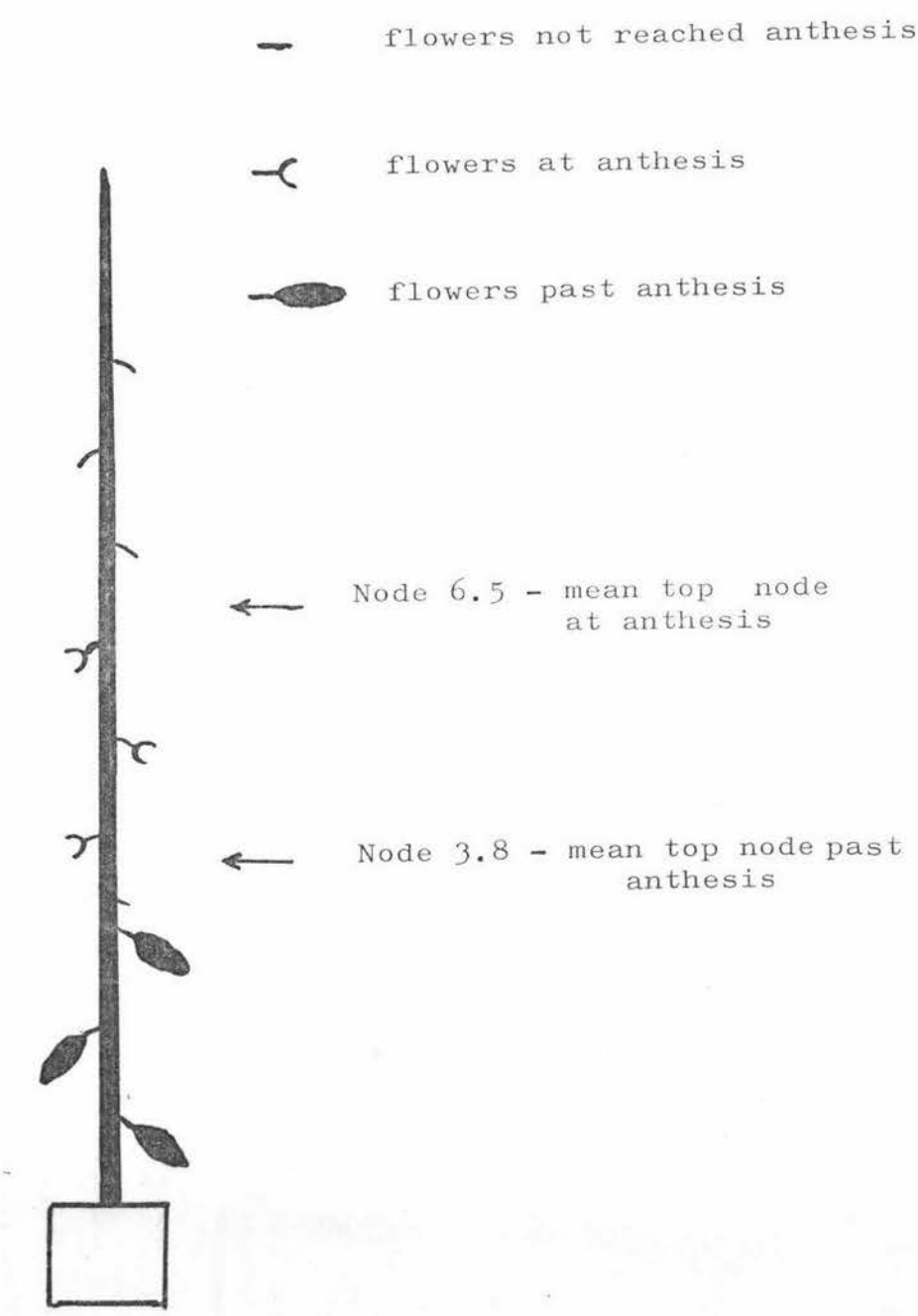

Fig. 3.1 Stage of flower development at time of growth substance application

3.2 Materials and methods

On 21 February 1978, seed of the cv. Princess was sown in 100 mm plastic pots containing coarse sand and germinated at 25° C. This is a long parthenocarpic cultivar which produces few male flowers and frequently several female flowers per node. Emergence occurred in four to six days and the seedlings were grown on in a greenhouse with a minimum temperature of 19° C and ventilation at 24° C. When two leaves had expanded, the plants were planted into black polythene bags containing 10 dm^3 of sand. From emergence the plants were fed once or twice daily with a NFT (nutrient film technique) nutrient solution (Appendix 1).

On 1 April two growth substances, chlorflurenol (methyl-2-chloro-9-hydroxyfluorene) and TIBA (2,3,5-triiodobenzoic acid), at three concentrations (0, 100 ppm, 200 ppm) were applied in factorial combination to two different sites (whole plant, fruit only). (Table 3.1). The growth substances were applied only once. At the time of application each plant had several flowers at anthesis, and several past athesis (Figure 3.1). The growth substances were sprayed on the whole plant to the point of runoff, and applied to the fruit with a brush. With application to the fruit only two or three nodes above the top node with a flower at anthesis were treated as the flowers in the higher nodes were too small for easy application. Therefore only seven to nine nodes were

treated. A wetting agent, Triton B 1956 at 0.1 cm^3/dm^3 was added to the solution.

Table 3.1 The Treatments

Growth substances	Site	Rate
Chlorflurenol = Chlor.	Plant = P	control = 0
TIBA = TIBA	Fruit = F	100 ppm = 100
		200 ppm = 200

Growth Substance x Site \ Rate	0	100	200
Chlor - P	Chlor-P0	Chlor-P100	Chlor-P200
Chlor - F	Chlor-F0	Chlor-F100	Chlor-F200
TIBA - P	TIBA-P0	TIBA-P100	TIBA-P200
TIBA-F	TIBA-F0	TIBA-F100	TIBA-F200

The plants were trained up strings and stopped at the wires (1.8 m from the base of the plant). All the laterals were removed when small, except near the wire where two laterals were allowed to develop, which is sometimes referred to as the umbrella training system. On 21 April block four was harvested, block one and three on 22 April and block two on 25 April. The dry weight of the individual fruit and the leaves, stem and roots was determined by drying them in an oven at 80° C.

3.3 Results

3.3.1 Introduction

This was a 2x3x2 factorial experiment and after analysis of variance was carried out on the relevant data the treatment means were compared by the Duncan's multiple range test. In the table of results treatment means with no letter in common are significantly different by this test at $p < 0.01$ (capitals) or $p < 0.05$ (lower case). All data expressed as a percentage was subjected to the arcsine transformation before analysis. In the tables of results actual percentages are given, not the transformed figure. Details of the analysis of variance are given in the appendices.

3.3.2 Total plant dry weight and dry weight of component organs

There was a significant effect ($p < 0.05$) of site of application on fruit dry weight (Table 3.2) (Appendix 2). Fruit dry weight was less when the growth substance was applied to the whole plant in comparison to application to the fruit. There was a significant interaction between the site of application and rate with respect to total plant dry weight and the dry weight of all the component organs, except the fruit (Table 3.3) (Appendices 3-6). Application of growth substances to the whole plant at 100 ppm or 200 ppm reduced the dry weight of the total plant, leaves, stem and root ($p < 0.01$).

Table 3.2 Effect of site of application on fruit dry weight (g/pl).

P	39.4 b
F	45.8 a

Table 3.3 Interaction between site of application and rate on total plant dry weight and weight of component organs (g/pl).

	Site \ Rate	0	100 ppm	200 ppm
Total plant	P	107.2 a A	85.5 b B	81.6 b B
	F	109.8 a A	112.2 a A	112.6 a A
Fruit	P	43.9 N.S.	38.9	35.4
	F	44.2 N.S.	45.6	47.8
Leaves	P	45.1 a A	34.8 a A	34.3 b B
	F	46.0 a A	46.6 a A	45.8 a A
Stem	P	12.4 a A	7.9 b B	7.6 b B
	F	12.9 a A	13.0 a A	12.8 a A
Root	P	6.0 a A	4.0 b B	4.2 b B
	F	6.7 a A	6.8 a A	6.3 a A

Fruit dry weight was significantly less ($p < 0.05$) with the application of TIBA in comparison to chlorflurenol and the reverse applied for stem dry weight (Table 3.4) (Appendice 2 and 5).

Table 3.4 Effect of growth substance on fruit and stem dry weight (g/pl)

Growth substance	Fruit	Stem
Chlor	45.4 a	10.9 b
TIBA	39.8 b	11.3 a

3.3.3 Partitioning of dry weight

3.3.3.1 Effect of site of application

With application of the growth substance to the plant the proportion of the dry weight in the roots was less ($p < 0.01$) in comparison to application to the fruit (Table 3.5) (Appendix 7).

Table 3.5 Effect of site of application on percent total dry weight in roots (%)

Site	Root
P	5.1 B
F	6.0 A

3.3.3.2 Effect of growth substances

A greater proportion of the dry weight was partitioned into the fruit ($p < 0.05$) and less into the leaves and stem ($p < 0.01$) with the application of chlorflurenol in comparison to TIBA (Table 3.6) (Appendices 8-10).

Table 3.6 Effect of growth substance on percent total dry weight in fruit, leaves and stem (%)

Growth substance	Fruit	Leaves	Stem
Chlor	43.4 a	40.5 B	10.4 B
TIBA	40.0 b	43.1 A	11.4 A

3.3.3.3 Interactions

There was an interaction between growth substance and site of application for the percent total plant dry weight in the leaves (Table 3.7) (Appendix 9). TIBA applied to the fruit was greater ($p < 0.05$) than the other treatments, and TIBA applied to the plant was greater ($p < 0.05$) than Chlorflurenol applied to the fruit.

Table 3.7 Interaction between growth substance and site of application on percent total dry weight in leaves (%)

Growth substance \ Site	P	F
Chlor	41.3 bc B	39.7 c B
TIBA	42.5 b AB	43.8 a A

There was an interaction between the site of application and the rate for the percent total plant dry weight in the stem (Table 3.8) (Appendix 10). The application of growth substance to the plant at 100 ppm and 200 ppm reduced the percentage in the stem ($p < 0.01$).

Table 3.8 Interaction between site of application and rate on percent total dry weight in stem (%)

Site \ Rate	0	100 ppm	200 ppm
P	11.7 A	9.4 B	9.4 B
F	11.9 A	11.8 A	11.5 A

3.3.4 Fruit set

3.3.4.1 Nodes 1-8

In this analysis fruit with a dry weight 1 g or greater was chosen to ensure the fruit had set, as abortion nearly always occurred when the fruit dry weight was less than 1 g. On these nodes there was a site x rate and site x growth substance interaction. Fruit set was increased ($p < 0.01$) with growth substance application to the plant at 100 ppm and 200 ppm (Table 3.9a). Fruit set was less ($p < 0.01$) with TIBA applied to the fruit than applied to the plant or chlorflurenol applied to the fruit or plant (Table 3.9b) (Appendix 11).

Table 3.9 Interactions between site and rate, and site and growth substance on fruit set on nodes 1-8

a.

Site \ Rate	0	100 ppm	200 ppm
P	4.0 b B	5.3 a A	5.4 a A
F	3.6 b B	3.7 b B	3.4 b B

b.

Growth substance \ Site	P	F
Chlor	4.8 a A	4.3 a A
TIBA	5.0 a A	2.8 b B

3.3.4.2 Nodes 3-5 and 6-8

With further analysis of only nodes 3-5 there was an interaction between growth substance and site and an effect of rate of application. TIBA applied to the fruit reduced fruit set on these nodes ($p < 0.05$, Table 3.10a) as with nodes 1-8 (Table 3.9b). With increasing concentration of growth substance there was a trend of decreasing fruit set but 200 ppm was only significantly less than the control ($p<0.01$, Table 3.10b) (Appendix 12).

Table 3.10 Effect of treatments on fruit set on nodes 3-5

a.

Growth substance \ Site	P	F
Chlor	2.4 a	2.5 a
TIBA	2.6 a	1.9 b

b.

Rate	0	100 ppm	200 ppm
	2.7 a A	2.4 a AB	2.0 b B

Fruit set on nodes 6-8 was greater ($p < 0.05$) with chlorflurenol than TIBA (Table 3.11a) (Appendix 13). There was a significant interaction between site and rate on these nodes. With growth substance application to the plant at 100 or 200 ppm, fruit set was greater

($p < 0.01$) than the control plants or with application to the fruit (Table 3.11b). In comparison to one of the controls fruit set was greater ($p < 0.05$) with application to the fruit (Table 3.11b).

Table 3.11 Effect of treatments on fruit set on nodes 6-8

a.

Growth substance	
Chlor	1.56 a
TIBA	1.15 b

b.

Site \ Rate	0	100 ppm	200 ppm
P	0.44 c B	2.13 a A	2.38 a A
F	0.81 bc B	1.25 b B	1.13 b B

3.3.4.3 Nodes 9-16

For the number of fruit set on nodes 9-16 there was an interaction between growth substance, site and rate. TIBA applied to the fruit at 200 ppm was greater ($p < 0.01$) than the other treatments (Table 3.12) (Appendix 14). TIBA applied to the plant at 100 or 200 ppm was less ($p<0.01$) than chlorflurenol applied to the plant at 200 ppm (Table 3.12). Fruit set occurred above node 16 but there was no significant difference between the treatments.

Table 3.12 Effect of treatments on the fruit set on nodes 9-16

	Chlor-P	Chlor-F	TIBA-P	TIBA-F
0	1.1 bc BC	1.6 b B	1.1 bc BC	1.6 b B
100 ppm	1.2 bc BC	2.0 b B	0.8 c C	1.6 b B
200 ppm	1.6 b B	1.8 b B	0.8 c C	3.3 a A

3.3.5 Fruit size

The mean fruit dry weight was significantly greater ($p < 0.01$) with application to the fruit than to the plant (Table 3.13) (Appendix 15).

Table 3.13 Effect of site application on mean fruit dry weight (g)

P	5.9 B
F	7.1 A

3.3.6 Distribution of fruit dry weight on various nodes

There was a greater proportion of the fruit dry weight on nodes 1-8 than 9-16 except with TIBA applied to the fruit at 200 ppm where the reverse occurred (Table 3.14) (Appendices 16 and 17). TIBA applied to the fruit at

200 ppm reduced the proportion of the fruit dry weight on nodes 1-8 but on nodes 9-16 it was greater ($p < 0.01$).

Table 3.14 Percent total fruit dry weight on nodes 1-8 and 9-16 (%)

Growth substance x site \ Rate	Nodes 1-8			Nodes 9-16		
	0	100ppm	200ppm	0	100ppm	200ppm
TIBA-P	77.7 A	78.5 A	84.0 A	10.3 B	19.7 B	16.0 B
TIBA-F	74.7 A	67.7 A	38.1 B	19.8 B	29.1 B	57.0 A
Chlor-P	76.9 A	82.2 A	73.8 A	14.1 B	17.7 B	26.2 B
Chlor-F	70.7 A	71.1 A	67.5 A	25.0 B	24.3 B	23.9 B

Except for these significant interactions the above analysis suggested that the growth substances had little influence on the distribution of fruit dry weight on the various nodes, but on grouping nodes 3, 4 and 5, and nodes 6, 7 and 8 together further significant effects were found (Table 3.15) (Appendices 18 and 19). On nodes 3-5 a decreasing proportion of the fruit dry weight occurred with an increasing concentration of growth substances. On nodes 6-8 there was an interaction between site and rate, and also between growth substance and rate (Table 3.15 b and c). Application to the plant at 100 ppm and 200 ppm increased the proportion of the total fruit dry weight on these nodes, as did chlorflurenol at 100 ppm and 200 ppm

and TIBA at 100 ppm ($p < 0.05$).

Table 3.15 Effect of treatments on percent total fruit dry weight on nodes 3-5 and nodes 6-8 (%)

Rate		0	100 ppm	200 ppm
a. Nodes 3-5		55.9 a A	35.7 b B	28.0 c B
b. Nodes 6-8	Site P	7.5 c C	43.1 a A	41.0 a A
	F	16.9 bcBC	25.1 b AB	18.4 bcBC
c. Nodes 6-8	Growth Chlor	9.3 c C	38.4 a A	36.5 a AB
	Substance TIBA	15.0 c CD	29.8 abABC	22.9 bcBCD

3.3.7 Misshapen fruit

The proportion of the fruit dry weight that was in misshapen fruit was greater ($p < 0.01$) with the application of growth substance to the plant at both rates or to the fruit at the 100 ppm rate. The increase was greater ($p < 0.01$) when sprayed on the whole plant (Table 3.16) (Appendix 20). Some of the misshapen fruit, with growth substance application to the fruit, was due to a small swelling at the point where the corolla was connected to the ovary. With application to the whole plant the fruit on the upper nodes did not swell at the distal end. Some of the fruit on the lower nodes was also misshapen, due to greater swelling at the distal end than at the proximal end.

Table 3.16 Percent fruit dry weight that was in misshapen fruit.

