STUDIES ON THE GROWTH AND DEVELOPMENT OF THE TOMATO (*Lycopersicon esculentum* Mill.)

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Keith James Fisher

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ABSTRACT

During the propagation of tomato plants a high and a low level of nitrogen was applied in factorial combination before and after initiation of truss 1. The high level of nitrogen prior to initiation produced earlier flowering and an increased yield in truss 1. It was suggested that a contributing factor to the latter response was that, where a change in nitrogen level was involved, the change from high nitrogen to low nitrogen produced a more productive plant response than when the sequence of applications was reversed. Flower number and earliness of flowering of certain trusses was increased by the high level of nitrogen applied after initiation. Initially the plants grew faster and cropped earlier in response to high nitrogen, but there were no differences in either the final amount of growth or the final crop.

The response of the plants to a change in nitrogen level suggested that some of the increase in yield due to exposure of young plants to cold temperatures, may be due to the change in temperature level. Warm and cold temperatures were therefore applied in factorial combination before flower initiation (9 nights) and for a subsequent period (14 nights) which included the flower initiation stage, with single-truss tomato plants. Cold temperatures during both stages increased yield and number of fruit and decreased

mean fruit weight. The early treatment was the most effective. It was suggested that low temperatures produced an enhanced supply of assimilates to the apex, which then initiated more flowers and that cold temperatures appeared to influence yield solely due to its effect on flower number. Shoot growth was reduced as yield increased and it was suggested that competition occurs for assimilates between the leaves and fruit.

The remaining investigations were devoted to the relationship between vegetative and reproductive growth (source sink relationship) in the tomato plant. By the use of leaf removal treatments a study on the importance of the amount and position of leaf tissue on the yield of single-truss tomato plants was carried out. A close positive relationship was shown to exist between leaf dry weight and yield, while leaf position did not appear to be important. The leaf and root tissues were shown to be in competition with the reproductive tissues for dry matter.

The nitrogen experiment indicated that competition occurred between fruit trusses for assimilates. By allowing plants to develop different numbers of trusses and then examining the effects of these treatments on the yield of a particular truss, competition effects between trusses were shown to exist with all trusses except truss 1.

The final investigation was designed to demonstrate that the yield of truss 1 could be reduced by competition for assimilates. The treatments consisted of 3 leaf levels, 2 pollination levels and 3 truss numbers in factorial combination. Competition effects reduced the

yield of truss 1 and it was shown that such effects were influenced by the level of sink strength. Total yield was increased by increases in leaf level when sink strength was high and by additional trusses or extra pollination when the amount of leaf tissue was adequate.

Evidence was presented in the last three studies that economic yield in the tomato plant can be limited simultanoously by lack of both source and sink strength. The studies on competition effects between trusses indicated that the net assimilation rate in the tomato plant can be depressed by lack of sink strength. Aspects of the source sink relationship in the tomato plant are discussed.

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INTRODUCTION

Commercial tomato production can be divided into two stages, the propagation stage and the planted out stage. During the propagation stage two important aspects of plant growth and development are the growth and development of the first inflorescence, and the rate of plant growth. The effects of temperature and light on the growth and development of the young tomato plant are well documented. Nutrition is another factor of the plant environment under grower control during propagation, but about which limited information is available. For this reason the effects of high and low levels of nitrogen were included in these investigations. Of particular interest was the effect of nitrogen level on the development of the first inflorescence and on early and total fruit yield.

The results of this experiment raised a question about whether the effect of low temperature in increasing flower number in the first inflorescence was due to low temperature per se, or as to whether the change itself from high to low temperatures was also a contributing factor. An investigation of this possibility formed the basis of further study.

The remainder of the work was devoted to the planted out crop. Of interest here was the relationship between vegetative and reproductive growth. It was considered that the source sink relationship in the tomato is particularly relevant to an understanding of this subject. The last three experiments were designed therefore to provide information about the source (leaves) sink (trusses) relationship and in particular about competition between sinks (trusses).

This included an examination of the effects of the amount and position of leaf on the supply of assimilates to the truss of single-truss tomato plants. The nitrogen investigation had indicated that a compensation mechanism might operate between the trusses of the tomato plant. The existence of such an effect has already been suggested by Cooper (1964c) and Cooper and Hurd (1968a). As only limited information was available on such competition effects between trusses a study was designed with this objective in mind. The final investigation was carried out to determine whether the first truss was affected by inter truss competition as the previous experiment had failed to establish this. This concluding experiment also studied the effects of the amount of leaf tissue, level of pollination and truss number on fruit yield.

At no point in these experiments was the effect of the treatments on fruit quality, apart from fruit size, assessed. The intention was at all times to produce fruit of acceptable quality.

CHAPTER ONE

REVIEW OF LITERATURE

1.1 The young tomato plant.

1.1.1 Introduction.

Good propagation usually has as its aim the control of the growth and development of the leaves and the first inflorescence with the intention of culminating in a large early yield. It is these aspects of the growth and development of the young tomato plant that are featured in this review.

The pattern of growth and development is such that at cotyledon expansion the first 2-3 true leaves have been initiated, but as yet are not visible to the naked eye. The apex will continue to initiate leaves, the number initiated being determined by the environmental conditions and the variety (Wittwer and Teubner, 1956; Calvert, 1957, 1959; Wittwer, 1963; Binchy and Morgan, 1970). During this time the apex will enlarge and change from a flat vegetative apex to a raised dome at the time of initiation of the first inflorescence. The time to flower initiation and the number of flowers in the inflorescence are influenced by the environmental conditions and variety (Lewis, 1953; Wittwer and Teubner, 1956; Calvert, 1957, 1959; Hussey, 1963a; Binchy and Morgan, 1970).

1.1.2 The rate of leaf production and the rate of leaf growth.

The rate of leaf initiation (Calvert, 1959; Hussey, 1963a; Binchy and Morgan, 1970), and the rate of leaf growth (Hussey, 1963a) in the tomato increase with both temperature and light intensity, with temperature having a greater effect on leaf growth than on the rate of leaf production.

1.1.3 Leaf number below the first inflorescence.

Leaf number is decreased by low temperatures (Wittwer and Teubner, 1956; Calvert, 1957, 1959; Hussey, 1963a) and high light intensities (Calvert, 1959; Hussey, 1963a; Wittwer, 1963) with the actual number depending on the variety of tomato grown (Calvert, 1957, 1959; Wittwer, 1963). The effect of temperature was greatest at low light intensities (Calvert, 1959; Hussey, 1963a), while the effect of light intensity was greatest at high temperatures (Calvert, 1959).

Wittwer and Teubner (1956) and Calvert (1957) presented data which indicate that short photoperiods favour a reduction in leaf number and this was later confirmed by Wittwer (1963) who found that when day length was increased by the use of low intensity light leaf number was increased.

The major supplier of carbohydrates to the plant immediately after pricking out are the cotyledons and Calvert (1959) has shown that the removal of all or a portion of them will increase leaf number. Saito and Ito (1965) have reported similar effects with the removal of cotyledons. It is interesting to note that conditions which reduce the supply of assimilates, such as low light intensity or cotyledon removal, or treatments which increase the competitive ability of young leaves, such as high temperatures (Hussey, 1963a) all increase leaf number. This could be explained in terms of these treatments delaying apical enlargement due to a reduced supply of assimilates. This delay will increase the time to flower initiation causing more leaves to be formed before the first inflorescence (1.1.4).

The value of a reduced number of leaves below the first inflorescence is that the first fruit truss should be closer to the ground and more trusses should be able to be carried below the wires.

1.1.4 Time to initiation of the first inflorescence.

Low temperatures and high light intensities reduce the time to flower initiation (Calvert, 1959; Hussey, 1963a) with the effect of light intensity being the more important (Hussey, 1963a).

The importance of light intensity has been further demonstrated by Binchy and Morgan (1970) who demonstrated that the larger the light integral the earlier flower initiation took place and at the same light integral flower initiation occurred with plants provided with the shortest days.

Wittwer and Teubner (1956) and Wittwer (1963) showed that a short photoperiod favoured earlier flowering as indexed by the number of nodes before the first inflorescence. Although Wittwer (1963) did not dissect his plants to determine the time of flower initiation it could be assumed that his measure of node number and time to first anthesis were indicative of early initiation. Wittwer (1963) concluded that despite the fact that no effect on flower number could be determined the tomato plant was a facultative short day plant.

The danger of low light intensities and high temperatures in delaying flower initiation and thus reducing early yield is well demonstrated by the data of Calvert (1959). He found that initiation occurred 18 days after cotyledon expansion with a light intensity of 10,760 lux and a temperature of 15°C and as late as 45 days with a light intensity of 2,590 lux and a temperature of 35°C.

Eguchi, Matsumura and Ishizawa (1958) showed that nutrition could affect the time to flower initiation. With the treatments that were capable of initiating flowers the time from seed sowing to initiation varied from 25-35 days. Attention has also been drawn (Calvert, 1959) to the difference between varieties with respect to the time to initiation when grown under the same environmental conditions.

Hussey (1963a) suggested that high temperatures increased the competitive ability of the expanding first two leaves which were able to utilize a larger proportion of the assimilates at the expense of the apex. Apical enlargement was slowed down so that more leaves were formed and flower initiation was delayed. The greater effect of high temperature at low light intensities in delaying apical enlargement is consistent with this concept as the dominant role of the leaves would now be operating in conditions of low assimilate availability. In a further experiment Hussey (1963b) confirmed his theory as plants grown at high temperatures had rapidly enlarging apicies and earlier flower initiation when the first two leaves were removed compared to plants where the leaves were left intact.

1.1.5 Flower number in the first inflorescence.

Low temperatures (Lewis, 1953; Wittwer and Teubner, 1956; Calvert, 1957, 1959) and high light intensities (Calvert, 1959; Wittwer, 1963) have been shown to increase flower number in the first inflorescence. Temperature also has a similar effect on flower number in the subsequent inflorescences (Went, 1957; Calvert, 1957).

Eguchi et al (1958) reported that initiation of the first inflorescence did not occur at extremely low levels of nutrition which is in contrast to Phatak (1965) who reported that initiation of the first inflorescence took place in the absence of nutrient elements.

The work of Calvert (1957) indicates that at cotyledon expansion the plant is sensitive to temperature with respect to leaf number and then becomes sensitive with respect to flower number some 9 days later. It is assumed that the point at which a plant becomes receptive to temperature with respect to flower number is at the time of flower initiation. Hence as the time to flower initiation is affected by light intensity and variety the time at which low temperatures should be applied to increase flower number will vary with both variety and time of the year.

As the size of the first inflorescence with single-truss tomatoes could markedly influence fruit yield, Hurd and Cooper (1967) set out to determine suitable cold treatments for different times of the year. Of the treatments applied they found that in summer 14 days chilling applied 15 days from seed sowing and in winter 14 days chilling applied 18 days from seed sowing were the most effective. With winter sowings the response to chilling was not as marked as with summer sowings and the authors point out that the treatments applied may have been too early and too short for winter sowings where initiation was likely to be taking place 25-33 days after seed sowing. The greater response to chilling with summer sowings would also be related to the better light conditions as control plants during summer months showed a tendancy towards truss branching. The cold treatments used were 10°C/10°C and 15.6°C/4°C day and night temperatures.

No difference between these treatments which produced the same mean temperature over 24 hours could be determined.

Hussey (1963b) states that he could find no consistent relationship between the size of the apex at flower initiation and the rate of enlargement. The data he has published indicates however that at the lower temperature (15°C) at flower initiation the dry weight of the apex was greater than at the higher temperature (25°C). On the assumption that the larger the apex at flower initiation the more flowers are likely to be formed these data would suggest that low temperatures prior to flower initiation may benefit flower number. Most of the published work in this area (Lewis, 1953; Calvert, 1957; Hurd and Cooper, 1967) has not precisely defined the time when tomato plants accept the cold stimulus to increase flower number. However, Lake (1967) has reported that low temperatures prior to flower initiation increased flower number as well as low temperatures applied during flower initiation.

Hurd and Cooper (1967) have suggested that variation between plants with respect to flower initiation may occur and this would make it hard to determine the time exactly. They found a 14 day cold treatment most suitable for increasing flower number and this, as they have suggested, may indicate a variation in the time of initiation between plants. It is suggested here that this could also imply that there is some benefit in cold treatment prior to flower initiation to produce a larger apex. Hussey's (1963a,b) observations did not proceed past the time of flower initiation.

In an earlier investigation Leopold and Lam (1960) removed varying numbers of young leaves as they reached approximately 1.5cm in length starting from node 3 upwards and varying numbers of mature leaves up to node five. The removal of young leaves increased flower number in the first inflorescence and the time of flowering was advanced. These observations are similar in nature to those of Hussey (1963b) and Saito and Ito (1965) and imply that the young leaves compete successfully with the apex for assimilates. The authors concerned however concluded that a floral inhibitor in the young expanding leaves was involved. There was a varietal response to the removal of young leaves with the later maturing varieties responding best. The removal of mature leaves delayed flowering and tended to reduce flower number.

From the above evidence it would seem reasonable to postulate that the increase in flower number at low temperatures is due to reduced competition for assimilates. Hurd and Coopers' (1967) observation that control plants grown under summer light conditions produced branched trusses without cold exposure is consistent with this hypothesis.

1.1.6 Seasonal effect on time to flowering of the first inflorescence.

Cooper (1964b) studied the flowering pattern of the tomato plant from weekly sowings over a 12 month period. These plants were planted into border soil soon after cotyledon expansion and were not subjected therefore to any form of "root restriction" during the early growth and development stage. The time from seed sowing to anthesis of the first flower varied from 46 days in summer to 110 days in winter. In some instances during the winter the first inflorescence did not flower at all so that flowering first occurred on the second inflorescence. This was presumably due to the lack of "root restriction". These seasonal trends could be related to day-length or total radiation and Cooper has tended to favour day-length.

Calvert (1964a) suggested that young tomato plants grown in containers were light saturated when they reached a daily mean of 10,000f.c.h. For in winter 400,000 f.c.h. (87-88 days from cotyledon expansion to flowering) were required while in summer due to the postulated light saturation 40 days were required from cotyledon expansion to flowering. Calvert suggests that the changing amount ot photosynthetic light determines the seasonal pattern of days to anthesis. In summer neither a reduction in day-length or light intensity reduced the number of days to anthesis. He was unable therefore to establish any effect of day-length on time to flowering.

The data presented by both Cooper (1961b) and Calvert (1964a) are remarkably similar. This however is not surprising when it is considered that in the first instance the number of days were measured from seed sowing and not cotyledon expansion and that with winter sowings Cooper did not at times obtain flowering in the first inflorescence. In both instances the minimum temperature was 15.6°C.

1.1.7 Arrested development of the first inflorescence.

After inflorescence initiation the flowers grow and develop and subsequently flower and set fruit. The major cultural problem of the early tomato growers in the United Kingdom until the 1960's, when improved technology came to their aid, was the problem of obtaining satisfactory fruit production from the first truss of plants sown during October to early December (Calvert, 1967). Such sowings had flowers initiating and developing under poor light conditions and the inflorescences consisted of few flowers which tended to abort prior to anthesis or flowers which after anthesis failed to set fruit. The data from successional sowings of plants grown without "root restriction" presented by Cooper (1964a) show for example that nearly all the flowers in sowings from early December to early August set fruit whereas none of the sowings between September and early December set fruit. It was suggested that where daylengths were less than 12 hours ovary swelling decreased rapidly and ceased.

An examination of the techniques used to achieve satisfactory truss production from winter sowings is pertinent as it leads to a better appreciation of the growth and development of the first inflorescence. These techniques include delayed planting ("root restriction"), use of supplementary lighting or growing rooms, temperature control and carbon dioxide enrichment.

Cooper and Hurd (1968b) showed that arrested development could be counteracted by the use of carbon dioxide enrichment and by delayed planting into the soil of the glasshouses with a range of varieties sown in November. The response of varieties varied, in some both treatments were required in others only one was required. The authors postulated that a shortage of assimilates was the cause of the arrested development. The role that carbon dioxide enrichment plays in increasing the supply of assimilates is apparent but the role that holding the plants in pots has was less certain.

Cooper (1972b) when studying the effects of container size on partitioning in tomato plants grown in nutrient culture found that as container size was reduced the proportion of dry matter in the roots and stem was not affected, but that in the leaves decreased, while that in the inflorescences increased. Thus the beneficial effect of "root restriction" appears to involve redirection of carbohydrates from leaves to inflorescences and not from roots to inflorescences as commonly thought. The same worker

(Cooper, 1971) had previously shown that when root pruning was used as a means of restricting the extent of the root system little effect was observed on dry matter partitioning in the tomato plant. The effect of delayed planting would appear therefore to be due not to physically restricting the roots but to a redistribution of assimilates between leaves and inflorescences.

The value of supplementary lighting (Canham, 1966) and growing rooms (Canham, 1967; Dempsey and Morgan, 1968) to obtain satisfactory inflorescence development with winter sowings is commercially practiced in Europe. Undoubtably the major factor here is the improved availability of assimilates to the inflorescence.

Calvert (1969) reported that a change from a high temperature (21.1 or 18.3°C) to a low temperature (15.6°C) at about the buds visible stage increased the number of buds that flowered and early fruit yield with plants from an October sowing. He offered a number of possible explanations for his results. These were the effect of the temperature change, the importance of adequate leaf area early and the possibility of effects on the activity of the roots.

It is suggested here that it is the change from high to low temperatures that was important. Brouwer (1968) reported that with maize a change from high to low temperature brought about the accumulation of carbohydrates in the leaves. He explained the accumulation of carbohydrates in terms of leaf growth being more sensitive than photosynthesis to the lowering of temperature. On the assumption that changes take place in the tomato plant similar to that in maize plants, then it is possible that the accumulation of carbohydrates in the leaves would enhance their supply to the developing inflorescence. Thus the treatment applied by Calvert (1969) would improve inflorescence development under conditions where carbohydrate supplies were limiting.