Site \ Rate	0	100 ppm	200 ppm
P	4.1 c C	65.7 a A	78.3 a A
F	4.0 c C	23.2 b B	16.9 bc BC

3.4 Discussion

3.4.1 Dry weight of component organs and partitioning between them.

3.4.1.1 Introduction

The effect of the site of application and rate on dry weight production and on the partitioning of the dry weight will be discussed in 3.4.1.2 and 3.4.1.3. However the difference between the two growth substances will not be discussed until section 3.4.3 as these results relate to the fruit set data (3.4.2).

3.4.1.2 Dry weight

Chlorflurenol and TIBA when applied to the whole plant at 100 ppm and 200 ppm reduced the total plant dry weight and the dry weight of the leaves, stem and roots (Table 3.3). Although the interaction between site and rate for the fruit dry weight was not significant (Table 3.3) fruit dry weight was less with the application of growth

substance to the plant than to the fruit (Table 3.2). Comparing the means for the non significant interaction (Table 3.3) it is more likely that the application to the plant reduced the fruit dry weight, rather than application to the fruit increasing fruit dry weight. Generally with application of chlorflurenol or TIBA to the cucumber plant there has been an increase in fruit yield (Cantliffe, Robinson and Bastdorff, 1972; Dean, 1978). Where fruit set has been increased total fruit yield has sometimes been reduced with chlorflurenol, but the proportion of fruit in the smaller size as required for pickling is increased (Cantliffe, Robinson and Shannon, 1972). Dean (1978) obtained the greatest response in yield to chlorflurenol with medium to strong genetic parthenocarpy cultivars. However in this experiment with a parthenocarpic cultivar, yield was not increased.

As these growth substances reduce vegetative growth and increase fruit set (3.4.2), yield soon after application should be greater, as found by Dean (1978) when the crop was harvested while most of the fruit was in the small pickle sizes. However if left for a longer period before harvesting, as in this experiment, non treated plants would be able to produce fruit on higher nodes and would have new leaves as sources for these fruit. For treated plants though, new sites would not occur as stem elongation is nearly nil, and so further fruit set is minimal. Had the present experiment been continued larger reductions in yields should have been detected.

3.4.1.3 Partitioning

Although application of growth substances to the plant reduced the dry weight of the leaves, stem and roots, it only reduced the percentage total plant dry weight in the stem (Table 3.8) and possibly the roots (Table 3.5). Application of growth substances to the plant almost stopped extension growth of the stem. These plants were about 1.3 m high when harvested whereas the other plants had reached the wire (1.8 m) and produced two laterals which were frequently 0.5 m each in length. The inhibition of the growth of the main shoot has been observed with a wide range of plants following application of TIBA or chlorflurenol to the whole plant (Bissaria and Prakash, 1978; Tanner and Ahmed, 1974; Bissaria, 1976). Associated with this is a reduction in apical dominance and increased branching (Bissaria and Prakash, 1978). However as all laterals had been removed when small in this experiment, little dry weight could be partitioned into the stem following application, thus accounting for the reduced proportion in the stem. A smaller percentage of the dry weight was partitioned into the roots with application of growth substance to the plant than the fruit (Table 3.5). This may be due to application to the plant reducing or application to the fruit increasing the percentage, or both, compared to the controls.

3.4.2 Fruit data

Fruit set on nodes 1-8 was increased with the application of growth substances to the whole plant (Table 3.9). However on nodes 9-16 fruit set was not significantly different to the controls (Table 3.11). The greater fruit set with the application of these growth substances to the plant has also been observed by Cantliffe (1972) with non-parthenocarpic cultivars and by Dean (1978) with parthenocarpic cultivars.

The difference in fruit set on nodes 1-8 between chlorflurenol and TIBA when applied to the fruit (Table 3.9b) is attributed to a reduction in fruit set with TIBA. It seems unlikely that chlorflurenol applied to the fruit increased fruit set or growth, as the nodes treated with growth substances were mainly nodes 1-8, and the proportion of fruit dry weight on these nodes was not greater (Table 3.14).

At 200 ppm TIBA applied to the fruit reduced the percentage fruit dry weight on nodes 1-8 (Table 3.14). The reduction in fruit set on the lower nodes with TIBA applied to the fruit (Table 3.9b) was partially compensated by greater fruit set on nodes 9-16 at the 200 ppm rate (Table 3.12) and a greater percentage of the fruit dry weight on nodes 9-16 at this rate (Table 3.14). Although the interaction between the three treatments was not significant it appears that only at the higher rate (200 ppm) fruit set is reduced on nodes 1-8. No difference was observed between 100 ppm and 200 ppm with chlorflurenol

(Table 3.9a, 3.12, 3.14). With application to the fruit only the lower nodes were treated with growth substance (3.2), so the increased fruit set on nodes 9-16 with TIBA at 200 ppm is likely to be an indirect effect. Two explanations are possible for the apparent compensatory mechanism following reduced fruit set on the lower nodes. Firstly the reduced fruit set on the lower nodes may allow greater fruit set on higher nodes due to the reduction in competition for assimilates. Secondly the lower fruit may produce an inhibitory factor or use up a promotory factor, which reduces fruit set on the higher nodes. Therefore if fruit set is reduced on the lower nodes less inhibitory factor is produced or less promotory factor is used up.

Application of growth substances to the plant reduced the fruit size (Table 3.13). The fruit on the upper nodes were frequently small due to the fruit not swelling at the distal end. Most of the fruit were misshapen with application to the plant (Table 3.16). However with the short type of cucumber cultivars, chlorflurenol and TIBA have little influence on the fruit shape (Cantliffe 1972, 1977; Cantliffe, Robinson and Bastdorff, 1972). Application of these growth substances to the fruit caused a small swelling at the point where the corolla was connected to the ovary (Table 3.16).

3.4.3 Effect of growth substances

The lower fruit dry weight, greater stem dry weight (Table 3.4), and reduced partitioning of the dry weight

into the fruit and more into the leaves and stem (Table 3.6 and 3.7) with TIBA application in comparison to chlorflurenol appears to be a redistribution effect between the fruit and vegetative parts of the plant. The reduction in fruit set on the lower nodes with TIBA applied to the fruit (Table 3.9), possibly reduced competition with the vegetative components until fruit set occurred on the higher nodes (Table 3.12). Fruit set was greater on nodes 9-16 with chlorflurenol than TIBA applied to the plant at 200 ppm (Table 3.12) even though fruit set was the same on nodes 1-8 (Table 3.9b) and this also may have increased the partitioning to the fruit with chlorflurenol compared to TIBA.

3.4.4 Relationship between stage of flower development and fruit set.

There was a decreasing trend in fruit set and per cent fruit dry weight on nodes 3-5 with increasing concentration of growth substance (Table 3.10, 3.15). With growth substance application fruit set and per cent fruit dry weight was greater on nodes 6-8 except for TIBA applied to the fruit at 200 ppm (Table 3.11 and 3.15). The increase on nodes 6-8 was greater with application to the plant than the fruit. Node 6.5 was the mean top node at anthesis at the time of growth substance application (Figure 3.1). This suggests that fruit set and growth are reduced on flowers past or at anthesis, and increased for flowers that

have not quite reached anthesis at the time of growth substance application.

These results are different to Cantliffe's (1972). With TIBA and chlorflurenol at 50 and 100 ppm they observed that fruit developed from flowers that reached anthesis approximately three days before spraying. However they were using a non-parthenocarpic cultivar. This difference in response may be due to the higher endogenous auxin levels in the ovaries of genetically parthenocarpic cultivars than non-parthenocarpic cultivars (Rudich, Baker and Sell, 1977).

3.5 Summary

Dry weight of the component organs was markedly reduced with application of chlorflurenol or TIBA to the whole plant, but the effect on the distribution of the dry weight between the component organs was small. Little stem elongation occurred after growth substance application to the plant, and this reduced the percentage total plant dry weight in the stem.

Both growth substances when sprayed on the whole plant increased fruit set on nodes 1-8. Chlorflurenol applied to the fruit did not influence the number of fruit set, but TIBA at 200 ppm reduced it on nodes 1-8 and increased it on nodes 9-16. As TIBA was only applied to about node 8, the increased fruit set on the higher nodes is likely to be an indirect effect. The greater fruit set on nodes 9-16 may be due to a reduced competition for

assimilates or a promotory factor, or reduced production of an inhibitory factor from the lower fruit. The reduction in fruit set on the lower nodes with TIBA applied to the fruit, reduced the fruit dry weight and the per cent total dry weight partitioned to the fruit.

These growth substances had an effect on the position where the fruit set. Fruit set and growth was reduced on flowers past or at anthesis, and increased on flowers that had not quite reached anthesis at the time of growth substance application. This shift was more marked with application to the plant than the fruit.

For an indeterminate crop, harvested over several months, the application of these growth substances to the whole plant has no commercial use, as the growth of the apex is markedly reduced and therefore later fruit sites and leaf growth. Also the fruit near the apex was very misshapen. Application to the fruit with chlorflurenol did not increase fruit set or yield, and TIBA reduced fruit set and yield. It is concluded that either of these growth substances when applied to either site, at the concentrations used in this experiment, have no place in a crop harvested over several months.

CHAPTER FOUR

THE EFFECT OF LEAF REMOVAL ON GROWTH AND DEVELOPMENT

4.1 Introduction

The sink strength of the fruit was not increased by the growth substances chlorflurenol or TIBA (Chapter 3). As there was no other easy method of possibly increasing sink-strength it was decided to study source-sink relationships by varying the degree of source strength.

By altering the rate of photosynthesis total dry matter production will be altered accordingly. However yield of the economic sink is influenced not only by total dry matter production but also by the way this is partitioned between the component organs. There is little information in the literature on the influence of source strength on the partitioning of dry weight for indeterminate plants.

Source strength may be reduced by shading or deleafing, and increased by carbon dioxide enrichment or by increasing the total PAR. Temperature influences source and sink strength. Deleafing is a simple method to reduce source strength. In this experiment source strength was reduced by various leaf removal treatments.

4.2 Materials and methods

On 19 April 1979 seed of the cv. Princess, as used in

3.2, was sown in 100 plastic pots containing coarse sand, and was germinated at 25° C. Following germination the seedlings were transferred to a greenhouse with a minimum temperature of 19° C and ventilation at 24° C. On 10 May, when the second leaf was expanding the plants were transferred to black polythene bags containing 10 dm^3 of coarse sand.

There were four treatments consisting of control and three levels of leaf removal. The level of leaf removal increased from treatment 1 (control) to treatment 4. Treatments 2, 3 and 4 had $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ of their leaves removed respectively (Table 4.1). The leaf removal treatments commenced on 11 May, and leaf 3 numbered from the base of the plant, was the first leaf to be removed. The leaves were removed when small, about 10 - 20 mm in width. At this size it was possible to remove them without damaging the apex, and there was little dry weight lost. There were four randomized blocks, with four plants per plot. Each plant had an area of 0.34 m^2 and a guard row was placed around the outside of this experiment.

Table 4.1 Leaf removal treatments.

Treatment	Per cent leaves removed	Leaves removed, numbered from the base of the plant
1. Control	0	None
2. Every 4th leaf removed	25	3, 7, 11 etc
3. Every 2nd leaf removed	50	3, 5, 7, 9, 11 etc
4. Every 4th leaf retained, the other three removed	75	3, 4, 5; 7, 8, 9; 11 etc

The plants were trained by the umbrella system and watered once a day with nutrient solution as in 3.2. On 15 July the plants were harvested and divided into fruit, leaves, stems and roots, dried at 90° C and their dry weights determined. The dry weight of individual fruit was recorded as well as the node number from which they were harvested.

4.3 Results

4.3.1 Introduction

All data expressed as a percentage was subjected to the arcsine transformation before analysing. In the tables of results actual percentages are given, not the transformed figure. Duncan's multiple range test was used to test for significant differences between treatment

means. Details of the analysis of variance are given in appendices 21-49.

4.3.2 Number of nodes per plant, total plant dry weight and dry weight of component organs.

There was no significance difference between the treatments for the number of nodes per plant when the plants were harvested. With increasing degree of leaf removal there was a reduction in total plant, fruit, leaf and root dry weight. However the reduction was not always significant (Table 4.2) (Appendices 21-26). Stem dry weight was little affected by the treatments, and was only significantly reduced at the highest leaf removal treatment.

Table 4.2 Effects of treatments on number of nodes, total plant dry weight and dry weight of component organs (g/plant).

Treatment	1	2	3	4
Number of nodes	27.6 N.S.	27.6	28.9	29.9
Total plant	90.1 a A	77.5 b B	66.0 c B	40.1 d C
Fruit	45.3 a A	37.1 b AB	31.6 b B	15.5 c C
Leaves	33.5 a A	29.5 b B	24.1 c C	15.7 d D
Stem	8.3 a A	8.1 a AB	8.0 a AB	7.0 b B
Root	3.0 a A	2.8 a A	2.3 b B	1.9 c C

4.3.3 Number and mean dry weight of fruit.

For the analysis on the fruit data, fruit with a dry weight of one gram or greater was used to ensure the fruit had set. With increasing degree of leaf removal the number and mean dry weight was reduced, but treatment 4 was only significantly less than the other treatments (Table 4.3) (Appendices 27-28).

Table 4.3 Number and mean dry weight of fruit with various leaf removal treatments (per plant).

Treatments	1	2	3	4
Number of fruit	4.3 a A	3.8 a A	3.5 a A	2.0 b B
Mean dry weight	10.6 a A	9.8 a A	8.7 a A	7.1 b B

4.3.4 Partitioning of the dry weight between the component organs.

Although the dry weight of all the component organs, except for the stem, was markedly reduced with increasing degree of leaf removal, the partitioning of the dry weight was little affected (Figure 4.1). The proportion of the dry weight in the fruit was significantly less for treatment 4. However the percentage in the leaves was not significantly different between the treatments (Table 4.4) (Appendices 29-32). The proportion in the stem increased

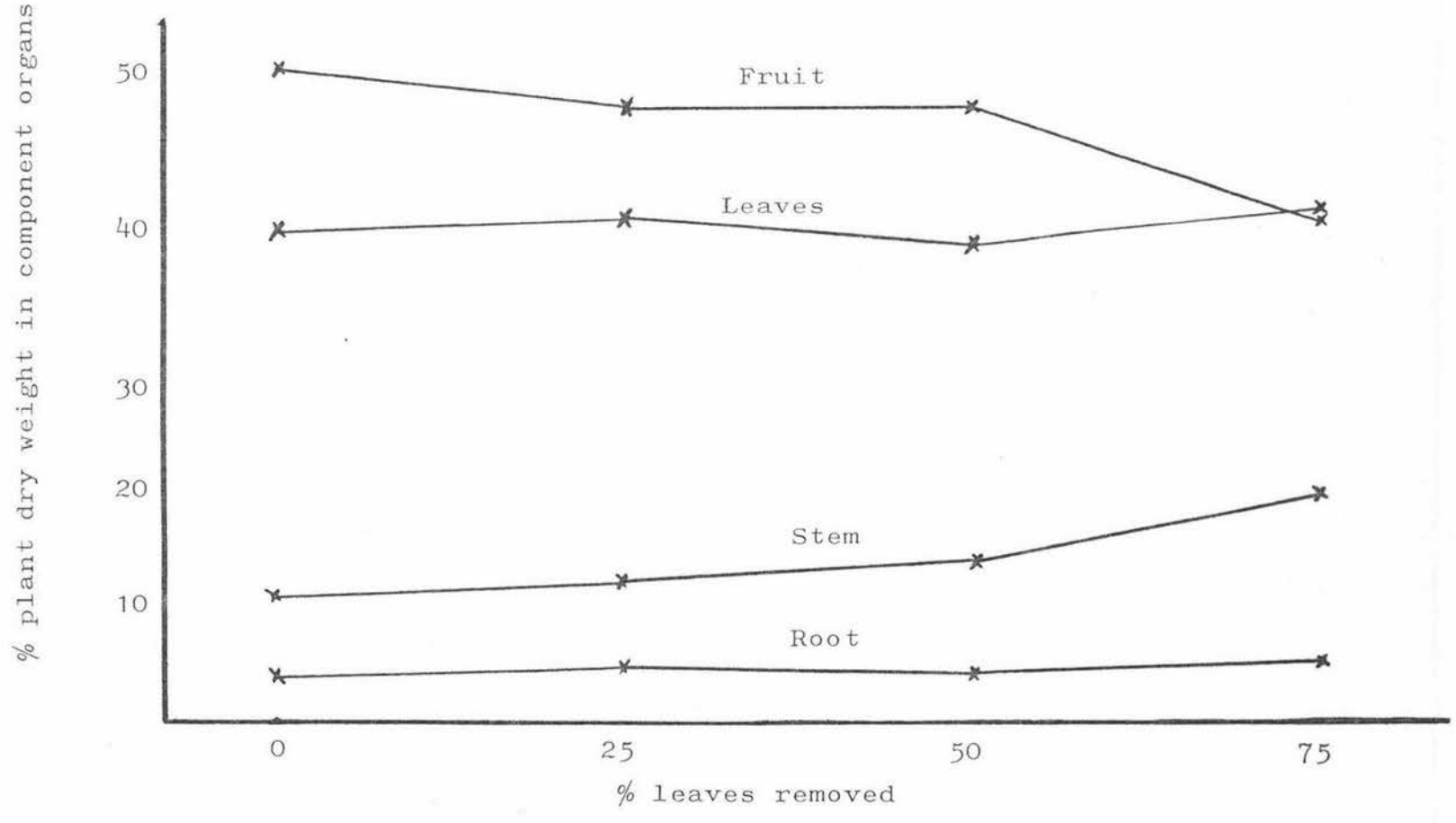

Fig. 4.1 Partitioning of dry weight with the leaf removal treatments

with increasing degree of leaf removal, although it was not significantly different between treatment 1 and 2. At the greatest leaf removal treatment a significantly greater proportion was partitioned into the roots.

Table 4.4 Percent total dry weight in the component organs (%).

Treatment	1	2	3	4
Fruit	50.1 a A	47.6 a A	47.8 a A	38.6 b B
Leaves	37.3 N.S.	38.3	36.5	39.3
Stem	9.2 c C	10.5 c C	12.2 b B	17.6 a A
Root	3.4 b B	3.7 b B	3.5 b B	4.6 a A

4.3.5 Fruit data.

4.3.5.1 Association between fruit and nodes with leaves.

It was observed that for treatment 3 and 4 the time to anthesis was delayed on nodes with no leaf, and that most of the fruit set on nodes with a leaf. The percentage of the fruit on nodes with a leaf decreased with increasing degree of leaf removal (Table 4.5) (Appendix 33). Due to the greater number of leafless nodes with increasing degree of leaf removal the chance of being associated with a leaf is less (Table 4.5). The number of fruit associated with a leaf is greater than expected if the distribution of fruit was due to chance.

Table 4.5 Association between a fruit and a node with a leaf.

Treatment	2	3	4
% fruit on nodes with a leaf.	90.9 a A	80.9 a A	59.2 b B
% fruit expected to be at a node with a leaf if the distribution was random.	75.0	50.0	25.0

4.3.5.2 Distribution of fruit dry weight and number of fruit on the plant.

Due to the association between fruit and nodes with a leaf, and as treatments were applied in groups of four nodes, the following nodes were grouped together for analysis (5 to 8, 9 to 12, 13 to 16, 17 to 20, and node 21 and above). There was no significant difference between the treatments for the proportion of the fruit dry weight on the various nodes except for nodes 13 to 16 (Table 4.6) (Appendices 34-38).

Table 4.6 Distribution of fruit dry weight on the various nodes (%).

Treatments	1	2	3	4
Nodes 5-8	18.0 N.S.	10.7	9.1	9.6
Nodes 9-12	20.0 N.S.	25.7	19.7	21.6
Nodes 13-16	16.5 a	11.6 ab	20.0 a	3.4 b
Nodes 17-20	9.5 N.S.	12.8	6.8	22.9
Node 21 and above	36.1 N.S.	39.2	44.5	42.6

Also for the number of fruit, with a dry weight greater than one gram, there was no significant difference between the treatments except for nodes 5 to 8. (Table 4.7((Appendices 39-43). The distribution of the fruit numbers on various nodes was not significantly different between the treatments.

Table 4.7 Effect of treatments on fruit numbers on various nodes (per plant).

Treatments	1	2	3	4
Nodes 5-8	0.8 a	0.4 ab	0.3 b	0.2 b
Nodes 9-12	1.0 N.S.	0.9	0.7	0.5
Nodes 13-16	0.7 N.S.	0.6	0.6	0.2
Nodes 17-20	0.4 N.S.	0.4	0.3	0.3
Node 21 and above	1.3 N.S.	1.4	1.5	0.8

4.3.6 Sex expression

No male flowers were produced after node 8 on the control plants, but with leaf removal male nodes were produced above this node. There was no significant difference between the treatments on the lower nodes (Table 4.8). For nodes 13 to 16 and 17 to 20 the number of nodes with male flowers was significantly greater for treatment 4 but there was no significant difference for nodes 21 to 24 (Table 4.8) (Appendices 44-49).

Table 4.8 Number of nodes with male flowers, on various nodes numbered from the base of the plant.

Treatments	1	2	3	4
1-4	2.1 N.S.	2.1	2.1	2.2
5-8	2.1 N.S.	1.9	2.3	2.1
9-12	0 N.S.	0.1	0.1	0.3
13-16	0 b B	0.8 b AB	0.8 b AB	2.2 a A
17-20	0 b B	0.4 b AB	0.6 b AB	1.8 a A
21-24	0 N.S.	0	0	0.2
Total	4.2	5.3	5.9	8.6

4.4 Discussion

4.4.1 Dry weight and partitioning of the dry weight between the component organs.

The reduction in leaf area (source size) with the leaf removal treatments reduced the total plant dry weight and the dry weight of the component organs. However the reduction in stem dry weight was small compared to the other organs and was only significant with the severest leaf removal treatment (Table 4.2). The stem was probably little affected by the treatments as this organ is part of the basic plant structure to which the other organs are attached. With leaf removal the plant produced more nodes for the development of each leaf and the treatments had

no significant effect on the number of nodes (Table 4.2).

Except for the severest leaf removal treatment, partitioning of the dry weight was little affected by the treatments (Table 4.4). The percentage of the total plant dry weight in the fruit was only significantly reduced with the severest leaf removal treatment. There was no significant differences with respect to the leaves. As the number of nodes was not altered by the treatments and leaf dry weight was only halved by 75% leaf removal (Table 4.2), the specific leaf area and/or the area of each leaf must have been greater. A greater percentage of the total plant dry weight was partitioned into the stem with treatment 3 and 4 and also the percentage partitioned into the roots increased with treatment 4. The greater percentage of the total dry weight partitioned into the stem at the higher leaf removal treatments, appeared to be at the expense of the percentage partitioned into the fruit.

With the severest leaf removal treatment a significantly greater proportion of the total dry weight was partitioned into the roots. In general the destination of exported assimilates is primarily to the nearest sink, and the lower leaves export primarily to the root (Thaine, Ovenden and Turner, 1959). As the two lowest leaves were not removed in this experiment, the close proximity of these to the roots may have allowed a greater proportion of the assimilates to be partitioned to them with the severest removal treatment.

Even with a marked reduction in total plant dry weight, resulting from leaf removal, the partitioning between the component organs was little affected. Stanhill (1977) has observed an increase in relative rate of leaf growth and reduced relative root growth following defoliation of carrots, to restore the relative size of organs to that preceding the treatment. Similar results have been described for leaf and root pruning treatments with Phaseolus vulgaris (Brouwer, 1962) and Beta vulgaris L. (Fick, Williams and Loomis, 1971). In these cases mature leaves were removed and the plant restored the balance between the component organs, whereas in this experiment the leaves were removed before they expanded, but similarly the plant maintained a balance between the component organs.

4.4.2 Fruit data

The number and mean dry weight of fruit was significantly reduced by the severest leaf removal treatment only, although the trend was the same for all treatments (Table 4.3). The reduction in fruit dry weight appears to be due more to a reduction in number than size. Wittwer and Robb (1964) also observed a reduction in number and mean weight of tomato fruit with a lower assimilation rate, as did Clifford (1979) with mung beans.

Most of the fruit developed at nodes with a leaf. The association between a leaf and fruit development at a node may be due to the close proximity of a source of

assimilates or the supply of other factors from the subtending leaf (2.2.1). Sinks tend to utilize local sources of assimilates preferentially, but can obtain assimilates from more distant sources upon removal of nearer sources (Cook and Evans, 1976; Wardlaw, Carr and Anderson, 1965). The removal of a mature subtending leaf on mung beans had no measurable effect on fruit number or seed weight at that node, due to a diversion of assimilates from other sources (Clifford, 1979). Flowers at leafless nodes for treatment 3 and 4 frequently reached anthesis later and were smaller than flowers at nodes above them with a leaf.

Only on nodes 13-16 was the distribution of the fruit dry weight significantly different between the treatments. Treatments 1 and 3 were greater than treatment 4 (Table 4.6). This may have been due to the larger fruit on the lower nodes being able to compete to a greater extent with the fruit on nodes 13-16 for the reduced supply of assimilates in treatment 4. The experiments of Peel and Ho (1970) with aphid colonies of various sizes, and Cook and Evans (1976) on wheat plants with two ears containing different numbers of grains both indicate that the distribution between two sinks of equal activity is not in proportion to the relative size of the two sinks but is heavily biased towards the larger sink, far more than would be expected from the relative sink sizes. With treatment 4 there may have been greater competition for assimilates and as the lower nodes have the larger fruit they may have

been able to compete to a greater extent for the assimilates, reducing the availability to nodes 13-16. Alternatively there may have been a marked reduction in fruit set on these nodes due to competition, and due to the reduced fruit set the proportion of the fruit dry weight on these nodes was reduced. However there was no significant difference between the treatments for fruit set on these nodes although the trend was in the same direction. Only on nodes 5-8 was the reduction in fruit set significantly different between the treatments (Table 4.7). However the trend was the same on the other nodes. With increasing degree of leaf removal the number of fruit that set decreased.

The distribution of the fruit dry weight and fruit set on the various nodes fluctuated in a similar manner (Table 4.6 and 4.7). Fruit set is greater on certain nodes but four to eight nodes later fruit set decreases. The reduction in fruit set for several nodes may be due to competition for assimilates or the lower fruit may produce an inhibitory factor or use up a promotory factor which reduces fruit set.

4.4.3 Influence of leaf removal treatments on the sex expression.

Although this cultivar is described as "all-female" some male flowers developed on the lower nodes (up to node 8), and then only female flowers developed on node 8 to 10 with all treatments. After this some male flowers

developed again with all the leaf removal treatments but was only significant for treatment 4 (Table 4-8).

The influence of daylength treatments applied to seedlings at different ages, designated by the number of unfolded leaves, was on nodes just above the last unfolded leaf at the time of treatment (Matsuo et al, 1969). In the present experiment leaf three was the first leaf to be removed. When the leaf removal treatments began the flower at node three had probably not differentiated but it was not until node thirteen that the sex expression was altered by the leaf removal treatments. In the cucumber plant several growth substances may participate in the regulation of sex expression. The ABA level is higher in gynoecious cucumber plants than monoecious plants (1.2.3.3). ABA is produced in many plants by the older leaves. With deleafing the plant has fewer older leaves and so ABA production may be less which could account for the increased maleness.

4.5 Conclusion

With increasing degree of leaf removal there was a reduction in total plant dry weight and dry weight of the component organs. The partitioning between the component organs was little affected, except for a greater proportion being partitioned into the stem and less into the fruit with the severest leaf removal treatment. The increased partitioning to the stem is attributed to the plant continuing to develop a basic structural framework.

The reduction in fruit dry weight with increasing degree of leaf removal was due to a reduction in numbers and weight of fruit. The distribution of the fruit dry weight and fruit set on the nodes appeared to occur in flushes, particularly with the severest leaf removal treatment. This may have been due to competition for assimilates or the lower fruit may produce on inhibitory factor or use up a promotory factor which reduces fruit set for several nodes.

Fruits generally set on nodes at which the leaf had not been removed. This may have been due to the close proximity of the source of assimilates or the supply of a growth factor from the leaf.

After the plants went into a pistillate phase, they went back to a monoecious phase with leaf removal. This is attributed to a shift in the balance between growth substances due to the changed ratio of mature to young leaves.

CHAPTER FIVE

THE EFFECT OF SHADING ON GROWTH AND DEVELOPMENT

5.1 Introduction

Deleafing appeared to have little influence on the partitioning of the dry weight except at the highest degree of leaf removal (4.3.3). Therefore the competitive ability of the component organs was not altered. When studying the partitioning of dry weight, deleafing as a method of reducing source strength has been criticised due to its effect on the distribution of hormones (Wareing, Khalifa and Treharne, 1968). Shading is another way of reducing source strength. In this experiment the influence of various degrees of shading will be studied when applied over different periods of time.

5.2 Materials and methods

Seed of the cv. Princess was sown on 28 July 1978 in 100 mm plastic pots containing coarse sand and was germinated at 28° C. At emergence (2 August) the seedlings were transferred to a greenhouse with a minimum temperature of 19° C and it was ventil ated at 24° C. On 18 August when the second leaf was just starting to expand, the plants were planted into black polythene bags containing 15 dm^3 of coarse sand. The treatments consisted of four shading treatments applied over two different fortnightly

periods. The first period was from 16 to 30 September and these plants were harvested on 30 September (H1). The second period was from 30 September to 14 October and these were harvested on 14 October (H2). Some plants reached anthesis on 6 September and when the first shading treatments were applied these fruit were 60 mm long. At the first harvest these fruit were 200 mm long and just marketable. The mean daily outdoor solar radiation received during the first period was 3,796 w.hr. m^{-2} and 4,949 w.hr. m^{-2} during the second period, as measured with an Eppley pyranometer at Plant Physiology Division, DSIR, Palmerston North.

Different shading materials were used to provide various degrees of shading. Using a Lambda light meter (LI-185) with a quantum sensor the reduction in PAR for the materials was measured outdoors (35%, 58%, 70%). The first material (35%) was 30% Sarlon shade cloth (green colour); the second material was a black shade cloth but the brand name is unknown; the third shading treatment (70%) was obtained by using two shading materials (a white on top of a black shading material).

Each plant was given an area of 0.34 m^2. A randomised complete block design was used. There were three blocks with four plants per plot giving thirty-two plants per block. A guard row was placed around the outside of this experiment. The plants were watered and trained as in the other experiments.

5.3 Results

5.3.1 Introduction

This was a 2 x 4 factorial experiment (two shading periods x four shading treatments) and after analysis of variance was carried out on the relevant data the treatment means were compared by the Duncan's multiple range test (3.3.1). Actual percentages are given in the tables but the arcsine transformation was used to determine significant differences. Details of the analysis of variance are given in the appendices.

5.3.2 Dry weight and partitioning

The leaf dry weight was reduced with increasing degree of shading, and was greater at the second harvest than the first (Table 5.1 and 5.2) (Appendix 50).

Table 5.1 Mean dry weight of the leaves with the different shading treatments (g/plant).

	S1	S2	S3	S4
Leaves	42.4 a A	37.6 b B	34.5 c C	32.7 d C

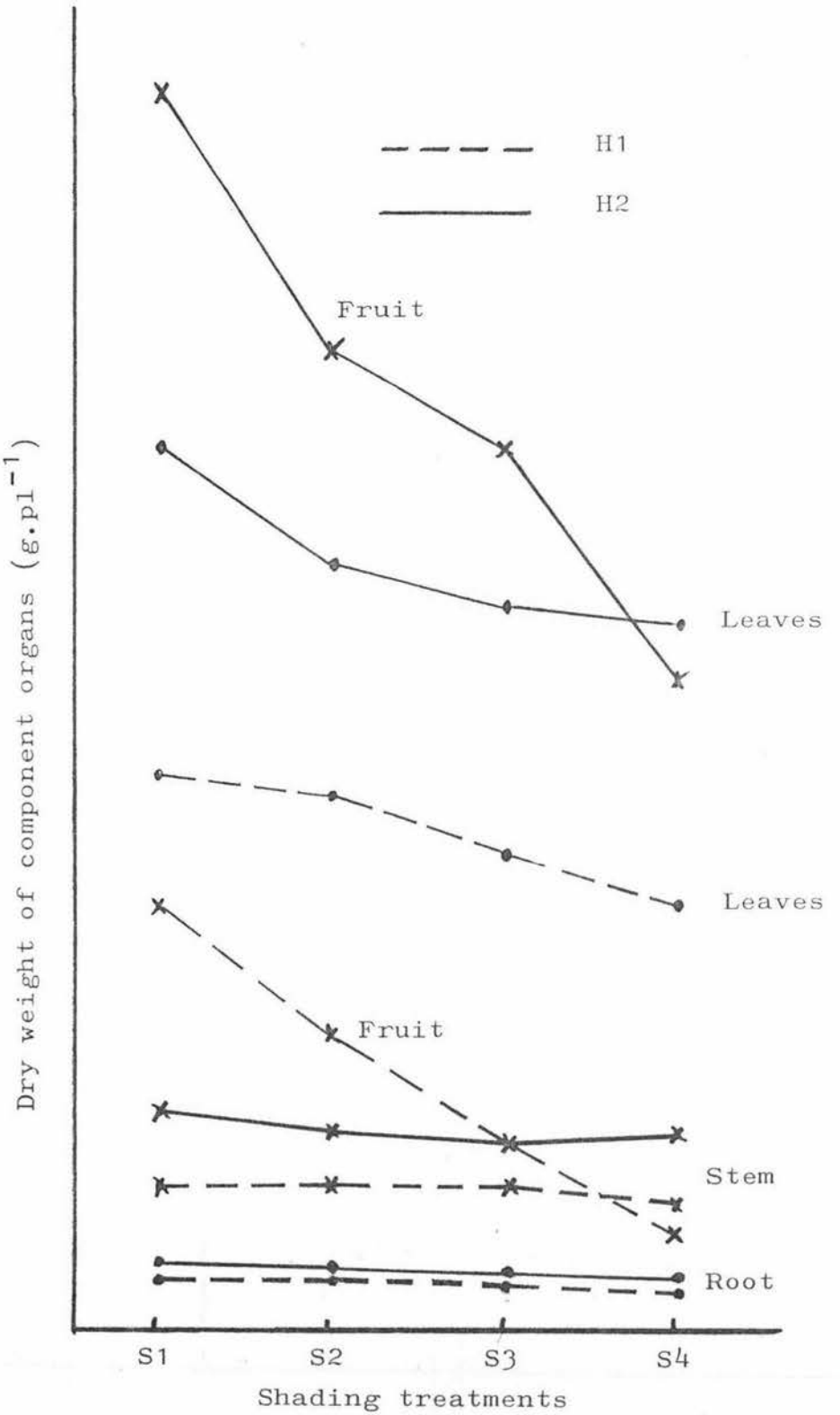

Fig. 5.1 Dry weight of component organs at two harvests and with different shading treatments

Table 5.2 Mean dry weight of the leaves at the two harvests (g/plant).