The most likely conclusion from the discussion of the above techniques is that inflorescence development is arrested in mid winter in the United Kingdom due to lack of carbohydrates. This has already been suggested by Cooper and Hurd (1968b). Thus at that time of the year any treatment increasing the availability of carbohydrates will favour inflorescence development and probably early yield. It should be noted that arrested development of the first inflorescence is not a significant problem in New Zealand due to our better winter light conditions.

1.1.8 The effects of temperature and light intensity on the growth of young tomato plants.

Some discussion of this topic has already taken place (1.1.2-1 1.5) and will not be repeated here. Calvert (1964b) investigated the effects of day temperatures in the 15.6-20°C range and night temperatures in the 13.3-22.2°C range on the vegetative growth of young tomato plants grown under natural light conditions during the winter months (October-March). He concluded that in winter light conditions in the United Kingdom, night temperature should not be less than 17.8°C and the day temperature not lower than 20°C. He could find no evidence to suggest that the night temperature should be lower than the day temperature.

Hussey (1965) examined the effect of constant and alternating day and night temperatures over the range from 10-30°C on tomato plants up to 9 days from cotyledon expansion. He was thus examining the response of very young tomato plants over a greater temperature range than Calvert (1964b). The maximum rate of dry matter accumulation occurred close to a constant temperature of 25°C. Here again there was no evidence of thermoperiodicity. Both the above authors draw attention to the fact that Went (1945) showed that thermoperiodicity did not occur in the tomato plant less than 40 cms high. Hurd and Cooper (1967) reached a similar conclusion with respect to the young plant with their work on cold treatments to induce increased flowering of single-truss tomatoes.

Calvert (1964a) has suggested that young tomato plants are light saturated in summer months as his data and that of Cooper's (1964b) indicate that the time from cotyledon expansion to anthesis of the first flower is fairly constant at 40 days for most of the summer months with plants grown at a minimum temperature of 15.0°C. A similar time to flowering has been obtained in New Zealand (Fisher, 1968). Calvert (1964a) suggested that young plants are light saturated when they received a daily mean of 10,000 f.c.h.

Cooper (1967) measured the net assimilation rate of plants at approximately the 8 leaf stage over a 2 year period. He concluded that under glasshouse conditions in England the photosynthetic system of the young tomato plant was not light saturated. This apparent contradiction to the work of Calvert (1964a) could be explained in terms of the two workers measuring two different aspects of plant growth and development, one the time to flowering and the other the net assimilation rate at one point in time.

1.1.9 Earliness.

This is usually taken as the yield in the first 4-6 weeks of harvest. Recommendations are selected on the basis of the programme most likely to maximize profits. In England this takes the form of the "Blueprints" which are available for the main planting dates and glasshouse conditions in that country.

The great weight of evidence indicates that warm propagation temperatures are necessary for earliness. Work at various Experimental Horticulture Stations and at the Glasshouse Crops Research Institute have culminated in these A.D.A.S. Blueprints (Anon 1968). The minimum temperature during the propagation stage for the various combinations of planting dates and glasshouse conditions is 15.6°C. The move towards these high temperatures to obtain earlier flowering and thus early yield represents a major change in approach to tomato plant propagation in that country (Calvert, 1967). Work in Holland (Verkerk, 1966) and New Zealand (Fisher, 1955) has also shown the value of warm temperatures during propagation in increasing early yield.

With a multitruss crop the use of cold temperatures during propagation to increase flower number and thus presumably yield in the first truss is no longer recommended. This is because the cold treatment necessary slows down vegetative growth and hence any increase in yield in the first truss would be at the expense of earliness (Calvert, 196[illegible]).

Hurd and Cooper (1970) reported that a chilling period of two weeks at an average temperature of 10°C increased yield of single-truss tomatoes by approximately 25% except with a September sowing. The chilling treatment was applied 15-25 days after sowing depending on the time of year. Lake (1967) on the other hand was unable to show an increase in yield with single truss tomatoes having branched inflorescences. In both instances the authors report that the increased flower number increased the fruit number but decreased fruit size. Hurd and Cooper (1970) consider the cold treatment was beneficial due to the level of increased yield and the fact that it delayed harvest by only 4 days in summer and rather more in winter while no effect on the length of the harvest period was observed.

1.1.10 Summary

The foregoing discussion has outlined the growth and development of the young plant with emphasis on the factors affecting leaf production and flower initiation and subsequent inflorescence development. There appears to be considerable evidence that competition occurs between the vegetative and reproductive organs. Under conditions of low assimilate production this competitive relationship becomes significant with the leaves having the dominant role such that flower initiation and development suffers.

The conclusion of Hussey (1963b) that such competition merely emphasises the relationship between these organs and does not in any way offer an explanation of the mechanism of control is worthy of particular note.

1.2 The Mature Plant

1.2.1 Introduction

The relationship between vegetative and reproductive growth of the planted out crop is regarded as of major importance by commercial tomato growers. Behind this interest is a belief that the tomato plant will favour the vegetative rather than the reproductive state and that vigorous vegetative growth is the forerunner of poor fruit yields. Thus a grower attempts to control vegetative growth by raising the osmotic strength of the liquid feed and perhaps by the use of low temperatures. The value of some vegetative growth restriction under poor light conditions to achieve satisfactory development of the first truss has been discussed in section 1.1.7.

It is also conceded that a liquid feed of moderate concentration may improve fruit quality early in the season. However in many instances the restriction of vegetative growth is likely to reduce yield (Cooper and Hurd, 1968a).

The intention of this review of the growth and development of the mature tomato plant (planted out crop) is not to examine the possible advantages and disadvantages of such grower techniques, but rather to examine the literature to gain an insight into the relationship between vegetative and reproductive growth and how it is modified by various factors. A better understanding of this relationship would aid a more critical assessment of grower techniques.

1.2.2 Seasonal effects on the growth and development of the tomato plant.

The study of work of this nature is of value as it provides information on the seasonal relationship between vegetative and reproductive growth and development. This knowledge of the seasonal pattern of growth and development also enables one to determine whether the response of a plant to a treatment over time is being modified by a seasonal effect.

1.2.2.1 Leaf growth

Cooper (1961a) studied the pattern of leaf growth from successional sowings. Leaf length was used as an estimate of leaf area (Cooper, 1958) and the weekly rate of leaf length production was obtained from the following equation.

$$P = (a_2 + b_2) - (a_1 + b_1)$$

where P = weekly rate of leaf length production
a = the leaf length present on the plant
b = the accumulated total of leaf length removed on senescence
1 = first week under consideration
2 = second week under consideration

All sowings, except that for September, had a similar basic leaf growth pattern. A rapid rise to a maximal rate was followed by a decline with the growth rate maintained at a relatively low rate. The September sowing did not achieve a leaf growth rate above this low level.

The swelling of the first ovaries coincided in all sowings with the attainment of the maximum leaf length production. In a later experiment (Cooper 1964c) it was shown that the increasing leaf growth rate ceased on average 1.75 weeks after ovary swelling began and with plants from October and December sowings the check to leaf growth occurred even on plants where no ovaries were allowed to swell. The check to leaf growth was therefore not due to the onset of fruiting. Cooper (1964c) in an attempt to explain this observation postulated "that when, or soon after, the first flower primordia were initiated, an internal reaction was stimulated that eventually resulted in the cessation of the progressive increase in the rates of shoot extension and growth in leaf length". Root growth has been shown to be checked at the same time (Cooper, 1958).

1.2.2.2 Flowering

Cooper (1961b) examined the weekly rate of flowers reflexing their petals from successional sowings planted in the border soil soon after cotyledon expansion. The rate of flowering rose to a maximum but then declined during shorter days to rise again later. Due to arrested flowering during the winter months at times the first inflorescence did not flower at all.

Further work by Cooper (1964b) produced results of a similar nature. He found that the seasonal pattern of flowering exhibited a rapid increase in the weekly rate of flowering from early March to early May, followed by a progressive decline until July. From July until March a low weekly rate of flowering was maintained.

Seasonal effects on time to anthesis of the first flower of the first inflorescence (1.1.6) and on the development of this inflorescence (1.1.7) have already been discussed.

1.2.2.3 Fruit production

Cooper (1961a) reported that with successional sowings that the rate of fruit volume production rose to a maximum and then declined. The weekly rate of fruit volume production was calculated in a similar way to that for the weekly rate of leaf length production (1.2.2.1). The estimate of fruit volume was obtained from the cube of the radius of the fruit. Fruit volume production was reduced to an extremely low level during November to January in all sowings that grew through this period.

Cooper (1963) discussed the relationship between fruit production and daylength from 56 weekly sowings. He reported similar patterns to that of his earlier work (Cooper, 1961a). He stated that the development of the plant could be divided into the following periods.

a) from germination to the start of fruiting,

b) an initial lag in fruit volume production,

c) rapidly increasing production,

d) declining production

and e) arrested development when fruit swelling virtually ceased.