	H1	H2
Leaves	29.3 B	44.3 A

There were significant interactions between the harvest dates and the shading treatments for the total plant dry weight of all the component organs except the leaves (Table 5.3 and Figure 5.1) (Appendices 51-54).

Table 5.3 Significant interactions on the dry weight of the component organs (g/plant).

		Total plant	Fruit	Stems	Roots
H1	S1	69.8 E	24.4 e D	8.5 c C	3.1 b ABC
	S2	59.3 F	17.0 f E	8.4 c C	3.0 bc BC
	S3	49.1 G	10.5 g EF	8.4 c C	2.6 c CD
	S4	40.0 H	5.6 h F	7.3 c C	2.2 c D
H2	S1	139.9 A	72.6 a A	12.5 a A	3.8 a A
	S2	115.5 B	56.5 b B	11.2 b A	3.5 ab AB
	S3	105.9 C	50.7 c B	10.5 b B	3.3 ab ABC
	S4	92.1 D	37.1 d C	11.4 ab A	3.1 b ABC

With increasing degree of shading the percentage of the dry weight in the roots increased (Table 5.4). The percentage in the roots decreased from H1 to H2 (Table 5.5) (Appendix 55).

Table 5.4 Percent dry weight in the roots with the various shading treatments.

	S1	S2	S3	S4
Roots	3.6 c B	4.0 b AB	4.2 a A	4.4 a A

Table 5.5 Percent dry weight in the roots at the two harvests.

	H1	H2
Roots	5.0 A	3.1 B

There were significant interactions between the harvest dates and the shading treatments, for the proportion of the dry weight in the fruit, leaves and stem (Table 5.6) (Appendices 56-58).

Table 5.6 Significant interactions on percent dry weight in the component organs.

		Fruit	Leaves	Stem
H1	S1	34.9 c BC	48.5 d C	12.2 c B
	S2	28.6 d C	52.1 c B	14.2 b B
	S3	22.0 e D	55.7 b B	17.0 a A
	S4	14.0 f E	62.2 a A	18.4 a A
H2	S1	51.9 a A	36.4 g E	8.9 d C
	S2	49.0 a A	38.4 fg E	9.7 d C
	S3	47.8 a A	39.1 f E	9.9 d C
	S4	40.3 b B	43.9 e D	12.4 c B

5.3.3 Absolute growth and partitioning of this growth over period two.

By deducting the dry weight of the control plants at the first harvest from the dry weight at the second harvest the growth over this two week period could be determined for the four shading treatments (Table 5.7) (Appendix 59). Also the distribution of this growth between the component organs was determined. The shading reduced the growth over this period but the distribution of this dry weight between the component organs was only significantly different at the highest shading treatment (Table 5.7) (Appendices 60-63). With the highest shading treatment a smaller proportion of the dry weight was partitioned into

the fruit and more into the leaves and stems. There was no significant difference between the treatments for the proportion of this dry weight in the roots.

Table 5.7 The absolute growth between H1 and H2 and the partitioning of this between the component organs.

	S1	S2	S3	S4
Absolute growth (g/pl)	70.0 A	45.7 B	36.2 B	22.3 C
Fruit (%)	68.8 a A	70.2 a A	72.6 a A	57.2 b B
Leaves (%)	24.5 b AB	22.8 b AB	21.1 b B	29.8 a A
Stem (%)	5.7 b	5.8 b	5.7 b	13.0 a
Roots (%)	1.0 N.S.	1.2	0.6	1.0

5.3.4 Fruit data.

5.3.4.1 Fruit set.

On nodes 1-10 the interaction was significant ($p < 0.01$). Fruit set was reduced with increasing degree of shading at the first harvest but there was no significant effect at the second harvest. (Table 5.8) (Appendix 64). With increasing degree of shading fruit set was reduced on nodes 11-20 and was greater at the second harvest than the first. (Table 5.8) (Appendix 65).

Table 5.8 Effect of shading on fruit set.

		Nodes 1-10		Nodes 11-20
H1	S1	4.1 A a	S1	2.8 a A
	S2	3.0 b A	S2	2.8 a A
	S3	1.7 c B	S3	2.0 b AB
	S4	0.7 d B	S4	1.3 c B
H2	S1	3.5 ab A		
	S2	3.7 ab A	H1	1.4 A
	S3	4.3 a A	H2	3.0 B
	S4	3.7 ab A		

5.3.4.2 Distribution of fruit dry weight on various nodes.

At the first harvest a decreasing proportion of the fruit dry weight occurred on nodes 1-10, and an increasing proportion on nodes 11-20 with increasing degree of shading. However at the second harvest the opposite trend occurred but few of the shading treatments were significantly different to each other (Table 5.9)(Appendices 66 and 67). The proportion of the fruit dry weight on nodes 21 and above was significantly greater at the second harvest than the first (Table 5.9) (Appendix 68).

Table 5.9 Percentage of fruit dry weight on various nodes (%).

		Nodes 1-10	Nodes 11-20		Node 21
H1	S1	80.5 a A	19.1 c B	H1	1.2 B
	S2	68.1 ab AB	31.0 bc AB	H2	5.8 A
	S3	59.8 bc ABC	39.7 ab AB		
	S4	45.7 cd BC	51.3 a A		
H2	S1	41.4 d C	51.4 a A		
	S2	51.1 bcd BC	39.9 ab AB		
	S3	61.3 bc ABC	33.2 abc AB		
	S4	58.8 bcd ABC	40.4 ab AB		

Using the control plants from the first harvest the distribution of the fruit growth over period two was calculated. There was no significant difference between S1, S2 and S3, but S3 was greater than S4 ($p < 0.05$) on nodes 1-10 and S2 and S3 were less than S4 on nodes 11-20 (Table 5.10) (Appendices 59-71).

Table 5.10 Distribution of the absolute fruit growth over period two on the various nodes (%).

	Nodes 1-10	Nodes 11-20	Nodes 20 and above
S1	21.1 ab	68.5 ab	10.4 N.S.
S2	27.4 ab	56.5 b	16.1
S3	42.3 a	47.7 b	10.0
S4	8.4 b	90.0 a	1.6

5.4 Discussion

5.4.1 Dry weight and partitioning of the dry weight.

With increasing degree of shading the growth of the total plant and the component organs was reduced (Table 5.1 and 5.3). With time a greater proportion of the plants dry weight was in the fruit and less in the vegetative organs (Table 5.5). The reduction in the percent total dry weight in the fruit with increasing degree of shading (Table 5.4 and 5.6) is attributed to a delay in the growth rate rather than a smaller percentage of the absolute growth being partitioned into the fruit, as in the second period there was no significant difference in the proportion of the dry weight partitioned into the various component organs for the three lowest shading treatments (Table 5.7). However at the highest shading (treatment 70%) a significantly smaller proportion of the absolute growth was partitioned into the fruit (Table 5.7).

When assimilate supply is low vegetative growth appears to have a greater priority over fruit growth. With sugar beet Ulrich (1952, 1955) concluded that storage beet growth and sugar accumulation required an excess of photosynthates beyond the needs for respiration and for growth of tops and fibrous roots. Fick, Williams and Loomis' (1973) simulations agreed well with field observations when the partitioning was based on a hierarchy of priorities. In order of importance these priorities were: respiration, top growth, fibrous root growth and storage root growth. Simulated growth did not match field observations if the sequence was changed. However with Callistephus chinensis and Chrysanthemum morifolium the distribution of the absolute growth at a certain total dry plant dry weight was not influenced by the carbon dioxide level or light intensity (Hughes and Cockshull, 1969, 1971).

5.4.2 Distribution of fruit dry weight on various nodes.

The reduction in the proportion of the fruit dry weight on the lower nodes with increasing degree of shading at the first harvest (Table 5.9) appeared to be due to a greater reduction in fruit set on nodes 1-10 than 11-20 (Table 5.8). At the second harvest fruit set was reduced on nodes 11-20 but not on nodes 1-10 as this would have been determined before the shading treatments were applied.

An increasing proportion of the fruit dry weight occurred on the lower nodes with increasing degree of shading at the second harvest (Table 5.9). There are two possible explanations for this. Firstly the delay in development with shading may account for this increase, as with ontogeny a greater proportion of the fruit dry weight occurs on the higher nodes. The increase in the proportion of the fruit dry weight on the higher nodes with ontogeny can be observed by comparing the distribution for the control plants at the two harvests (Table 5.9).

Secondly where several sinks are competing for a limited supply of assimilates, the relative magnitude of the sinks may be of overriding importance with a pronounced bias in favour of the largest sink (2.1.1). Due to the fruit on the lower nodes having developed a high sink strength by this stage they may markedly reduce fruit growth on the higher nodes when the supply of assimilates is reduced by the shading treatments. However with the highest shading treatment most of the fruit growth occurred on the higher nodes (Table 5.10). Besides the sink strength, the proximity of the various sinks, modified to some extent by the pattern of vascular connections, determines the distribution of assimilates (Evans, 1975). With 70% shading the lower leaves were probably near the compensation point, and so the proximity of the fruit on the higher nodes to the source of assimilates may have determined where the fruit growth occurred.

5.5 Conclusion

For a young fruiting cucumber plant that has developed several medium sized fruit, shading up to 58% had no effect on the partitioning of the absolute growth between the component organs. However with an increase in shading from 58% to 70% the per cent absolute growth partitioned into the fruit was reduced. It appears that below a critical level of assimilate supply the vegetative organs have a higher priority than the fruit. Above this critical level the partitioning of the absolute growth between the component organs was not significantly different. At this stage of development about 70% of the absolute growth was partitioned into the fruit, 23% into the leaves, 6% into the stem and 1% into the roots. However with 70% shading the proportion of the absolute growth partitioned into the fruit was reduced to 57%.

Over this period the greatest degree of shading (70%) markedly reduced fruit growth on the lower nodes. With this degree of shading the lower leaves were probably near the compensation point and the proximity of the fruit to the source of assimilates appears to have determined where the fruit growth occurred. Fruit set was reduced with increasing degree of shading.

CHAPTER SIX

THE EFFECT OF CARBON DIOXIDE ENRICHMENT ON GROWTH AND DEVELOPMENT

6.1 Introduction

In the two previous experiments, source strength was reduced by leaf removal or shading, with little influence on the partitioning of assimilates, even though the dry weight was markedly reduced. The present investigation was designed to study the influence of increasing source strength on the partitioning of assimilates and on the growth and development of the cucumber plant. Carbon dioxide enrichment to 1000 ppm was used to increase source strength.

6.2 Materials and methods

On the 16 March 1979 seed of the cv. Princess was sown in 100 mm plastic pots containing coarse sand and was germinated at 25° C. At emergence the seedlings were transferred to a greenhouse with a minimum temperature of 19° C and ventilated at 24° C. When the second leaf was just expanding (4 April), the plants were planted into black polythene bags containing 15 dm^3 of coarse sand. These were randomized between two greenhouses on 9 April, given an area of 0.34 m^2/plant and with guard rows placed around the outside. The minimum temperature of these

greenhouses was 19° C and they were ventil ated at 28° C. The plants were watered once or twice daily with a nutrient solution (Appendix 1) and trained by the umbrella training system.

The first flower reached anthesis on 19 April, and the first weekly harvest from each house was taken on 20 April. From this date onwards the carbon dioxide level was maintained in one greenhouse at 1000 ppm from dawn to dusk. The carbon dioxide was supplied from pressurised cylinders and the level controlled by a carbon dioxide indicator/controller (Gas-O-Mat). This conductimetric carbon dioxide analyser, similar to that described by Slack (1974), is based on the principle of measuring the increase in electrical conductivity of recirculated, deionized water, when a sample air stream is bubbled through the water.

Six weekly harvests from each house were taken, with eight plants on the first harvest and the final harvest. On the other four harvests, two sets of eight plants were harvested weekly. This allowed a separate set of plants to be used for calculating the growth over the preceeding week compared to the following week. The plants were taken at random and the remaining plants moved to fill up the gaps. A sample of one leaf in three for the first three harvests and one leaf in four for the last three harvests were taken and its leaf area measured with a Lambda leaf area machine. The total leaf area was

estimated by multiplying the sample leaf area by the inverse of the proportion of the leaf dry weight in the sample. The dry weight of the component organs and individual fruit were determined at each harvest. Also the number of leaves with a diameter greater than 20 mm was recorded.

The NAR and RGR were determined from the following formulae (Hunt, 1978):

$$NAR = \frac{{}_2W - {}_1W}{{}_2T - {}_1T} \cdot \frac{\log_{e2}L_A - \log_{e1}L_A}{{}_2L_A - {}_1L_A}$$

$$RGR = \frac{\log_{e2}W - \log_{e1}W}{{}_2T - {}_1T}$$

If the leaf area at the beginning of a week is multiplied by the reduction in specific leaf weight, the leaf weight loss from these leaves can be determined. This assumes that the specific leaf weight of the new leaves is the same as the old leaves.

$$\text{Leaf weight loss from existing leaves} = \left(\frac{{}_1L_w}{{}_1L_A} - \frac{{}_2L_w}{{}_2L_A}\right) \cdot {}_1L_A$$

6.3 Results

6.3.1 Introduction

The treatments were not replicated because of the limit to the number of plants that could be grown in each greenhouse, and therefore determinations of significant differences were not possible.

6.3.2 Absolute growth rate

The absolute growth rate for the total plant and the fruit was greater with carbon dioxide enrichment for each weekly period (Table 6.1). It was also greater for all the component organs on week 1, 2 and 5, but on week 3 and 4 was greater for the fruit but not the vegetative organs.

Table 6.1 Absolute growth rate of total plant and component organs ($g.pl^{-1}.day^{-1}$).

	Week	1	2	3	4	5
Control						
	Total plant	2.12	2.05	1.75	1.82	1.76
	Fruit	0.13	0.51	0.80	0.89	1.28
	Leaf	1.21	0.59	0.45	0.45	0.38
	Petiole	0.26	0.30	0.18	0.11	0.07
	Stem	0.40	0.43	0.33	0.25	0.10
	Root	0.12	0.22	-0.01	0.12	-0.07
Enrichment						
	Total plant	2.76	4.72	2.37	3.06	6.38
	Fruit	0.16	0.79	2.24	2.95	4.45
	Leaf	1.55	2.19	-0.21	0.18	1.30
	Petiole	0.37	0.62	0.15	-0.15	0.26
	Stem	0.50	0.63	0.18	0.07	0.28
	Root	0.18	0.49	0.01	0.01	0.09

6.3.3 Partitioning of the absolute growth

Over the first week the partitioning between the component organs was similar for the two treatments, but in the second week a greater percentage of the growth was partitioned into the leaves and less into the fruit and stem with enrichment (Table 6.2). In the third and

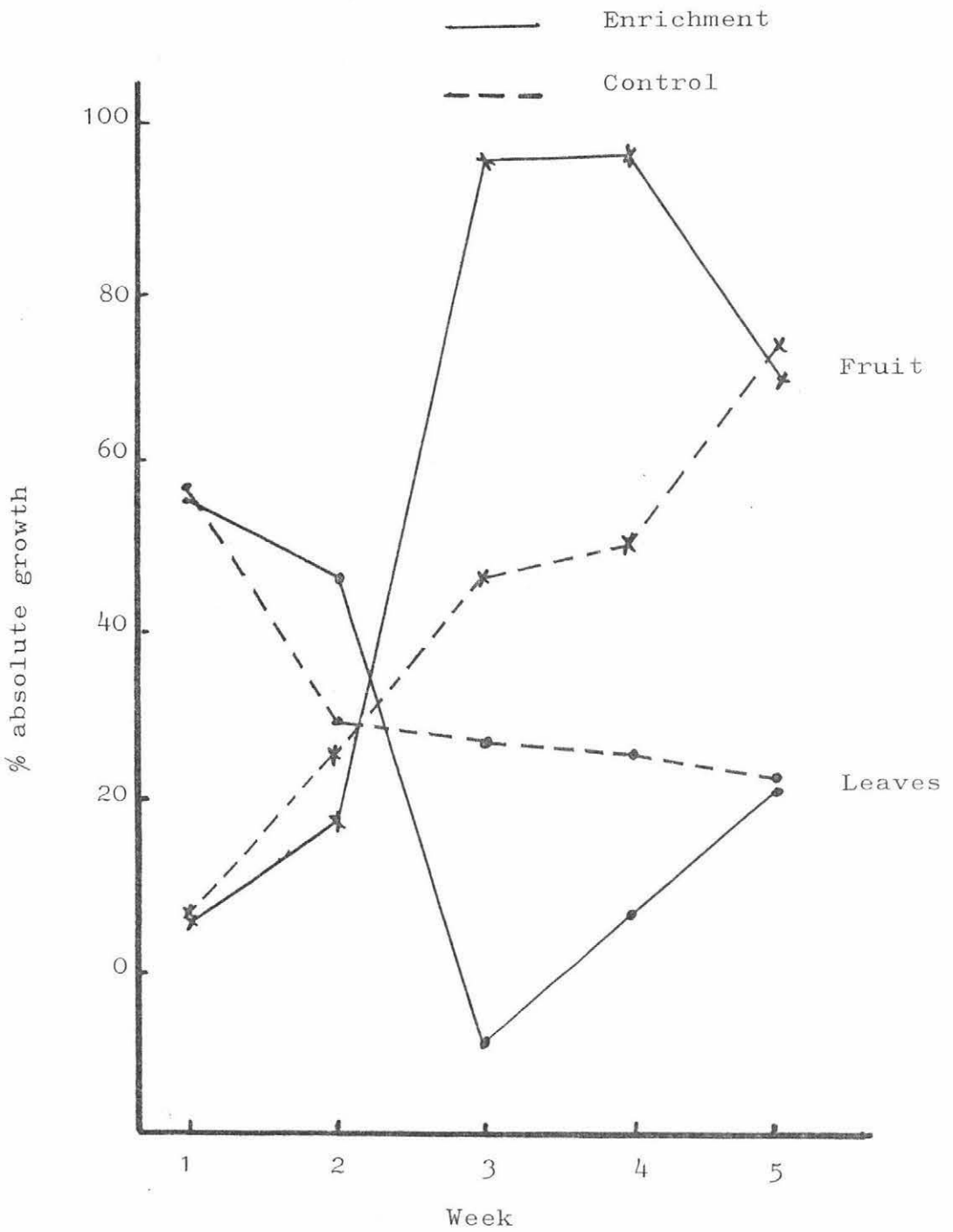

Fig. 6.1 Per cent absolute growth partitioned into fruit and leaves in each week

fourth week, with enrichment most of the growth was partitioned into the fruit and there appeared to be a loss of dry weight from the leaves in the third week and petiole in the fourth week. Without enrichment an increasing proportion of the growth was partitioned into the fruit and less into the leaves, stem and petiole. The percentage partitioned into the root fluctuated from week to week. With enrichment the percentage partitioned into the fruit was 94.9 and 96.0% in week 3 and 4 respectively but was reduced to 69.9% in week 5. The partitioning was very similar for both of the treatments in week 5 (Table 6.2). The partitioning data is also shown in Figure 6.1 and 6.2.

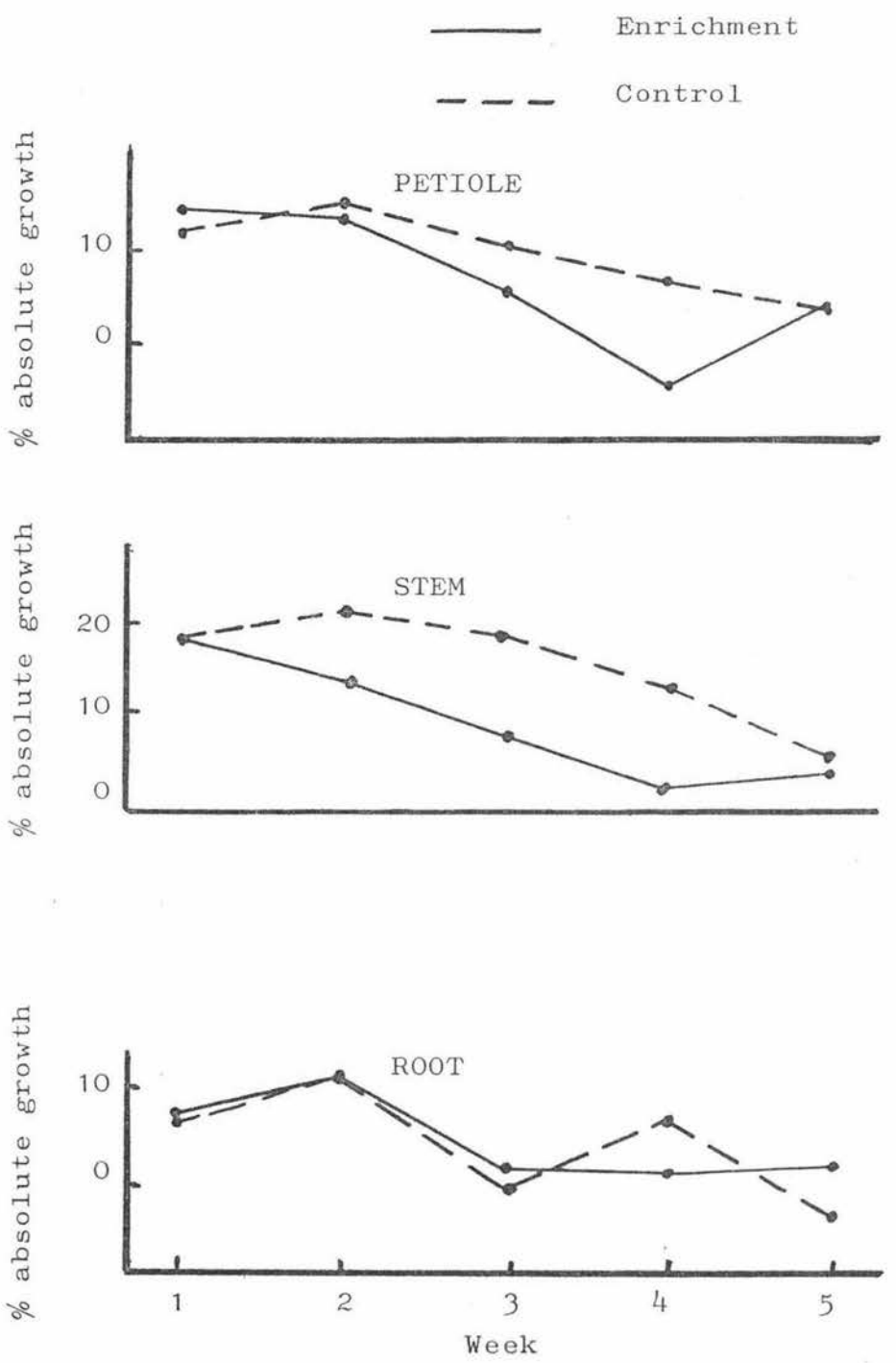

Fig. 6.2 Per cent absolute growth partitioned into petioles, stem and roots in each week

Table 6.2 Partitioning of the absolute growth (%).

	Week	1	2	3	4	5
Control						
	Fruit	6.3	24.8	45.9	49.0	72.8
	Leaf	57.2	28.6	25.8	24.5	21.5
	Petiole	12.2	14.8	10.3	6.2	3.9
	Stem	18.6	20.9	18.8	13.8	5.7
	Root	5.6	10.9	-0.8	6.5	-3.9
Enrichment						
	Fruit	5.7	16.9	94.9	96.0	69.9
	Leaf	56.2	46.3	-9.1	6.0	20.3
	Petiole	13.4	13.1	6.2	-4.8	4.0
	Stem	18.1	13.4	7.6	2.3	4.4
	Root	6.7	10.4	0.4	0.5	1.5

6.3.4 Fruit data

6.3.4.1 Fruit growth and set

The absolute growth rate and the relative growth rate of the fruit was greater with enrichment for each week (Table 6.1 and 6.3).

Table 6.3 Relative growth rate of the fruit (g/g/day).

Week	1	2	3	4	5
Control	0.307	0.195	0.109	0.061	0.055
Enrichment	0.326	0.234	0.186	0.094	0.084

There appeared to be little difference in the percentage fruit growth on nodes 1-10 over each weekly period except for week five. During this week little growth occurred on these nodes for the control plants (Table 6.4).

Table 6.4 Per cent absolute fruit growth in week 5 on nodes 1-10.

Week	1	2	3	4	5
Control	89.8	72.9	67.1	75.2	8.1
Enrichment	89.6	81.9	88.8	74.2	59.2

At harvest six the number and mean dry weight of fruit was greater with enrichment (Table 6.5). Fruit with a dry weight of one gram or greater was considered

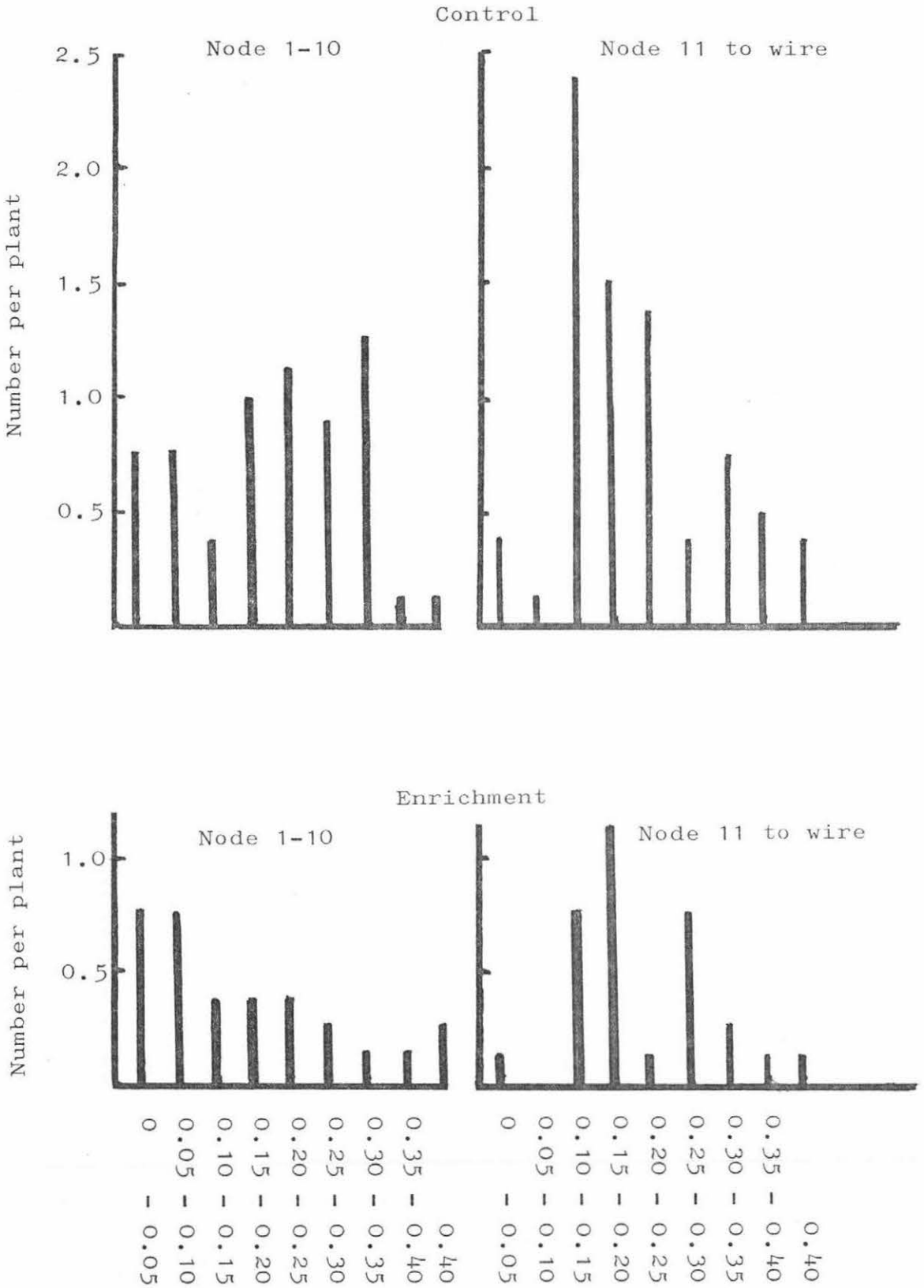

Fig. 6.3 Distribution of aborted fruit dry weight at harvest six with and without enrichment

as having set as abortion usually always occurred before this weight.

Table 6.5 Number and mean dry weight of fruit at harvest six.

	Number	Mean dry weight (g)
Control	4.5	5.7
Enrichment	9.9	6.9

6.3.4.2 Aborted fruit

The distribution of the size of the aborted fruit at harvest six for nodes 1-10 and 11 to the wire where the plants were stopped (mean 9.25 nodes for both treatments) is shown in Figure 6.3. On node 1-10 for the control plants most of the fruit aborted in the 0.15-0.35 g size but with enrichment most aborted at a smaller size. The number of aborted fruit in the small (< 0.15 g) and larger sizes (> 0.35 g) was not different between the two treatments. Also on nodes 11 to the wire there were more aborted fruit with the control plants than with enrichment, but there appeared to be little difference in the distribution of the sizes between the two treatments (Figure 6.3). At harvest six a greater dry weight and per cent fruit dry weight occurred in aborted fruit

with the control plants than the enriched (Table 6.6).

Table 6.6 Dry weight and per cent total fruit dry weight in aborted fruit at harvest six.

	Dry weight (g/plant)	Per cent total fruit dry weight
Control	3.0	10.8
Enrichment	1.7	2.5

6.3.5 Leaf data

The leaf area was greater at harvest three to six with enrichment, but the number of leaves (> 20 mm width) was very similar for the two treatments (Table 6.7). At harvest six the leaf area of leaf ten and fifteen, measured from the base of the plant, was greater with enrichment (Table 6.8).

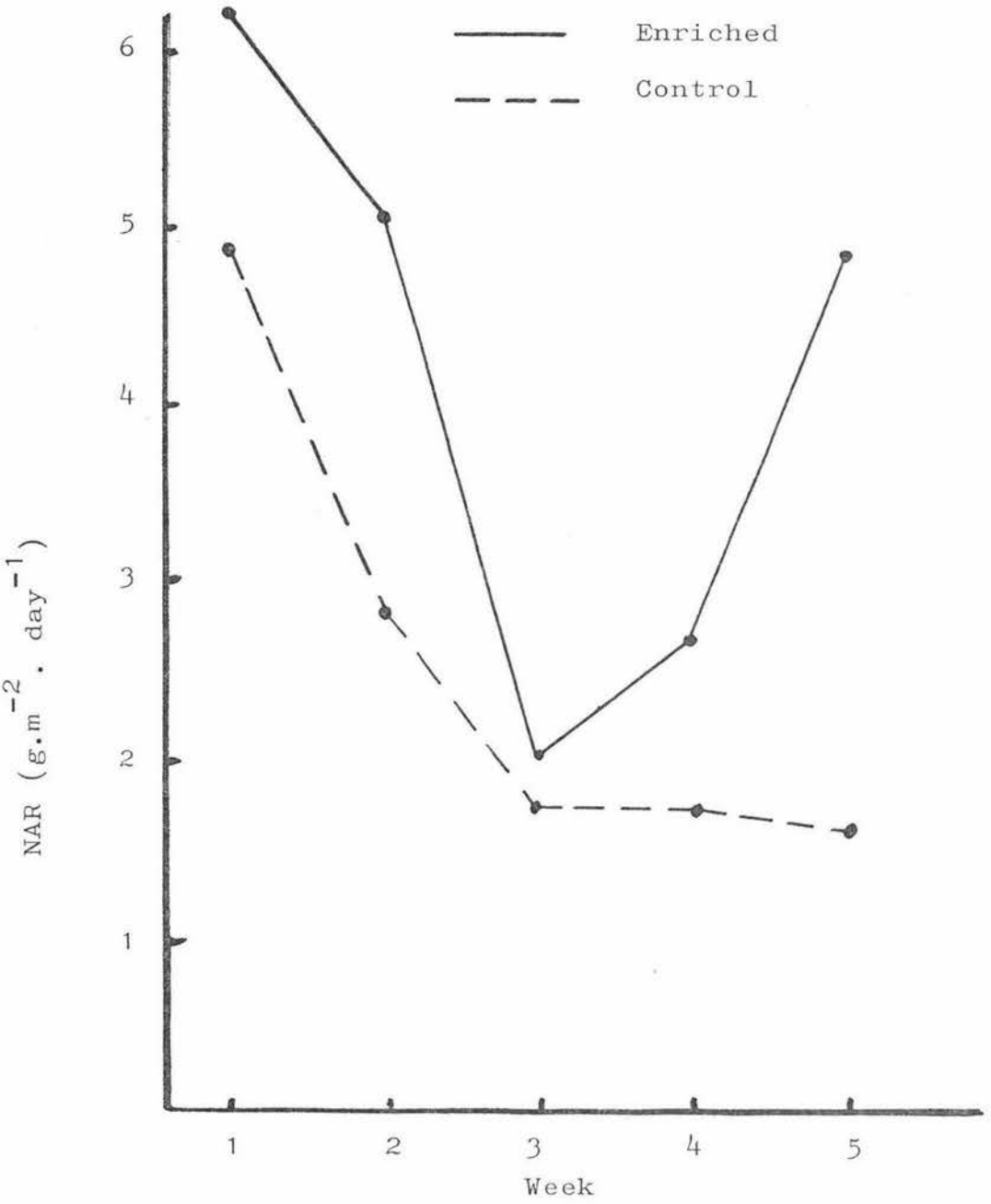

Fig. 6.4 Net assimilation rate in each week

Table 6.7 Leaf area and number of leaves per plant.