This pattern is not unlike the one for the number of flowers reflexing their petals (Cooper, 1964b) and the depression in flowering during the winter months would obviously reduce the number of potential ovaries. The statement by Cooper (1961a) that with the September sowing "although each ovary began to swell, this swelling was largely arrested and fruit development was very slow" implies that the swelling of individual fruit was also slowed down during the winter period. The fall in fruit volume production is therefore a likely reflection of the reduced supply of assimilates limiting flowering, fruit set and fruit swelling.

Cooper (1963) found that when the daylength was greater than 12 hours (March onwards) the rate of fruit volume production was rapid and was curvilinear in its relationship to daylength. It continued to increase until mid summer when it began to decline as did the daylength and the relationship between the two was now linear. Figure 1.1 shows the seasonal pattern of fruiting of plants that have attained their initial maximal rate

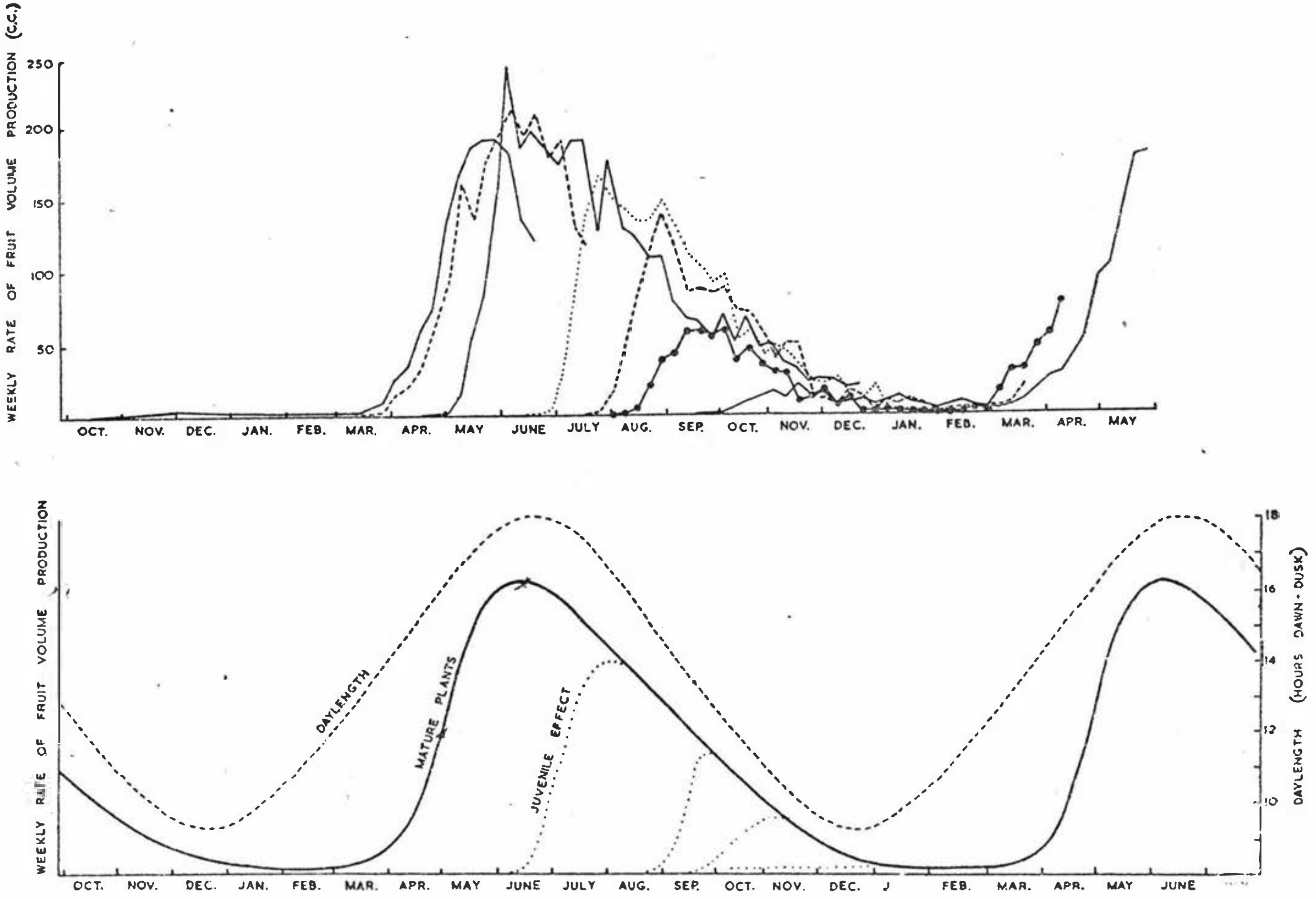


Fig. 1.1 The experimentally determined (upper) and diagrammatic (lower) seasonal pattern of fruit volume production (Cooper, 1963).

of fruit production. The shape of the curve will obviously be determined by the variety, geographic situation and type of crop management.

It could be suggested that a pattern of this nature was only to be expected, but the presentation of such data is of considerable value. Thus Cooper (1961a) has pointed out that with respect to the amount of fruit picked within 280 days of seed sowing then the nearer germination was to the shortest day the greater was total yield. Figure 1.1 also illustrates that the later seed is sown after mid summer for an autumn crop then the lower will be total yield. The importance of the seasonal effects on leaf and fruit production and the consequential effects on nutrient uptake (Brice, 1972) and possible response to temperature, it is suggested, has often been overlooked and could help to explain anomalies in the literature.

The maximum rate of fruit volume production was associated with the attainment of a minimal ratio of leaf area to fruit volume present on the plant (Cooper, 1961a). This ratio was constant for sowings that began fruiting between the shortest day and the longest day. The ratio was higher for sowings that began fruiting between the longest day and the shortest day and increased as the shortest day approached. Once this minimal ratio was reached it varied very little except during November-January when it rose sharply to fall again later. Cooper suggested that the data on leaf area/fruit volume ratio suggested the existance of a balance between leaf and fruit growth as apart from the November-January period the leaf area/fruit volume ratio was maintained throughout the life of the plant.

It is suggested here that the increase in the leaf area/fruit volume ratio during the winter months indicates a shift of such a balance in favour of vegetative growth under poor light conditions. This is supported by the later work of Cooper (1971), who compared the absolute growth rates of the component parts of the tomato plant from winter and summer sowings. He found that the increase in dry weight during the summer was mainly due to the increase in dry weight of the reproductive tissues. This clearly demonstrates that it is the reproductive tissues that are mainly affected by poor winter light. Cooper concluded that the demands of the roots, stems and leaves appear to be met before assimilates are made available to the reproductive tissues.

1.2.3 Partitioning of dry matter in the tomato.

Cooper (1972a) studied the partitioning of dry matter between the organs of the tomato plant for a period of 3-4 months with plants growing under winter (October sowing) and spring (February sowing) conditions. Such plants had very different growth rates, but despite this partitioning between organs was very similar until just after the start of rapid ovary swelling. This suggested that partitioning is not greatly influenced by the growth rate of the plant.

Initially the proportion of dry matter going to the leaves and stems increased and that going to the cotyledons and roots decreased. The proportion going to the roots in fact declined steadily throughout the whole of the observation period. Immediately after flower initiation the proportion of dry matter going to the leaves ceased to increase and started to decrease slowly.

At the onset of rapid ovary swelling the proportion of the dry matter going to the stem declined for both sowings, whereas the proportion going to the leaves, which had been decreasing slowly, began to decrease rapidly for the February sowing. For the October sowing, where ovary swelling was limited due to the poor light conditions (1.2.2.3), no rapid decline in the proportion of dry matter going to the leaves occurred. It is suggested here that this indicates that leaf and reproductive tissue compete directly for dry matter. The data presented by Cooper (1972b) in a later paper on the effects of container size on partitioning would support such a conclusion. Here container size affected the proportion of dry matter in the leaves and reproductive tissues only. The smaller container favoured reproductive growth with no effects being observed on the roots.

It was concluded when discussing the seasonal effects of light conditions on fruit growth and development (1.2.2.3), that under poor light conditions, there was a shift in balance between vegetative and reproductive growth in favour of vegetative growth. The above study (Cooper, 1972a) produced results of a similar nature. Thus with the October sowing fruit production was limited and as it appears that these tissues are in competition with leaf tissues the proportion of dry matter going to the leaves was not greatly affected.

1.2.4 Effects of modifying the fruit load.

Salter (1958) studied the effects of soil moisture and differing fruit loads on vegetative growth. The greater the fruit load the more vegetative growth was depressed.

Cooper (1964c) studied the effect of fruit removal with an October and December sowing. He found that the removal of all flower buds or alternate fruits as they appeared stimulated total leaf length by at least 7%. The removal of alternate fruits in each inflorescence as they appeared did not affect fruit volume as their removal caused buds which otherwise would not have produced fruit to do so. Thus on May 30th the total fruit volume present on the plants or harvested for both sowings was 3,682 cc and 3,667 cc respectively, for the treatments where no fruit were removed and were alternate immature fruit were removed. This was a difference of 0.5% in total fruit volume production, when in fact one treatment had had 50% of the fruits set removed at ovary swelling.