Harvest	1	2	3	4	5	6
Leaf Area (m^2).						
Control	0.34	0.58	0.93	1.15	1.27	1.39
Enrichment	0.31	0.60	1.31	1.34	1.48	1.57
Number of leaves.						
Control	11.1	16.0	19.7	25.9	32.2	36.2
Enrichment	11.0	16.2	19.9	25.8	30.1	33.9

Table 6.8 Leaf area of individual leaves at harvest six (cm^2/plant)

	Leaf 10	Leaf 15
Control	634	556
Enrichment	758	746

The NAR of the control plants declined markedly until week 3 and then levelled off. However the NAR for the enriched plants, declined until week three and then increased to a level three times the control plants on week five (Table 6.9 and Figure 6.4).

Table 6.9 Net assimilation rate ($g/m^2/day$).

Week	1	2	3	4	5
Including senescing leaves					
Control	4.80	2.82	1.65	1.57	1.41
Enrichment	6.24	5.02	1.89	2.44	4.57
Excluding senescing leaves					
Control	4.80	2.82	1.67	1.65	1.55
Enrichment	6.24	5.02	1.97	2.62	4.79

6.3.6 Stem data

The stem length per plant was very similar for the two treatments at each harvest but the stem dry weight per length was greater with enrichment (Table 6.10).

Table 6.10 Stem length and stem weight per length for each harvest.

Harvest	1	2	3	4	5	6
Mean stem length (m)						
Control	0.85	1.40	1.93	2.71	3.42	3.73
Enrichment	0.77	1.35	1.90	2.52	3.17	3.69
Stem dry weight per length (g/m)						
Control	3.16	4.00	4.52	3.96	3.70	3.66
Enrichment	3.31	4.38	5.35	4.65	4.03	4.05

6.3.7 Redistribution of assimilates

During week 3 with the enriched plants there was a loss of leaf dry weight (Table 6.1) even though the leaf area increased (Table 6.7). Using the formula to determine leaf weight loss from existing leaves (6.2) it was calculated that the redistribution of assimilates would have contributed to 24% of the plants growth. With enrichment there was little increase in leaf area over this week so if the specific leaf weight of the new leaves was different it would have had little influence on this calculation.

6.4 Discussion

6.4.1 Absolute growth rate and partitioning.

As expected carbon dioxide enrichment increased the absolute growth rate of the total plant and the fruit over the five weeks (Table 6.1). However due to the partitioning of this growth between the component organs, the absolute growth rate of the vegetative organs was less in week three and four with enrichment (Table 6.1). In week two a smaller percentage of the absolute growth was partitioned into the fruit and more into the leaves with enrichment than for the control plant. The increase in leaf dry weight over week two was four-fold greater with enrichment than the control plants, however the increase in leaf area was only twice as great (Table 6.1 and 6.7). It appears as though the mobilising ability of the growing points was limiting plant growth and there was an accumulation of assimilates which may have caused the reduction in NAR (2.2.2).

In week three there was a reduction in leaf dry weight and in week four a small reduction in petiole dry weight. These reductions occurred even though the leaf area and number of leaves were still increasing slowly (Table 6.7 and 6.8). It appears that there was a redistribution of assimilates from the leaves and petioles to the fruit over these two weeks. This redistribution coincided with a large increase in the absolute fruit growth rate (Table 6.1). It is estimated that 24% of

the growth would have relied on stored assimilates. With enrichment the absolute fruit growth rate was even greater in week five but the per cent absolute growth partitioned into the fruit was reduced from 96.0 (week four) to 69.9 (Table 6.2). This suggests that the stored assimilates were depleted by this stage. Associated with this apparent depletion of stored assimilates was an increase in the NAR (Fig 6.4). With many of the grains there is a build up of reserves in the stem which are mobilized during the storage phase. These contribute to a relatively small proportion of the final grain yield, unless the plant is under stress (Evans, 1975). Also with soybean, temporary storage of carbohydrates occurs in the pod walls, which is later exported to the seeds (Thorne, 1978). Hughes and Cockshull (1969) observed some loss of leaf and stem dry weight as flowers matured on Chinese Aster. They concluded that stored assimilates were translocated from the stem or that no further imports occurred and the loss was due to respiration.

For the control plants the partitioning data does not suggest that there was a redistribution of assimilates. An increasing proportion was partitioned into the fruit and less to the vegetative organs over the five week period (Table 6.2).

The partitioning in week five was similar for the two treatments. Unfortunately this experiment did not continue to see if these figures were maintained over a

longer period. This is an indeterminate cucumber cultivar and presumably maintains a balance between vegetative and reproductive growth.

The root growth nearly ceased from week three onwards except in week five there appeared to be some growth with enrichment (Table 6.1). This reduction in root growth was associated with an increasing proportion of the absolute growth being partitioned to the fruit for both treatments (Table 6.2). Similarly Van der Post (1968) observed that root growth stopped when cucumber fruits were developing, but upon removal the root growth was stimulated again. Also with tomato plants, root growth ceased one month after anthesis, and renewed growth a month later only replaced roots which had died (Hurd and Gay, 1977).

6.4.2 Fruit data

There was a large loss of the fruit dry weight in aborted fruit for the control plants (Table 6.6). With enrichment it was less due to fewer fruit aborting, and on nodes 1-10 most of this fruit was in the smaller sizes compared to the control plants (figure 6.3). There appeared to be a critical stage the fruit had to reach to ensure fruit set, and this size was less on the lower nodes with enrichment. When fruit set was occurring on these nodes there was an abundant supply of assimilates.

Carbon dioxide enrichment increased the absolute fruit growth rate (Table 6.1) and the relative growth rate of the fruit (Table 6.3). The large reduction in the per cent fruit growth on nodes 1-10 in week five for the control plants, and little reduction for the enriched (Table 6.4) suggest that the reduction in partitioning to the fruit with enrichment from week four to week five (Table 6.2) was not due to the loss in growth ability of the older fruit. The suggestion that it is due to the redistribution of mobilizable carbohydrates appears to be more feasible (6.4.1).

Enrichment increased the number and size of fruit (Table 6.5). Yield of many crops is increased with carbon dioxide enrichment, but its effect on the components of yield varies between crops. With tomatoes the number and size of fruit was increased (Wittwer and Robb, 1964), but with eggplants and peppers the number of fruit was increased but the mean weight was little affected (Milhet and Costes, 1975). The number of musk melon fruit and total weight was increased but mean fruit weight was slightly reduced (Milhet and Costes, 1975). Similarly with soybean the number of seed was increased but the size was reduced (Hardman and Brun, 1971).

With a commercial greenhouse cucumber crop the fruit is harvested at a fixed size so only an effect on numbers is likely to be observed. Enrichment appeared not to influence the number of nodes or stem length (Table 6.10).

Therefore the number of fruit per node must have been greater with enrichment.

6.4.3 Leaf data

Carbon dioxide enrichment had little influence on the number of leaves per plant but increased the area of the leaves (Table 6.7 and 6.8). The NAR declined over the five week period for the control plants but with enrichment it declined over the first three weeks but markedly increased over the following two weeks. Generally the NAR decreases with ontogeny due to greater mutual shading and leaf ageing. The big reduction in NAR in week three and four with enrichment appeared to be due to an accumulation of assimilates in the leaves (6.4.1). Following its depletion the NAR increased.

6.5 Summary

The growth and partitioning of dry weight of cucumber plants maintained at ambient carbon dioxide levels in a greenhouse was compared with enrichment to 1000 ppm from early anthesis.

Carbon dioxide enrichment increased the absolute growth rate of the total plant and the fruit. During week three and four, with enrichment there was a loss of leaf and petiole dry weight even though the leaf area and numbers were still increasing. This loss may have been due to a redistribution of mobilizable reserves. The

partitioning in week five was very similar for the two treatments. Unfortunately this experiment was not continued for a longer period to see if these partitioning figures were maintained over a longer period.

The NAR was greater with carbon dioxide enrichment in every week. It declined over the first three weeks for the control and enriched plants, and for the control plants there was little difference between weeks three, four and five. However with enrichment the NAR increased from week three. This coincided with an apparent redistribution of stored assimilates.

Fruit set and to a lesser extent, size, was increased with enrichment. The aborted fruit were smaller on the lower nodes with enrichment. The critical stage the fruit had to reach to ensure fruit set appeared to be smaller with an abundant supply of assimilates. Enrichment did not appear to influence the stem length or number of leaves but the leaf area was increased. Little root growth occurred from week three onwards which was associated with a marked increase in the fruit growth.

CHAPTER SEVEN

SOURCE-SINK RELATIONSHIPS IN THE CUCUMBER PLANT

7.1 Partitioning of dry weight

The partitioning of dry weight between the component organs is an important factor influencing crop yield (Evans, 1975; Duncan, McCloud, McGraw and Boote, 1978). However there is little information in the literature about partitioning for indeterminate crops and the variation that occurs between cultivars and with different environmental conditions.

The per cent partitioning of dry weight in the young fruiting cucumber plant was little affected by a range of treatments (growth substances, deleafing, shading and carbon dioxide enrichment). Although TIBA and chlorflurenol had a marked effect on leaf production and stem elongation, per cent partitioning was little affected. The main effect was a reduction in the proportion partitioned into the stem with growth substance application to the whole plant. With the application of TIBA to the fruit, fruit set was reduced on the lower nodes and this reduced the fruit dry weight and partitioning to the fruit (3.3.3). Fruit set was greater on the higher nodes (3.4.2) thus establishing the apparently fixed ratio between the component organs.

Similarly with various degrees of leaf removal the partitioning of the dry weight between the component organs was little affected. With beans (Brouwer, 1962), sugar beet (Fick, Williams and Loomis, 1971) and carrots (Stanhill, 1977), the plant restored the balance between the component organs following leaf and root pruning. In the cucumber deleafing experiment the leaves were removed before they expanded but still the plant maintained a balance between the component organs (4.3.4). However with the severest degree of leaf removal a greater percentage was partitioned into the stem and less into the fruit. The plant continued to develop a basic structural framework and the number of nodes was not altered by the leaf removal treatments. The percentage partitioned into the leaves was not altered. Denna (1973) concluded that the cucumber plant possesses a regulatory mechanism that controls the proportion of the dry weight that can be devoted to fruit and seed production. When he compared parthenocarpic fruit development with fertilised fruits, seed dry weight accummulated at the expense of fruit rather than vine growth. With deleafing partitioning to the stem was at the expense of partitioning to the fruit rather than to the leaves. It appears that the cucumber's regulatory mechanism ensures the per cent partitioning to the leaves is maintained.

Shading up to 58% for a two week period did not alter the partitioning of the absolute growth on a cucumber

plant that had developed several medium sized fruit (5.3.2). However the partitioning to the fruit was reduced when the shading was increased to 70%. When assimilate supply is low vegetative growth appears to have a greater priority than the fruit. The mean outdoor daily solar radiation during this period (early October) was 4948 w.h.r.m^{-2}. During the winter months the mean outdoor solar radiation would sometimes be less than 70% of this in N.Z. Therefore the partitioning to the fruit may be reduced during the winter months unless this was an adaptive response to the sudden reduction in irradiance.

With carbon dioxide enrichment from first anthesis the partitioning in the first week was not different to the control plants (6.3.3). However in week two, three and four the partitioning was quite different. In week two there appeared to be an accumulation of assimilates in the leaves due to the mobilising ability of the growing regions being insufficient for the higher rate of photosynthesis. Following this accumulation there was a reduction in the NAR. In week three and four the mobilising ability of the growing regions increased and there appeared to be a redistribution of stored assimilates from the leaves and petioles. Following this apparent redistribution of assimilates the NAR recovered (Figure 6.4). Many workers have observed a correlation between the accumulation of carbohydrates in leaves and the rate

of photosynthesis. However the idea of a direct feedback system in controlling the rate of photosynthesis has been criticised (2.2.2).

Other workers have also observed net dry matter transfer from other organs to the fruit (Hughes and Cockshull, 1971; Incolls and Neales, 1970; Moorby, 1970). However Hall (1977) did not detect any net transfer of dry matter from other organs to the fruit in pepper plants even though the fruit was the major sink. Ho (1979) observed a loss of up to one-sixth the leaf's carbon within twentyfour hours when tomato leaves were exposed to low levels of irradiance. Similarly at low rates of assimilation in week three and four with enrichment there was a loss of stored assimilates.

For the control plants the per cent absolute growth partitioned into the fruit increased from first anthesis to 73% five weeks later. However with the enriched plants in week three it was 95% due to a redistribution of assimilates from the leaves (6.4.1). In the fifth week it decreased to 70%. By the fifth week the whole plant appeared to have adapted to the new environment. Unfortunately this experiment was not continued for several weeks longer to see if the plants maintained these partitioning figures.

The partitioning of the absolute growth in the fifth week with and without enrichment (Chapter 6) and with the various shading treatments (Chapter 5) for plants at a

similar stage of development was about 70% into the fruit, 23% into the leaves, 6% into the stem and 1% into the roots. For an indeterminate crop, once a fruit load is established on a plant and this is not removed, it is likely that the partitioning of the absolute growth between the component organs will not change. New sinks will constantly develop on the plant to replace older ones.

The cucumber plant appears to possess a regulatory mechanism that maintains the partitioning of dry weight between vegetative and reproductive growth constant under a wide range of environmental conditions that alter the supply of assimilates.

7.2 Source or sink limitation

With an increase in irradiance and with carbon dioxide enrichment the cucumber plants growth rate and the growth rate of the fruit was increased (5.3.2 and 6.3.2). This shows that under these environmental conditions the plant was source limited (Fischer and Wilson, 1975; Fisher, 1978).

A reduction in partitioning to the fruit with higher rates of assimilation would suggest that the mobilising ability of the fruit may be limiting yield (Gifford, Bremner and Jones, 1973; Fischer and Wilson, 1975). In the second week of carbon dioxide enrichment the percentage partitioned into the fruit was less with enrichment than

for the control plants (6.3.3). This appeared to be due to an accumulation of assimilates in the leaves due to the limited mobilising ability of the growing regions. If the plants had been given enrichment from an earlier stage the mobilising ability of the growing regions may have been greater as this is likely to be partially determined by the environment they developed under (enrichment was applied from first anthesis).

In the third week the partitioning to the fruit was greater with enrichment (95%) than for the control plants (46%) (6.3.3). It appears that following an adaption period the mobilising ability of the growing regions increased so that by week five all the available photosynthates were utilised. The bulk of the stored assimilates are separated from the transport system and current assimilates are utilised first (Wardlaw, 1976). The depression of the NAR allowed the stored assimilates to be utilised.

When the plant had developed several medium sized fruit it was able to partition about 70% of the absolute growth into the fruit with no shading (Chapter 5) and with carbon dioxide enrichment (Chapter 6). At these higher rates of assimilation the percentage partitioned into the fruit was not reduced. The ability of the plant to partition 70% of the absolute growth into the fruit under these environmental conditions does not imply that this proportion can be maintained at higher rates of

assimilation. However this is a gynoecious cultivar, so there is a potential fruit site at nearly every node. The maximum fruit set occurred on the lower nodes with 50% of the nodes having a fruit (3.4.2 and 5.3.4.1). However many of these nodes would have had several flowers but only one flower set at each node. Therefore this cultivar has many potential fruit sites and with greater assimilate supply fruit set will increase and should be capable of utilising the greater supply.

The method devised by Gifford et al (1973) or Fischer and Wilson (1975) to determine sink or source limitation (2.3.2) cannot be used for indeterminate plants as it is essential that vegetative growth continues. If all of the absolute growth is partitioned into the fruit then according to those methods the plant is not sink limited. However if some growth is partitioned into the vegetative organs then the crop is considered to be partially sink limited. During week three and four 95% - 96% of the absolute growth was partitioned into the fruit (6.3.3). According to Gifford et al's scale the plant would mainly be source limited and not sink limited. In week 5, 70% of the absolute growth was partitioned into the fruit due to some growth of vegetative organs. This is essential for an indeterminate crop that is harvested over several months as new leaves are required to supply assimilates for the fruit that develops later as the efficiency of leaves falls soon after full expansion (Hopkinson, 1964).