After consideration of these results Cooper postulated "that the amount of fruit a given tomato plant is able to produce in a given environment is a fixed quantity". He also agreed with Salter (1958) that there was a negative relation between fruit load and vegetative growth. It should not be concluded from this statement however that vigorous vegetative growth is detrimental to fruit yield, but rather that the carrying of fruit places alternative demands on the plants supply of assimilates. The existence of competition between leaf and reproductive tissues for assimilates was also supported by the data discussed on partitioning in the tomato (1.2.3).

1.2.5 Effect of leaf removal treatments and the presence of extra leaves.

Cooper (1964c) studied the effects of the removal of alternate young leaves and mature leaves from two winter sowings, on leaf length and fruit volume production. The removal of alternate immature leaves decreased total leaf length by 38% and 30% for the two sowings not 50%. Removal of mature leaves increased total leaf length by 7% and 5% in the two sowings. Thus both leaf removal treatments stimulated leaf growth. Aung and Kelly (1966) reported a similar response to leaf removal of young or mature leaves below the first inflorescence. These treatments caused the remaining leaves to grow larger and the increase in leaf area was greater than from control plants. The stimulated leaf growth as a result of the leaf removal treatments of the above workers is to be expected as the plants would attempt to re-establish the shoot root ratio pertaining to those environmental conditions (Brouwer, 1962).

Cooper (1964c) reported that the removal of alternate young leaves had a greater effect than the removal of mature leaves on fruit volume production. Fruit volume was decreased 47% and 30% by the removal of young leaves and by 37% and 19% by the removal of mature leaves for the two sowings. In both instances the treatments could be regarded as severe and not necessarily comparable. As already suggested these leaf removal treatments would require the plant to attempt to re-establish the balance between shoot and root for those conditions and this readjustment would divert assimilates from reproductive growth. The reduction in leaf area present on the plant would also contribute to a reduction in fruit volume

The removal of mature leaves in this experiment was from widely spaced plants so that the lower leaves should have still been photosynthetically active.

Cooper, Large, Proctor and Rothwell (1964) reported on de-leafing trials in commercial crops at a number of research stations in the United Kingdom. No effect on total yield was observed and early yield was reduced in one instance, but here the de-leafing treatment was severe. It would appear therefore that the commercial technique of removing lower leaves up to the truss where fruit is colouring does not reduce yield. Where more severe treatments are applied (Cooper, 1964c) then yield will be reduced. The data presented by Wiebe (1969) support this suggestion. Here the retaining of the top 4 feet of leaves or the removal of overlapping leaves did not significantly reduce the yield below that of plants where only the yellow leaves were removed. Where only 2 feet of leaves were retained or where alternate leaves were removed then yield was reduced.

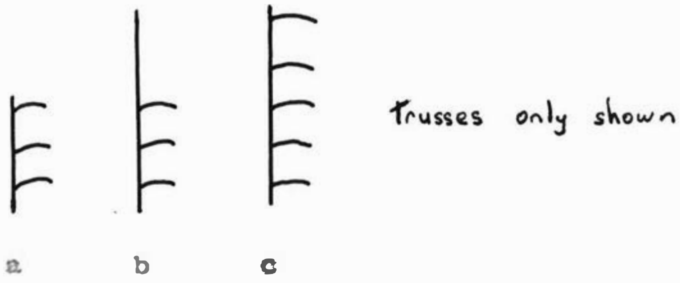
Wiebe (1969) also reported that the light intensity near the bottom of the plant was less than 10% of that at the top and that these lower leaves did not deplete CO_2 levels to the same extent as leaves higher up the plant. He suggests that these lower leaves are not photosynthetically very active. It could be expected therefore that the removal of leaves from densely shaded parts of the canopy would not greatly effect the supply of assimilates available for fruit production.

It is possible that the lower leaves if below their compensation point could become parasitic with respect to photosynthates. This would imply that the removal of lower leaves could benefit fruit production but the data presented by Cooper et al (1964) showed no signs of any such benefit.

The work of Khan and Sagar (1969a) could be taken as a further indication that leaves of the tomato plant, when below their compensation point do not become parasitic. These workers found that where light was excluded from all but the leaf treated with $^{14}CO_2$ that the darkened leaves, which were below their compensation point, had not imported the products of photosynthesis from the treated leaf by the end of the test period.

Verkerk (1963) examined the effects of pollination and number of leaves on earliness and total yield. The experiment was carried out in summer in an unheated glasshouse. The treatments applied are represented diagramatically in Fig. 1.2.

Fig. 1.2 Treatments applied by Verkerk (1963).



Half the plants in each treatment were pollinated using an electric vibrator with the other plants setting fruit naturally. With respect to the first three trusses the leaf number per truss increased from c to a to b. The more leaves per truss the later harvest started but the greater total yield.

The extra leaves increased the yield in particular of those trusses nearest them. Extra pollination gave an earlier and usually higher total yield and was necessary to gain the maximum benefit from the extra leaves.

Key to Fig. 1.2.

a stopped 2 leaves above truss 3
b stopped 2 leaves above truss 5, trusses 4 and 5 removed
c stopped 2 leaves above truss 5

1.3.6 Effect of nutrition.

Kraus and Kraybill (1918) carried out experiments which have often been regarded as the classical work on the relationship between vegetative and reproductive growth in the tomato. They found that plants given an abundant supply of nitrogen and conditions favouring carbohydrate production were not fruitful. These plants when transferred to a moderate level of nitrogen were less vegetative but fruitful. Where plants were transferred from an abundant supply of nitrogen to a low supply both vegetative and reproductive growth was poor.

The work of Kraus and Kraybill (1918) was carried out in the early days of crop experimentation and the levels of nitrogen were achieved by using techniques which would not be accepted today. It is not possible, for example, to determine quantitatively what the levels of nitrogen were in their experiments. It is suggested here that too often the effects of high nitrogen reported by these workers has been used as evidence to support the concept of low nitrogen feeds. Kraus and Kraybill in fact suggested that a moderate level of nitrogen was necessary for fruiting and the reduction in vegetative growth they noted would have been due to the diversion of carbohydrates to fruit production. Similar reductions in vegetative growth with increased fruitful~~l~~ness has been reported by other workers (Salter, 1958; Cooper, 1964c).

Murneek (1926) found that tomato plants grown at low levels of nitrogen had their vegetative growth inhibited by the presence of a single fruit. Plants grown at high level of nitrogen required the presence of up to 30 fruit before growth was restricted. The removal of fruits lead to a recovery of vegetative growth. Murneek states that he had studied plants at "one extreme only, the lowest plane of nutrition" and his results are not unlike those of Kraus and Kraybill (1918). It would appear that at a low level of nitrogen the presence of a few fruits so overloads the plants that both vegetative and reproductive growth are markedly reduced.

It is not possible to present a clear picture on the effects of nutrition on the relationship between vegetative and reproductive growth. Thus low nitrogen will bring both vegetative and reproductive growth to a standstill (Kraus and Kraybill, 1918; Murneek, 1926) and the effect of nitrogen level will interact with the prevailing light conditions (Brice, 1972). Where adequate levels of nutrients are applied then fruitfulness is likely to be encouraged and this itself will reduce vegetative growth. At times the effect of an element may be specific as for example low calcium, which affects fruit growth first, and providing the level is not too low, vegetative growth will not be effected. Vegetative growth may in fact be encouraged due to lack of competition for assimilates (Fisher, 1964).

1.2.7 Assimilate distribution in the tomato plant.

1.2.7.1 Export of assimilates from leaves.

Khan and Sagar (1966, 1967, 1969a, 1969b) have carried out investigations into the distribution of assimilates in the tomato plant. They found that in the vegetative phase lower leaves exported more carbon up than down and upper leaves a larger proportion downwards. During the development of the crop upper leaves continued to export more carbon down than up and lower leaves developed a similar tendency. Each leaf added assimilates to the shoot system, but few leaves had exported more than 20% of the carbon they fixed after 24 hours after application of $^{14}CO_2$ (Khan and Sagar, 1966).

The same workers (Khan and Sagar, 1967) studied the export characteristics of leaves on plants with a rapidly developing first truss and 17 leaves. 24 hours after treatment with $^{14}CO_2$ they found that leaves 1-13 (numbered from the base up) had exported approximately 30% of the carbon they fixed, but younger leaves exported less (13-15 20%, 16-17 10%). Young leaves appeared to export at a very early age as leaf 17 exported 13% when it was only ¼ expanded. Data on export figures over a longer period were reported from a later experiment (Khan and Sagar, 1969b), when the export pattern of C^{14} products from the second leaf of young tomato plants was studied. Export had started 10 minutes after $^{14}CO_2$ was applied and 17% had been exported in the first day and a further 23% the following week, with 44% remaining at the death of the leaf. It appeared that the roots re-exported a large proportion of the carbon products originally imported.