These experiments show that source is limiting yield of this cultivar.

To determine if sink is limiting yield, some method of altering sink strength is required and studying this effect over several months, as increased sink strength will reduce vegetative growth and may increase fruit yield over the first month but due to the reduced vegetative growth, yield may be lower in the following month (Anon, 1969; Denna, 1973).

Increasing the activity of the fruit would increase the competitive ability of the fruit and presumably increase the partitioning to the fruit. For an indeterminate plant the important factor is the partitioning between the fruit and vegetative organs and it is necessary to determine the optimum proportion to partition into the fruit to maximise yield. There is little information in the literature about the proportion indeterminate plants partition into the fruit and what is the optimum proportion. The optimum proportion may vary with environmental conditions that effect the assimilation rate (e.g. level of irradiance, carbon dioxide concentration).

In the above discussion the optimum proportion is in relation to fruit yield. The partitioning of dry matter for plants in the wild is likely to be quite different as their strategy is to survive (Bidwell, 1979).

7.3 Fruit set

A reduction in the supply of assimilates by leaf removal or shading reduced the size of the fruit and fruit set (number). An increase in assimilate supply by carbon dioxide enrichment increased the fruit size and fruit set. There appeared to be a critical stage the fruit had to reach to ensure fruit set (less than 0.5 g dry weight). On the lower nodes, with CO_2 enrichment, this size was less than for the control plants, but this pattern did not occur on the higher nodes (Figure 6.3). The abundant supply of assimilates appears to have reduced the critical stage necessary to ensure fruit set. On the higher nodes when fruit set was occurring, competition for assimilates would have been greater due to increased fruit growth.

Even though with enrichment there appeared to be an accumulation of assimilates in the first two weeks following anthesis, some abortion occurred on the lower nodes.

The mobilising ability of these young fruit appears to be very low. Alternatively the ability of these sinks to attract assimilates may be limited by poor development of the vascular strands. Therefore the resistance to carbohydrate transport into the young fruit would be high. An abundant supply of assimilates may be capable of overcoming this resistance. Several reports suggest that in some circumstances the transport system may restrict

transfer of assimilates from source to sink (Geiger, Saunders and Cataldo, 1969; Jenner, 1974).

A reduction in fruit set on the lower nodes with TIBA application to the fruit (3.4.2) was compensated by greater fruit set on the higher nodes. This reduction in fruit set may have reduced competition for assimilates thus allowing greater fruit set on higher nodes. Alternatively the fruit may produce an inhibitory factor or use up a promotory factor, and with less fruit set on the lower nodes greater fruit set occurs on the higher nodes as less inhibitory factor would be produced or less promotory factor would be used up. With leaf removal most of the fruit developed at nodes with a leaf (4.3.5.1). This may have been due to the close proximity of a source of assimilates or the supply of a factor from the subtending leaf.

In all of the experiments it was noticed that the plant set three to four fruit on consecutive nodes on the lower nodes, and then for several nodes the fruit aborted. The plant appeared to set fruit in flushes and this was more marked with a greater degree of leaf removal (4.3.5.2). With distance the competition for assimilates may be less. Alternatively the fruit may produce an inhibitory factor or consume a promotory factor and the effect of this factor is less with distance.

High auxin levels in the ovary appear to be responsible for parthenocarpic fruit development in

cucumber plants (Rudich, Halevy and Kedar, 1972; Beyer and Quebedeaux, 1974). However why some ovaries cease growing and others develop into fruit is unknown, but is presumably associated with the regulatory mechanism that limits the percentage of the plants dry matter that can be devoted to fruit.

7.4 Distribution of fruit growth on various nodes

In the shading experiment (Chapter 5) with up to 58% shading most of the fruit growth was on the lower nodes. Sink size appears to have determined where the growth occurred at these rates of assimilation. However with the severest shading treatment (70%) little fruit growth occurred on the lower nodes. Similarly in the carbon dioxide experiment (Chapter 6) for the control plants in the fifth week little fruit growth occurred on the lower nodes, whereas with enrichment most of the fruit growth was still on the lower nodes. In these two instances the lower leaves were probably near the compensation point. It appears that at a low rate of assimilation the growth of individual fruit ceases at an earlier stage and this may be due to the proximity of the source of assimilates. Similarly Bremner and Rawson (1978) concluded that the major influence on the weight of grains within a spikelet was the relative ease with which assimilates could reach the grains, and the potential for growth seemed to play only a minor role.

7.5 Conclusion

The partitioning of dry matter is an important factor influencing fruit yield. From the present investigation it is clear that the cucumber plant possesses a regulatory mechanism that maintains the partitioning of dry matter between vegetative and reproductive growth constant under a wide range of treatments that alter the supply of assimilates. However the per cent partitioned into the fruit was less at low rates of assimilation. Further studies are required to see if there is a redistribution of dry matter in the early stages of fruit growth when the plant has a high rate of assimilation as occurred with carbon dioxide enrichment, or whether this was an adaptive response due to the plants only receiving enrichment from first anthesis.

Studies are also necessary to determine the optimum proportion to partition into the fruit in cucumber plants and other indeterminate crops to obtain maximum fruit yield. Also work is required to see if the optimum proportion is the same under a wide range of assimilation rates. The plants regulatory mechanism controls the proportion partitioned into the fruit by controlling the fruit set and growth. One simple way to reduce the partitioning to the fruit would be to reduce fruit set by removing flowers and leaving various numbers of fruit to develop on the plants. However increasing partitioning to the fruit is more difficult. Also investigations

are necessary to determine the mechanism that controls the degree of fruit set.

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44. Analysis of variance of number of male nodes on nodes 1-4.

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46. Analysis of variance of number of male nodes on nodes 9-12.

47. Analysis of variance of number of male nodes on nodes 13-16.

48. Analysis of variance of number of male nodes on nodes 17-20.

49. Analysis of variance of number of male nodes on nodes 21-24.

50. Analysis of variance of leaf dry weight.

51. Analysis of variance of total plant dry weight.

Appendix 1

Nutrient Solution.

Salt	Formula	g/100 l
Potassium nitrate	KNO_3	65.8
Calcium nitrate	$Ca(NO_3)_2 \cdot 4H_2O$	98.8
Magnesium sulphate	$Mg\ SO_4 \cdot 7H_2O$	49.7
Potassium phosphate	$K\ H_2\ PO_4 \cdot 2H_2O$	27.2
Iron chelate	Fe Na EDTA	7.888
Manganous sulphate	$Mn\ SO_4\ 4H_2O$	0.6154
Boric acid	$H_3\ BO_3$	0.1714
Copper sulphate	$Cu\ SO_4 \cdot 5H_2O$	0.0275
Zinc sulphate	$Zn\ SO_4 \cdot 7H_2O$	0.0308
Ammonium molybdate	$(NH_4)_6\ Mo_7O_{24} \cdot 4H_2O$	0.0092

Appendix 2

Analysis of variance of fruit dry weight.

Source	SS	df	MS	F	Result
Blocks	1,238	3	413	5.28	* *
Growth substance	366	1	366	4.69	*
Rate	51	2	26	0.33	n.s.
Site	493	1	493	6.31	*
GxR	294	2	147	1.88	n.s.
GxS	245	1	245	3.14	n.s.
SxR	293	2	147	1.88	n.s.
GxRxS	64	2	32	0.41	n.s.
Error	2,577	33	78		
Total	5,621	47			

Appendix 3

Analysis of variance of total plant dry weight.

Source	SS	df	MS	F	Result
Blocks	1,437	3	479	4.06	*
Growth substance	265	1	265	2.24	n.s.
Rate	1,237	2	618	5.24	* *
Site	4,798	1	4,798	4.07	n.s.
GxR	564	2	282	2.39	n.s.
GxS	248	1	248	2.10	n.s.
SxR	1,912	2	956	8.11	* *
GxRxS	97	2	49	0.39	n.s.
Error	3,892	33	118		
Total	14,450	47			

Appendix 4

Analysis of variance of leaf dry weight.

Source	SS	df	MS	F	Result
Blocks	41	3	14	1.09	n.s.
Growth substance	7	1	7	0.53	n.s.
Rate	289	2	145	11.57	* *
Site	783	1	783	62.60	* *
GxR	20	2	10	0.79	n.s.
GxS	2	1	2	0.14	n.s.
SxR	305	2	152	12.19	* *
GxRxS	14	2	7	0.57	n.s.
Error	411	33	12.5		
Total	1872	47			

Appendix 5

Analysis of variance of stem dry weight.

Source	SS	df	MS	F	Result
Blocks	7.39	3	2.46	4.76	* *
Growth substance	2.52	1	2.52	4.87	*
Rate	59.49	2	29.75	57.54	* *
Site	151.23	1	151.23	292.51	* *
GxR	0.05	2	0.03	0.05	n.s.
GxS	0.19	1	0.19	0.37	n.s.
SxR	57.21	2	23.61	45.67	* *
GxRxS	0.73	2	0.37	0.72	n.s.
Error	17.07	33	0.52		
Total	295.88	47			

Appendix 6

Analysis of variance of root dry weight.

Source	SS	df	MS	F	Result
Blocks	3.25	3	1.08	0.74	n.s.
Growth substance	3.31	1	2.31	1.58	n.s.
Rate	11.86	2	5.93	4.06	*
Site	42.56	1	42.56	29.15	* *
GxR	5.76	2	2.88	2.05	n.s.
GxS	0.27	1	0.27	0.33	n.s.
SxR	9.61	2	4.81	3.29	*
GxSxR	0.09	2	0.05	0.03	n.s.
Error	48.21	33	1.46		
Total	124.13	47			

Appendix 7

Analysis of variance of percent plant dry weight in roots.

Source	SS	df	MS	F	Result
Blocks	12.54	3	4.18	3.07	* *
Growth substance	0.66	1	0.66	0.49	n.s.
Rate	3.14	2	1.57	1.15	n.s.
Site	13.23	1	13.23	9.73	* *
GxR	2.44	2	1.22	0.90	n.s.
GxS	2.43	1	2.43	1.79	n.s.
SxR	3.52	2	1.76	1.29	n.s.
GxRxS	1.10	2	0.55	0.40	n.s.
Error	44.72	33	1.36		
Total	83.78	47			

Appendix 8

Analysis of variance of percent plant dry weight in fruit.

Source	SS	df	MS	F	Result
Blocks	104.80	3	34.93	4.80	* *
Growth substance	49.41	1	49.41	6.80	* *
Rate	18.34	2	9.17	1.26	n.s.
Site	20.94	1	20.94	2.88	n.s.
GxR	10.69	2	5.35	0.74	n.s.
GxS	22.82	1	22.82	3.14	n.s.
SxR	11.86	2	5.93	0.82	n.s.
GxRxS	4.81	2	2.41	0.33	n.s.
Error	240.00	33	7.27		
Total	483.67	47			

Appendix 9

Analysis of variance of percent plant dry weight in leaves.

Source	SS	df	MS	F	Result
Blocks	54.47	3	18.16	6.16	* *
Growth substance	45.83	1	45.83	15.54	* *
Rate	4.51	2	2.26	0.77	n.s.
Site	1.17	1	1.17	0.40	n.s.
GxR	0.48	2	0.24	0.08	n.s.
GxS	17.88	1	17.88	6.06	* *
SxR	12.64	2	6.32	2.14	n.s.
GxRxS	11.07	2	5.54	1.88	n.s.
Error	97.24	33	2.95		
Total	245.29	47			

Appendix 10

Analysis of variance of percent dry weight in stem.

Source	SS	df	MS	F	Result
Blocks	23.34	3	7.78	6.48	* *
Growth substance	8.84	1	8.84	7.37	* *
Rate	14.98	2	7.49	6.24	* *
Site	24.37	1	24.37	20.31	* *
GxR	4.66	2	2.33	1.94	n.s.
GxS	2.90	1	1.45	1.21	n.s.
SxR	9.91	2	4.96	4.13	* *
GxRxS	3.06	2	1.53	1.28	n.s.
Error	39.67	33	1.20		
Total	131.73	47			

Appendix 11

Analysis of variance of fruit set on nodes 1-8.

Source	SS	df	MS	F	Result
Blocks	1.11	3	0.33	0.52	n.s.
Growth substance	5.33	1	5.33	8.32	* *
Rate	4.20	2	2.20	3.43	*
Site	21.33	1	21.33	33.28	* *
GxR	1.08	2	0.54	0.84	n.s.
GxS	7.55	1	7.55	11.78	* *
SxR	5.99	2	3.00	4.67	*
GxRxS	3.75	2	1.88	2.93	n.s.
Error	21.14	33	0.64		
Total	71.48	47			

Appendix 12

Analysis of variance of fruit set on nodes 3-5

Source	SS	df	MS	F	Result
Blocks	0.9	3	0.30	0.94	n.s.
Growth substance	0.4	1	0.40	1.25	n.s.
Rate	3.9	2	1.95	6.09	*
Site	1.4	1	1.40	4.38	*
GxR	0	2	0	0	n.s.
GxS	2.0	1	2.00	6.25	*
SxR	0	2	0	0	n.s.
GxRxS	1.0	2	0.50	1.56	n.s.
Error	10.6	33	0.32		
Total	20.2	47			

Appendix 13

Analysis of variance of fruit set on nodes 6-8.

Source	SS	df	MS	F	Result
Blocks	1.27	3	0.42	1.21	n.s.
Growth substance	2.08	1	2.08	5.93	*
Rate	12.79	2	6.40	18.19	* *
Site	4.08	1	4.08	11.61	* *
GxR	1.79	2	0.90	2.55	n.s.
GxS	1.02	1	1.02	2.90	n.s.
SxR	5.79	2	2.90	8.24	* *
GxSxR	0.54	2	0.27	0.77	n.s.
Error	11.60	33	0.35		
Total	40.98	47			

Appendix 14

Analysis of variance of fruit set on nodes 9-16.

Source	SS	df	MS	F	Result
Blocks	10.94	3	3.65	22.81	* *
Growth substance	0.08	1	0.08	0.50	n.s.
Rate	1.64	2	0.82	5.13	*
Site	8.33	1	8.33	52.06	* *
GxR	0.82	2	0.41	2.56	n.s.
GxS	1.70	1	1.70	10.62	* *
SxR	0.95	2	0.48	3.00	n.s.
GxRxS	2.84	2	1.42	8.87	* *
Error	5.18	33	0.16		
Total	32.48	47			

Appendix 15

Analysis of variance of mean fruit dry weight.

Source	SS	df	MS	F	Result
Blocks	35.81	3	11.94	4.87	* *
Growth substance	2.71	1	2.71	1.11	n.s.
Rate	13.39	2	6.70	2.73	n.s.
Site	19.00	1	19.00	7.76	* *
GxR	15.43	2	7.72	3.15	n.s.
GxS	0.12	1	0.12	0.05	n.s.
SxR	2.48	2	1.24	0.51	n.s.
GxRxS	2.89	2	1.45	0.59	n.s.
Error	80.93	33	2.45		
Total	172.76	47			

Appendix 16

Analysis of variance of percent fruit dry weight on nodes 1-8.

Source	SS	df	MS	F	Result
Blocks	462	3	154	1.24	n.s.
Growth substance	150	1	150	1.21	n.s.
Rate	881	2	441	3.55	*
Site	2312	1	2312	18.63	* *
GxR	287	2	143	1.16	n.s.
GxS	441	1	441	3.55	n.s.
SxR	983	2	491	3.96	n.s.
GxRxS	1151	2	575	4.64	*
Error	4094	33	124		
Total	10761	47			

Appendix 17

Analysis of variance of percent fruit dry weight on nodes 9-16.

Source	SS	df	MS	F	Result
Blocks	281	3	94	1.25	n.s.
Growth substance	60	1	60	0.80	n.s.
Rate	713	2	356	4.75	*
Site	995	1	995	13.27	* *
GxR	220	2	110	1.47	n.s.
GxS	321	1	321	4.28	*
SxR	120	2	60	0.80	n.s.
GxRxS	551	2	276	3.68	*
Error	2474	33	75		
Total	5735	47			

Appendix 18

Analysis of variance of per cent fruit dry weight on nodes 3-5.

Source	SS	df	MS	F	Result
Blocks	119.93	3	39.98	0.97	n.s.
Growth substance	7.60	1	7.60	0.18	n.s.
Rate	2350.55	2	1265.28	30.79	* *
Site	0.16	1	0.16	0	n.s.
GxR	17.82	2	8.91	0.22	n.s.
GxS	38.53	1	38.53	0.94	n.s.
SxR	175.23	2	87.62	2.13	n.s.
GxRxS	191.49	2	95.75	2.33	n.s.
Error	1356.01	33	41.09		
Total	4437.32	47			

Appendix 19

Analysis of variance of per cent fruit dry weight on nodes 6-8.