In another series of experiments (Khan and Sagar, 1969b) the leaf below truss 1 was treated with $^{14}CO_2$ and then 24 hours later the distribution pattern was determined. This was carried out at 7 different stages in the development of the crop. The percentage exported from this leaf (24 hours sample) rose to a peak of 30% early in the life of the plant and then fell sharply. The pattern of distribution varied during the life of the plant. Heavy accumulation occurred in the internode below leaf 10 early and later more reached the roots. Truss 1 had a dominant role and although as the importance of this truss decreased and more was exported to the other trusses it did not account for a large proportion of that that was exported.

By removing leaves or by shading all but the treated leaf or by increasing the growth of fruit by the application of growth substances, Khan and Sagar (1969a) decreased the number of sources on the plant or increased sink strength. They found that with plants with a rapidly developing first truss and 18 leaves that the treatments exported 40-45% of C^{14} products from leaf 9 24 hours after treatment. This was a marked increase over the control plants. They suggested that if these results represent the increase in performance which could occur over a longer period of time, then the whole plant has leaves whose efficiency could be increased by between 30-50%. This lead them to conclude that the limited activity of the sinks, as indicated by the increased export on the application of growth substances, indicates that fruit production is not limited by leaf area or photosynthetic activity.

It is however hard to accept this proposal of Khan and Sagar (1969a) that yield is not likely to be limited by the photosynthetic system, though this would apply during the early stages when sink strength is building up. Verkerk (1963), for example, was able to obtain further increases in yield from extra pollination by the addition of extra leaves, which would suggest that in the first instance the leaves of the plant were at their export maximum. The work of Cooper (1964c) where alternate immature fruit were removed causing fruit that otherwise would not have developed to develop, is a further indication that a lack of assimilates at times limits yield. The well established response of commercial crops to carbon dioxide enrichment also implies that at some stage the photosynthetic system of the plant limits yield. The presentation of Cooper et als' (1964) work on leaf removal as supporting their view (Khan and Sagar 1969a) is not conclusive for these leaves were at the base of the crop.

It is suggested here that it is unlikely that the percentage of C^{14} carbon exported from the leaf could be maintained at the level achieved by Khan and Sagar (1969a) as it would be at the expense of later leaf growth. The reduction in leaf area that would result, it is suggested, would reduce later fruit yield.

Khan and Sagar (1969a) stated that it was not clear from their experiment as to whether the lack of activity of the sinks and the accumulation of materials in stem caused any reduction in photosynthesis.

1.2.7.2 Pattern of distribution of assimilates.

During the early fruiting stage all leaves exported to all trusses, but as the truss number increased more definite relationships between groups of leaves and trusses developed (Khan and Sagar, 1966). Initially truss 1 dominated the distribution pattern in the plant with the direction of export from a leaf primarily being determined by its position relative to truss 1 (Khan and Sagar, 1967). Later other trusses dominated in series up the plant as the major sink (Khan and Sagar, 1969b). The relationship between a truss and the leaves closest to them however is not an absolute relationship as shown by the work of Drollinger (1957) who found that the removal of a few leaves nearest to a truss did not reduce the yield of that truss.

Khan and Sagar (1967) proposed that due to the varied origins of the carbon found in the various sinks it was hard to imagine that the vascular arrangement of the tomato plant had an important role in the overall distribution pattern of assimilates. At the end of these studies Khan and Sagar (1969b) concluded that the leaf appeared to have some control over the rate at which carbon products leave the leaf and the subsequent distribution pattern appeared to be greatly influenced by the relative activity of the various trusses which were the dominant sinks on the tomato plant.

1.2.8 Compensation effects between inflorescences and trusses.

Cooper (1964c) compared total fruit volume production between plants where alternate immature fruit had been removed and plants that were allowed to develop normally. The difference in total fruit volume between these two groups of plants was less than 0.5%, which was presented as evidence of the ability of the tomato plant to compensate for the removal of young fruit, by allowing fruit that otherwise would not have developed to develop and take their place (1.2.4).

Cooper and Hurd (1968a) examined the effects of 2 sowing dates, mid-November and late-December, with control plants pricked out at seedling emergence into the border soil and plants planted out at buds visible and at anthesis. The control plants bore an average of 5.5 - 5.8 fruits per plant in the first 7 inflorescences more than the plants planted at anthesis for both sowing dates. A similar but less marked reduction in fruit number occurred with the buds visible treatment. The response of individual trusses differed with sowing date, thus with the November sowing delayed planting increased fruit number on the first two inflorescences.

The authors proposed that the influence of one inflorescence on another could explain the oscillating pattern in fruit number for successive trusses of the delayed planting treatments compared to the control plants. They suggest that the compensating effect previously reported by Cooper (1964c) may in some way be involved. The results presented by Cooper and Hurd (1968a) as evidence of the influence of one inflorescence on another were as follows.

1. With the November sowing the increase in fruit number in inflorescences 1-2 resulting from delayed planting, was compensated for by a decrease (greater) in later inflorescences, particularly inflorescences 3-4.

2. With the December sowings (which were made in both 1965 and 1966) the decrease in fruit number of the plants planted at anthesis followed an oscillating pattern. The decrease declined from the first to the third inflorescence to rise to a maximum at the sixth inflorescence and then began to decline. Again a compensation type response.

The patterns described above involved the 7th inflorescence and there was no reason to expect that later trusses would not also have been effected.

It is suggested here, that in the work discussed above, the term competition could equally well have been used in place of the term compensation. This is because it is considered these effects were due to competition for assimilates between inflorescences or fruit trusses.

1.2.9 Summary

The above review has featured research work relevant to the relationship between vegetative and reproductive growth. Leaf growth rises to a peak level and then starts to fall just after ovary swelling commences. This peak is depressed by low winter light conditions and the fall occurs irrespective of whether the plant is carrying fruit or not. Both flowering and fruiting follow a seasonal pattern rising to a maximum in mid summer and falling to a low level in mid winter. This depression in fruit production, it is suggested, would be due to a reduced supply of assimilates limiting flowering, fruit setting and fruit swelling.

The data available on leaf area/fruit volume ratio imply that this ratio is constant for a particular management programme except in mid winter when it rises. This is presumably due to the low light levels reducing reproductive growth more than vegetative growth. The work reported on partitioning of dry matter supports this conclusion and also indicates that competition for dry matter between leaf and reproductive tissues occur. The decrease in vegetative growth resulting from an increase in fruit load supports the latter conclusion.

The relationship between vegetative and reproductive growth in the mature plant is similar therefore to that in the young plant. That is the leaf and reproductive tissues compete for assimilates and under conditions of low light (poor assimilate production) leaf tissue has the dominant role. The seasonal change in light conditions appears to be the major factor affecting this relationship.

Data on fruit removal treatments indicate that the plant is able to maintain the balance between vegetative and reproductive growth (leaf area/fruit volume) that is relevant to the prevailing environmental conditions. Severe leaf removal treatments will bring about fruit yield reductions, while the removal of lower leaves as practised commercially is not likely to affect yields. This is because the contributions these leaves make to the supply of available assimilates is limited. These responses to leaf removal are further indications that the relationship between leaf and reproductive tissues is primarily determined by the level of photosynthesis taking place in the leaves. Providing of course, that there are an adequate number of potential sites of fruit production present on the plant.

Adequate nutrition is necessary for satisfactory vegetative and reproductive growth and development. High or deficiency levels of elements should be avoided and their effects on the relationship between vegetative and reproductive growth is often specific to the element concerned.

The pattern of assimilate distribution appears to be dominated by the relative activity of the fruit trusses which are the major sinks present on the plant. These tend to be supplied by the leaves which are closest to them, but this is not an absolute relationship. Very young leaves (½ expanded) export assimilates and leaves appear to export only up to 30% of the carbon they fix during the subsequent 24 hour period. There is some evidence that inflorescences and trusses influence the growth and development of each other. This could be due to competition between themselves for their share of the assimilates available for reproductive tissues.

CHAPTER TWO

THE EFFECT OF NITROGEN SUPPLY DURING PROPAGATION ON FLOWERING AND FRUITING.*

2.1 Introduction

During the propagation of tomato plants it is possible to achieve a high degree of control of the plant environment. This is because plants can be grown in a small area and as these plants are pot grown the below ground environment can be influenced to a greater extent than with the planted out crop.

The effects of temperature and light during propagation on the performance of the planted out crop have been discussed by a number of workers (Canham, 1966; Calvert, 1967; Canham, 1967; Dempsey and Morgan, 1968), but there is limited information available on the effects of nutrition. In this experiment the effects of nitrogen level before and after initiation of the first inflorescence on early and total yield was examined. The treatment period was divided into these two stages in an attempt to partition the effects of nitrogen on the first inflorescence into effects on flower initiation and effects on inflorescence growth and development. Both these processes influence fruit yield in the first truss. Nitrogen was the only element studied as it was considered it would have the greatest single effect on the rate of growth of the young plant.

* The investigation discussed in this chapter has been published as follows:
Effects of nitrogen supply during propagation on flowering and fruiting of glasshouse tomatoes. J.hort.Sci., (1969) 44, 407-11.
Effects of nitrogen supply in nutrient culture on fruit yield in the first truss of the tomato. J.hort.Sci., (1971) 46, 273-6.

2.2 Materials and methods

Seed of tomato cv. Potentate was sown on 1st May 1967 in vermiculite, which was the growing medium used throughout the experiment. The seedlings were pricked out on 9th May into 8cm plactic pots and on the appearance of the first truss (18th June) the plants were transferred to 4.8 litre containers. Minimum temperatures of 15.5°C were maintained in a 6 x 8 m section of a partitioned glasshouse.

High (340 ppm) and low (57 ppm) levels of nitrogen, representing twice and one-third respectively of the nitrogen level used in the nitrate-type nutrient solution described by Hewitt (1966), were applied in factorial combination before and after initiation of the first truss. That is from 9th to 24th May (truss initiation) and from 24th May to 5th July. The time of flower initiation was determined by the regular examination of spare plants. As the time of initiation will vary from plant to plant and as it is not an instantaneous process the before initiation treatments included part of the flower initiation period as did the after initiation treatments. As there would be some carry over, after the removal of a treatment, it is considered that with respect to truss 1 the before treatment effects were due to effects on initiation, while the after treatment effects were due to effects on inflorescence development. The high level of nitrogen (+N) was obtained by the addition of NH_4NO_3 to Hewitt's nutrient solution; for the low level (-N) the $Ca(NO_3)_2$ was replaced by $CaCl_2$. Hewitt's solution unmodified was used from 5th July to the end of the experiment.

There were nine randomized blocks each containing eight plants. On 5th July (8 weeks from pricking out) one plant per treatment was sampled from each block and the leaf area and the fresh and dry weights of the shoot were recorded. The remaining plants (4 per block) were spaced 0.6m apart in a square pattern and fed daily with nutrient solution. No fruit-setting sprays were used and the plants were all stopped two leaves above the fifth truss.

Anthesis of the first flower of the first truss of most treatments had occurred by 5th July, which was 13 days after the shortest day. The monthly mean of outdoor solar radiation received during June 1967 at Palmerston North was 136 cal/cm^2/day, as measured with an Eppley pyranometer at the Plant Physiology Division, D.S.I.R.

Records of number of flowers that reached anthesis, days to anthesis of the first flower for truss 1, days between trusses for trusses 2-5, number and fresh weight of fruit harvested for each truss and date of harvest of fruit were collected. The final harvest of fruit was on 30th October (6 months from seed sowing) and the final shoot dry weight was determined on this date.

2.3 Results

2.3.1 Introduction

The data were analysed as a 2 x 2 factorial experiment with the main effects being reported in 2.3.2 and the interactions in 2.3.3. The response of the plants to the change in nitrogen level was of interest and results relevant to the discussion on this subject are presented in 2.3.4. The t test was used to calculate significant differences where two means were compared and Tukey's w procedure was used where more than two means were involved.

2.3.2 Main effects

2.3.2.1 Flower number, days to flowering and shoot dry weight.

The results of the analysis of variance carried out on the relevant data are presented in summarized form in table 2.1 (Appendices 1-9).

Table 2.1 Main effects of nitrogen levels before and after flower initiation on flower number, days to flowering, and shoot dry weight.

	Before flower initiation of truss 1		After flower initiation of truss 1		Significant differences	
	-N	+N	-N	+N	Before	After
			Flower number			
Truss 1	6.9	6.8	6.3	7.4	n.s.	0.7**
" 2	10.0	9.8	8.8	10.9	n.s.	1.9*
			Days to flowering			
Truss 1	70.0	65.4	70.0	65.4	1.3**	1.3**
" 2	14.7	15.2	16.6	13.3	n.s.	1.9**
" 3	9.3	9.8	10.3	8.8	n.s.	1.4**
" 4	7.5	8.4	7.6	8.3	n.s.	n.s.
" 5	8.9	8.7	9.5	8.1	n.s.	1.2**
			Shoot dry weight (g)			
Dry weight (8 weeks)	4.8	5.9	3.4	7.3	0.6**	0.6**
Final dry weight	192	181	185	187	n.s.	n.s.

* P, 0.05 ** P, 0.01

Flower number in trusses 1 and 2 was increased by high nitrogen applied after initiation of the first truss. The number of days to flowering was reduced for truss 1 by high nitrogen before or after initiation and for trusses 2, 3 and 5 by high nitrogen applied after initiation of truss 1.

Shoot dry weight at 8 weeks after pricking out was increased by high nitrogen before or after initiation. There were no significant effects on final shoot dry weight.

2.3.2.2 Yield, mean weight and number of fruit.

The results of the analysis of variance carried out on the relevant data are presented in summarized form in table 2.2 (appendices 10-18).

Table 2.2 Main effects of nitrogen levels before and after flower initiation on yield, mean weight and number of fruit.

	Before flower initiation of truss 1		After flower initiation of truss 1		Significant differences	
	-N	+N	-N	+N	Before	After
			Fruit yield (g)			
Truss 1	385	536	430	491	136**	n.s.
Early crop	754	1,083	627	1,210	258**	258**
Final crop	3,656	3,455	3,511	3,600	n.s.	n.s.
			Mean fruit weight (g)			
Truss 1	70.5	88.8	78.2	81.1	14.1*	n.s.
" 2	91.1	82.4	92.7	80.8	n.s.	9.3*
" 3	99.6	87.9	96.0	91.4	11.6**	n.s.
Early crop	80.6	93.2	80.8	93.0	11.7*	11.7*
Final crop	83.6	80.4	85.0	79.0	n.s.	n.s.
			Fruit number			
Early crop	8.9	12.0	7.6	13.3	2.5*	3.4**

* P 0.05 ** P 0.01

The yield of the first truss was increased by high nitrogen before initiation. The early crop, which was designated as the first 4 weeks of harvest, was increased by high nitrogen before or after initiation of truss 1. There were no significant effects on the final weight of crop.

The mean fruit weight of truss 1 was increased by high nitrogen before initiation, but that of trusses 2 and 3 was decreased by high nitrogen after and high nitrogen before initiation of truss 1 respectively. The size of fruit in the early crop was increased by high nitrogen before or after initiation, but there were no significant differences in mean fruit weight of the final crop.

Increases in the number of fruit harvested in the early crop were produced by high nitrogen before or after initiation. There were no significant differences in fruit number per truss or total number of fruits harvested. The trend in fruit number for trusses 1 and 2 were however similar to those reported in Table 2.1 for flower number.

2.3.3 Interactions.

Table 2.3 Significant interactions of nitrogen level before and nitrogen level after initiation of truss 1.

		Days to flowering				Shoot dry weight at 8 weeks(g)		Early crop (g)	
		Truss 1		Truss 3					
Before \ After		-N	+N	-N	+N	-N	+N	-N	+N
-N		73.9	66.1	9.4	9.2	2.4	7.1	336	1,171
+N		66.0	64.7	11.2	8.4	4.3	7.5	918	1,248
Significant differences:	P 0.05	1.8		1.9		0.8		359	
	P 0.01	2.3		2.4		1.1		452	

Significant interactions between nitrogen level before and after initiation of truss 1 occurred with respect to days to flowering, shoot dry weight (8 weeks) and early crop (Table 2.3) (Appendices 3,5,8,11). In no instance was there a significant difference between the combinations which received high nitrogen after flower initiation.

The number of days to flowering of truss 1 was increased where low nitrogen was applied both before and after initiation. The plants receiving high nitrogen before initiation flowered later on truss 3, when this was combined with low nitrogen rather than high nitrogen after flower initiation.

Plants receiving low nitrogen after initiation had lower shoot dry weights (8 weeks) than plants receiving high nitrogen after initiation. This was particularly marked with plants that received low nitrogen early.

The early crop was reduced where plants received low nitrogen at all stages compared with plants which had received high nitrogen at some stage during the treatment period.

2.3.4 Response of plants to a change in nitrogen level.

Of particular interest here was the response of plants to the change in nitrogen level, either from high to low or vice versa. The results of the analysis of variance carried out on the relevant data are presented in summarized form in Table 2.4 (Appendices 10,8,19,20).

Table 2.4 Fruit yield in first truss, shoot dry weight, leaf area per unit shoot dry weight and shoot dry matter content.

	Treatment means				Significant differences	
Nitrogen level before flower initiation	N+	N-	N+	N-	P 0.01	P 0.05
Nitrogen level after flower initiation	N+	N+	N-	N-		
Fruit yield in first truss (g)	574	408	498	362	n.s.	189
* Shoot dry weight (g)	7.5	7.1	4.3	2.4	1.1	0.8
* Leaf area per unit shoot dry weight (dm^2/g)	3.04	3.03	2.92	3.18	0.12	0.10
* Shoot dry matter content $\left(\frac{\text{dry wt}}{\text{fresh wt}} \times \frac{100}{1}\right)$	7.56	7.41	8.14	7.18	0.41	0.32

* all at 8 weeks

The only significant difference in fruit yield was between the two treatments containing high nitrogen and low nitrogen at all stages. In the results reported in 2.3.2.2 factorial analysis showed that the high level of nitrogen prior to initiation increased fruit yield in the first truss.