Source	SS	df	MS	F	Result
Blocks	202.11	3	67.37	0.94	n.s.
Growth substances	180.58	1	180.58	2.51	n.s.
Rate	2154.63	2	1077.32	14.98	* *
Site	522.06	1	522.06	7.26	*
GxR	605.56	2	302.78	4.21	*
GxS	124.48	1	124.48	1.73	*
SxR	1394.24	2	697.12	9.69	* *
GxRxS	202.06	2	101.03	1.41	n.s.
Error	2373.14	33	71.91		
Total	7758.86	47			

Appendix 20

Analysis of variance of per cent fruit dry weight in misshapen fruit.

Source	SS	df	MS	F	Result
Blocks	733	3	244	1.87	n.s.
Growth substance	6	1	6	0.05	n.s.
Rate	10,954	2	5477	41.97	* *
Site	6,843	1	6843	52.44	* *
GxR	24	2	12	0.09	n.s.
GxS	163	1	163	1.25	n.s.
SxR	3,709	2	1855	14.21	* *
GxSxR	27	2	14	0.10	n.s.
Error	4,307	33	131		
Total	26,766	47			

Appendix 21

Analysis of variance of number of nodes.

Source	SS	df	MS	F	Result
Blocks	8.58	3	2.53	0.62	n.s.
Treatments	14.70	3	4.90	1.21	n.s.
Error	37.40	9	4.16		
Total	60.69	15			

Appendix 22

Analysis of variance of total plant dry weight.

Source	SS	df	MS	F	Result
Blocks	2,177	3	726	1.63	n.s.
Treatments	87,503	3	29,168	65.52	* *
Error	4,007	9	445		
Total	93,687	15			

Appendix 23

Analysis of variance of fruit dry weight.

Source	SS	df	MS	F	Result
Blocks	1,251	3	417	1.33	n.s.
Treatments	30,394	3	10,131	32.35	* *
Error	2,819	9	313		
Total	34,463	15			

Appendix 24

Analysis of variance of leaf dry weight.

Source	SS	df	MS	F	Result
Blocks	41	3	14	0.46	n.s.
Treatments	11,412	3	3,804	128.25	* *
Error	267	9	30		
Total	11,720	15			

Appendix 25

Analysis of variance of stem dry weight,

Source	SS	df	MS	F	Result
Blocks	47.05	3	15.68	3.42	n.s.
Treatments	70.39	3	23.46	7.82	* *
Error	41.22	9	4.58		
Total	158.66	15			

Appendix 26

Analysis of variance of root dry weight.

Source	SS	df	MS	F	Result
Blocks	0.78	3	0.26	0.59	n.s.
Treatments	50.99	3	17.00	38.64	* *
Error	3.95	9	0.44		
Total	55.72	15			

Appendix 27

Analysis of variance of number of fruit.

Source	SS	df	MS	F	Result
Blocks	11.19	3	3.73	0.85	n.s.
Treatments	145.69	3	48.56	11.05	* *
Error	39.56	9	4.40		
Total	196.44	15			

Appendix 28

Analysis of variance of mean fruit dry weight.

Source	SS	df	MS	F	Result
Blocks	0.29	3	0.10	0.06	n.s.
Treatments	35.66	3	11.89	7.37	* *
Error	14.51	9	1.61		
Total	50.46	15			

Appendix 29

Analysis of variance of per cent dry weight in fruit.

Source	SS	df	MS	F	Result
Blocks	7.97	3	2.66	1.04	n.s.
Treatments	105.24	3	35.08	13.70	* *
Error	23.01	9	2.56		
Total	136.22	15			

Appendix 30

Analysis of variance of per cent dry weight in leaves.

Source	SS	df	MS	F	Result
Blocks	4.96	3	1.65	0.99	n.s.
Treatments	6.14	3	2.05	1.24	n.s.
Error	14.90	9	1.66		
Total	26.00	15			

Appendix 31

Analysis of variance of percent dry weight in stem,

Source	SS	df	MS	F	Result
Blocks	1.84	3	0.61	0.97	n.s.
Treatments	113.59	3	37.87	60.11	* *
Error	5.65	9	0.63		
Total	121.08	15			

Appendix 32

Analysis of variance of per cent plant dry weight in roots.

Source	SS	df	MS	F	Result
Blocks	1.13	3	0.38	1.65	n.s.
Treatments	8.19	3	2.73	11.87	* *
Error	2.08	9	0.23		
Total	11.40	15			

Appendix 33

Analysis of variance of per cent fruit on nodes with a leaf.

Source	SS	df	MS	F	Result
Blocks	252.15	3	84.05	2.52	n.s.
Treatments	1254.00	2	627.00	18.83	* *
Error	199.74	6	33.29		
Total	1705.89	11			

Appendix 34

Analysis of variance of per cent fruit dry weight on nodes 5-8.

Source	SS	df	MS	F	Result
Blocks	185.34	3	61.78	0.88	n.s.
Treatments	256.12	3	85.37	1.22	n.s.
Error	630.33	9	70.04		
Total	1071.78	15			

Appendix 35

Analysis of variance of per cent fruit dry weight on nodes 9-12.

Source	SS	df	MS	F	Result
Blocks	828.15	3	276.05	2.28	n.s.
Treatments	121.49	3	40.50	0.33	n.s.
Error	1091.48	9	121.28		
Total	2041.12	15			

Appendix 36

Analysis of variance of per cent fruit dry weight on nodes 13-16.

Source	SS	df	MS	F	Result
Blocks	135.89	3	45.30	n.s.	
Treatments	775.74	3	258.58	*	
Error	577.24	9	64.14		
Total	1488.86	15			

Appendix 37

Analysis of variance of per cent fruit dry weight on nodes 17-20.

Source	SS	df	MS	F	Result
Blocks	43.24	3	14.41	0.10	n.s.
Treatments	722.32	3	240.77	1.66	n.s.
Error	1308.04	9	145.34		
Total	2073.59	15			

Appendix 38

Analysis of variance of per cent fruit dry weight on nodes 21 and above.

Source	SS	df	MS	F	Result
Blocks	185.42	3	61.81	0.89	n.s.
Treatments	7.01	3	2.34	0.03	n.s.
Error	618.97	9	68.77		
Total	811.48	15			

Appendix 39

Analysis of variance of fruit numbers on nodes 5-8.

Source	SS	df	MS	F	Result
Blocks	1.25	3	0.42	0.37	n.s.
Treatments	15.25	3	5.08	4.47	*
Error	10.24	9	1.14		
Total	26.73	15			

Appendix 40

Analysis of variance of fruit numbers on nodes 9-12.

Source	SS	df	MS	F	Result
Blocks	29.49	3	9.83	3.88	*
Treatments	10.79	3	3.60	1.42	n.s.
Error	22.78	9	2.53		
Total	63.06	15			

Appendix 41

Analysis of variance of fruit numbers on nodes 13-16.

Source	SS	df	MS	F	Result
Blocks	2.22	3	0.74	0.68	n.s.
Treatments	12.36	3	4.12	3.80	n.s.
Error	9.75	9	1.08		
Total	24.33	15			

Appendix 42

Analysis of variance of fruit numbers on nodes 17-20.

Source	SS	df	MS	F	Result
Blocks	4.19	3	1.40	0.68	n.s.
Treatments	0.23	3	0.08	0.04	n.s.
Error	18.50	9	2.06		
Total	22.92	15			

Appendix 43

Analysis of variance of fruit numbers on nodes 21 and above.

Source	SS	df	MS	F	Result
Blocks	346.94	3	115.65	1.05	n.s.
Treatments	261.43	3	87.14	0.79	n.s.
Error	993.43	9	110.38		
Total	1601.80	15			

Appendix 44

Analysis of variance of number of male nodes on nodes 1-4.

Source	SS	df	MS	F	Result
Blocks	14.75	3	4.92	3.11	n.s.
Treatments	0.75	3	0.25	0.16	n.s.
Error	14.25	9	1.58		
Total	29.75	15			

Appendix 45

Analysis of variance of number of male nodes on nodes 5-8.

Source	SS	df	MS	F	Result
Blocks	6.69	3	2.23	3.05	n.s.
Treatments	4.69	3	1.56	2.14	n.s.
Error	6.56	9	0.73		
Total	17.94	15			

Appendix 46

Analysis of variance of number of male nodes on nodes 9-12.

Source	SS	df	MS	F	Result
Blocks	2.19	3	0.73	1.52	n.s.
Treatments	3.44	3	1.15	2.40	n.s.
Error	4.31	9	0.48		
Total	9.94	15	0.66		

Appendix 47

Analysis of variance of number of male nodes on nodes 13-16.

Source	SS	df	MS	F	Result
Blocks	12.5	3	4.2	6.00	*
Treatments	159.5	3	53.2	7.60	* *
Error	63.0	9	7.0		
Total	235.0	15	15.7		

Appendix 48

Analysis of variance of number of male nodes on nodes 17-20.

Source	SS	df	MS	F	Result
Blocks	29.69	3	9.89	1.13	n.s.
Treatments	117.69	3	39.23	4.47	*
Error	79.06	9	8.78		
Total	226.44	15	15.10		

Appendix 49.

Analysis of variance of number of male nodes on nodes 21-24.

Source	SS	df	MS	F	Result
Blocks	0.69	3	0.23	1.00	n.s.
Treatments	1.69	3	0.56	2.43	n.s.
Error	2.06	9	0.23		
Total	4.44	15			

Appendix 50

Analysis of variance of leaf dry weight .

Source	SS	df	MS	F	Result
Blocks	6.61	2	3.30	1.95	n.s.
Harvest	1348.50	1	1348.50	797.93	* *
Shading	325.42	3	108.47	64.18	* *
HxS	13.08	3	4.36	2.58	n.s.
Error	23.66	14	1.69		
Total	1717.27	23			

Appendix 51.

Analysis of variance of total plant dry weight.

Source	SS	df	MS	F	Result
Blocks	0.90	2	0.45	0.04	n.s.
Harvest	20,732.88	1	20,732.88	1705.01	* *
Shading	4,866.64	3	1,622.21	133.41	* *
HxS	273.23	3	91.08	7.49	* *
Error	170.27	14	12.16		
Total	26,043.92	23			

Appendix 52

Analysis of variance of fruit dry weight.

Source	SS	df	MS	F	Result
Blocks	29.48	2	14.74	5.05	*
Harvest	1169.01	1	1169.01	400.34	* *
Shading	370.65	3	123.55	42.31	* *
HxS	57.80	3	19.27	6.60	* *
Error	40.92	14	2.92		
Total	1667.86	23			

Appendix 53

Analysis of variance of stem dry weight.

Source	SS	df	MS	F	Result
Blocks	4.25	2	2.12	5.05	*
Harvest	62.40	1	62.40	148.57	* *
Shading	4.73	3	1.58	3.76	*
HxS	4.30	3	1.43	3.40	*
Error	5.83	14	0.42		
Total	81.50	23			

Appendix 54

Analysis of variance of root dry weight.

Source	SS	df	MS	F	Result
Blocks	0.36	2	0.18	2.25	n.s.
Harvest	3.08	1	3.08	38.5	* *
Shading	2.30	3	0.77	9.63	* *
HxS	0.19	3	0.63	7.88	* *
Error	1.14	14	0.08		
Total	7.07	23	0.31		

Appendix 55

Analysis of variance of per cent dry weight in roots.

Source	SS	df	MS	F	Result
Blocks	1.66	2	0.83	3.95	*
Harvest	49.02	1	49.02	233.43	* *
Shading	5.24	3	1.75	8.33	* *
HxS	0.19	3	0.06	0.29	n.s.
Error	2.89	14	0.21		
Total	59.00	23			

Appendix 56

Analysis of variance of per cent dry weight in fruit.

Source	SS	df	MS	F	Result
Blocks	29.48	2	14.74	5.05	*
Harvest	1169.01	1	1169.01	400.34	* *
Shading	370.65	3	123.55	42.31	* *
HxS	57.80	3	19.27	6.60	* *
Error	40.92	14	2.92		
Total	1667.86	23			

Appendix 57

Analysis of variance of per cent dry weight in leaves.

Source	SS	df	MS	F	Result
Blocks	5.96	2	2.98	4.45	*
Harvest	467.28	1	467.28	697.43	* *
Shading	124.85	3	41.62	62.12	* *
HxS	11.68	3	3.89	5.81	* *
Error	9.35	14	0.67		
Total	619.12	23			

Appendix 58

Analysis of variance of per cent dry weight in stem .

Source	SS	df	MS	F	Result
Blocks	6.53	2	3.26	4.79	*
Harvest	119.71	1	119.71	176.04	* *
Shading	54.95	3	18.32	26.94	* *
HxS	7.93	3	2.64	3.88	*
Error	9.53	14	0.68		
Total	198.65	23			

Appendix 59

Analysis of variance of the absolute growth.

Source	SS	df	MS	F	Result
Blocks	34.53	2	17.27	2.79	n.s.
Treatments	3637.25	3	1212.42	195.55	* *
Error	37.27	6	6.21		
Total	3709.05	11			

Appendix 60

Analysis of variance of per cent absolute growth partitioned into fruit.

Source	SS	df	MS	F	Result
Blocks	26.75	2	13.38	1.76	n.s.
Treatments	155.72	3	51.91	6.83	* *
Error	45.60	6	7.60		
Total	228.07	11			

Appendix 61

Analysis of variance of per cent absolute growth partitioned into leaves.

Source	SS	df	MS	F	Result
Blocks	10.53	2	5.27	2.46	n.s.
Treatments	53.56	3	17.85	8.34	* *
Error	12.83	6	2.14		
Total	76.92	11			

Appendix 62

Analysis of variance of per cent absolute growth partitioned into stem.

Source	SS	df	MS	F	Result
Blocks	3.96	2	1.98	0.19	n.s.
Treatments	114.06	3	38.02	3.62	*
Error	62.95	6	10.49		
Total	180.97	11			

Appendix 63

Analysis of variance of per cent absolute growth partitioned into roots ,

Source	SS	df	NS	F	Result
Blocks	173.30	2	86.65	5.58	*
Treatments	25.46	3	8.49	0.55	n.s.
Error	93.17	6	15.53		
Total	291.93	11			

Appendix 64

Analysis of variance of fruit set on nodes 1-10.

Source	SS	df	MS	F	Result
Blocks	0.25	2	0.13	0.56	n.s.
Harvest	12.05	1	12.05	52.39	* *
Shading	8.51	3	2.84	12.35	* *
HxS	12.64	3	4.21	18.30	* *
Error	3.21	14	0.23		
Total	36.66	23			

Appendix 65

Analysis of variance of fruit set on nodes 11-20.

Source	SS	df	MS	F	Result
Blocks	1.88	2	0.94	3.03	n.s.
Harvest	15.44	1	15.44	49.81	* *
Shading	9.57	3	3.19	10.29	* *
HxS	0.82	3	0.27	0.87	n.s.
Error	4.29	14	0.31		
Total	32.00	23			

Appendix 66

Analysis of variance of per cent fruit dry weight on nodes 1-10.

Source	SS	df	MS	F	Result
Blocks	136.83	2	68.42	2.27	n.s.
Harvest	241.94	1	241.94	8.01	*
Shading	111.99	3	37.33	1.24	n.s.
HxS	842.66	3	280.89	9.30	* *
Error	422.76	14	30.20		
Total	1756.18	23			

Appendix 67

Analysis of variance of per cent fruit dry weight on nodes 11-20 .

Source	SS	df	MS	F	Result
Blocks	182.74	2	91.37	2.75	n.s.
Harvest	84.00	1	84.00	2.53	n.s.
Shading	170.75	3	56.92	1.71	n.s.
HxS	614.87	3	204.96	6.18	* *
Error	464.63	14	33.19		
Total	1516.99	23			

Appendix 68

Analysis of variance of per cent fruit dry weight on nodes 21 and above.

Source	SS	df	MS	F	Result
Blocks	39.34	2	19.67	0.66	n.s.
Harvest	333.76	1	333.76	11.18	* *
Shading	49.52	3	16.51	0.54	n.s.
HxS	235.99	3	78.66	2.64	n.s.
Error	417.93	14	29.85		
Total	1076.54	23			

Appendix 69

Analysis of variance of per cent absolute fruit growth on nodes 1-10 ,

Source	SS	df	MS	F	Result
Blocks	98.30	2	49.15	0.69	n.s.
Treatments	1080.96	3	360.32	5.06	*
Error	427.12	6	71.19		
Total	1606.38	11			

Appendix 70

Analysis of variance of per cent absolute fruit growth on nodes 11-20 .

Source	SS	df	MS	F	Result
Blocks	1.49	2	0.74	0.01	n.s.
Treatments	1553.96	3	517.99	5.28	*
Error	588.46	6	98.08		
Total	2143.91	11			

Appendix 71

Analysis of variance of per cent absolute fruit growth on nodes 21 and above.

Source	SS	df	MS	F	Result
Blocks	140.17	2	70.09	0.87	n.s.
Treatments	375.58	3	125.19	1.55	n.s.
Error	485.32	6	80.89		
Total	1001.07	11			