The shoot dry weights were in the expected order. The longer the period of time that the high nitrogen level was received, the greater was the shoot dry weight, although the difference between the treatments containing high nitrogen after initiation was not significant.

The leaf area per unit dry weight of shoot was the lowest for the treatment with high nitrogen before and low nitrogen after initiation, and highest for the treatment with low nitrogen at all stages. There was no significant difference between the treatments containing high nitrogen after initiation.

The dry matter content of shoots from plants receiving low nitrogen at all stages was significantly lower than that of any of the others except those receiving low nitrogen before and high nitrogen after initiation. High nitrogen applied before initiation followed by low nitrogen after initiation resulted in a significantly greater shoot dry matter content than any of the other treatments. The restricted range of values precluded use of the arcsine transformation for these data. The dry matter content of the shoot appeared, therefore, to vary in the opposite direction to the leaf area per unit shoot dry weight.

2.4 Discussion

2.4.1 Flower initiation and number (Table 2.1).

Phatak (1965) found that the initiation of the first truss occurred even in the absence of nutrient elements and suggested that the role of nutrition was only indirect in flowering. The data obtained in the present investigation supported this contention, because the level of nitrogen before initiation of truss 1 had no significant effect on flower number of that truss.

The high level of nitrogen after initiation of truss 1 increased flower numbers in trusses 1 and 2. In the case of truss 1 this could only have resulted from the production of conditions favourable for the development of initiated flowers and not to an effect on flower initiation. Wittwer and Teubner (1957), Saito, Hatayama and Ito (1963), Fisher (1964) and Adams, Winsor and Donald (1973) have previously reported that high nitrogen levels increased flower number.

2.4.2 Early growth and yield.

High nitrogen treatments during propagation produced earlier flowering, more rapid vegetative growth (Table 2.1) and an increased early crop (Table 2.2). A similar relationship between vegetative growth rate and earliness has been outlined by Verkerk (1966), when reviewing the effects of propagating temperatures. The increased early crop obtained with the high nitrogen treatments was accounted for by increases in the number and size of fruits harvested (Table 2.2). High nitrogen levels applied at planting (later planting than in the present experiment) have also produced increased early yields, as reported by Winsor and Hart (1964) when examining the nutrition of the early tomato crop in the United Kingdom.

The greater weight of fruit produced in truss 1 by the high level of nitrogen prior to initiation (2.4.4) was the result of increased fruit size (Table 2.2). This was possibly due to the diversion of increased amounts of carbohydrates to this truss at the expense of later trusses; hence the decrease in fruit size of trusses 2 and 3. Such a response could be controlled by a compensation mechanism, such as has previously been suggested by Cooper (1964c) and Cooper and Hurd (1968a).

The interaction observed with truss 3 as regards days to flowering is in contrast to that obtained with truss 1 (Table 2.3). Once again a compensation effect could be involved. The other interactions imply that, where nitrogen levels were high for most of the propagating period, there was little to be gained in terms of better growth and early crop from high levels in the first few weeks after pricking out. It should be pointed out however that under winter light conditions inferior to those experienced in the present experiment then this statement may not apply. For the improvement in yield of truss 1 due to high nitrogen early, as discussed in 2.4.4, may be such that early yield would be increased.

2.4.3 Final growth and yield.

The lack of any differences in final shoot dry weight and final crop suggests that propagating conditions may often influence the rate of growth and distribution of crop rather than the final amount of growth and final crop. Comparable responses with respect to fruit yields have been observed with different propagating temperatures, although in some instances under poor light conditions high temperatures have reduced total yields (Verkerk, 1966). Seasonal effects on leaf and fruit growth as described by Cooper (1961a, 1963) could well modify the effects of propagating treatments on total yield.

Cooper (1964a) proposed the concept of a fixed fruit load for a particular set of environmental conditions. The existence of a compensation mechanism in the tomato is an essential part of this proposal. In the present investigation the plants were grown under the same environmental conditions after propagation, so that the absence of differences in final crop is acceptable in terms of this fixed fruit load theory.

There is a considerable body of opinion amongst commercial tomato growers that vigorous vegetative growth is the forerunner of poor yields. This was certainly not true under the conditions of light in the present experiment, but it should be noted that the nitrogen treatments were not maintained for a long period and that the plants were container-grown. Abdalla and Verkerk (1970) reached a somewhat similar conclusion with respect to nitrogen level and yield.

2.4.4 Explanation of the effect of high nitrogen prior to truss initiation increasing fruit yield in truss 1.

In 2.4.2 it was reported that high nitrogen prior to flower initiation increased the yield of truss 1. The treatments receiving high nitrogen before initiation were the high nitrogen at all stages and the high nitrogen before and low nitrogen after initiation treatments. The following discussion attempts to offer an explanation of this result (Table 2.4).

High nitrogen supplied throughout all stages produced a greater yield of fruit in the first truss than low nitrogen. It is suggested that this was due to this treatment providing favourable conditions for plant growth and development throughout the propagating stage.

The mechanism by which the other treatment containing high nitrogen before initiation was associated with increased fruit yield was thought to be different. This is because it was considered that a diversion of increased amounts of carbohydrates to the truss was essential if fruit yield was to be improved. An explanation in these terms involving a direct effect of high nitrogen before initiation could not be postulated. It is considered, however, that the interpretation offered below is possible.

The following plant responses were associated with a change from a high to a low nitrogen level at flower initiation: the shoot dry weight was lower than that in either of the two treatments which included high nitrogen after flower initiation; the leaf area per unit of shoot dry weight was the lowest, whereas the shoot dry matter content was the highest, of the four treatments.

These responses were similar to those reported by Brouwer (1968) when discussing the effects of a lowering of temperature on maize. He explained the accumulation of carbohydrates in the leaves in terms of leaf growth being more sensitive than photosynthesis to adverse conditions. In his case the adverse condition was low temperature, while in the present experiment it was low nitrogen. It is suggested therefore that the high shoot dry matter content produced by the change from a high to a low level of nitrogen was accompanied by an increased supply of carbohydrates to the developing truss, and later, this promoted fruit growth.

Calvert (1969) has reported that when tomatoes were grown under poor light conditions a change from high to low temperature at the stage when buds became visible improved the flowering capacity of the early inflorescences. Presumably changes took place in these tomato plants similar to those reported for maize, and it is therefore probable that a high dry matter content in the leaves was associated with enhanced carbohydrate supply to the developing inflorescences.

Hurd and Cooper (1970) found that, with single-truss tomatoes, 14 days' treatment at low temperature applied 15-25 days after sowing increased the yield by approximately 25% at most times of the year. They suggested that the increased flower number may not have been the only cause of the increased yield, and the possibility of a direct effect of low temperature was discussed.

It is again feasible that such a direct effect could be caused by an increase in the supply of carbohydrate to the truss as a result of leaf growth being more adversely affected than photosynthesis by the change from high to low temperature. That a change to a lower level of temperature may contribute to increased yield is supported by the work of Lake (1967), who reported that he could find no difference in yield between single-truss plants with branched and unbranched trusses. Here the effect of static temperature levels was examined as distinct from the effect of a change in temperature level. An examination of the possibility that the change itself from a high to a low temperature level contributes to the increased yield of truss 1 formed the basis of a later study (Chapter Three).

Thus the increased yield of fruit in the first truss produced by high nitrogen applied before flower initiation was due partly to high nitrogen at all stages being better than low nitrogen, and partly because, where a change in nitrogen level occurred, the change from high to low nitrogen produced more favourable plant responses than when the change was the other way round.

These results also suggest that in New Zealand, where plants are planted out at a relatively young stage, that high nitrogen feeds at planting during the winter months should be avoided as they may detrimentally effect the growth and development of truss 1. The effect of nitrogen level at different times of the year on the yield of truss 1 and early yield with plants grown in the soil of a glasshouse, it is suggested, should be investigated.

2.5 Summary

During the propagation of tomato plants, which were later stopped at the fifth truss, a high and a low level of nitrogen was applied in factorial combination before and after initiation of the first truss. The high level of nitrogen prior to initiation produced earlier flowering and an increased weight of fruit in the first truss. The data suggested that the increased fruit yield in this truss in response to high nitrogen applied before initiation was due to high nitrogen at all stages being superior to low nitrogen, and that, where nitrogen applications before and after initiation were different, a change from high nitrogen to low nitrogen produced a more productive plant response than when the sequence of applications was reversed. Flower number and earliness of flowering of certain trusses was increased by the high level of nitrogen applied after initiation.

Initially the plants grew faster and cropped earlier in response to high nitrogen, but there were no differences in either the final amount of growth or the final crop. The constancy of the final crop was explained in terms of the concept of a fixed fruit load.

Under the conditions of light in this experiment the results did not suggest that vigorous early growth was detrimental.

CHAPTER THREE

THE EFFECT OF TEMPERATURE LEVEL AT DIFFERENT STAGES DURING PROPAGATION ON THE YIELD OF SINGLE-TRUSS TOMATOES.

3.1 Introduction

It was concluded in Chapter Two (2.4.4) that where a change from high to low nitrogen occurred during propagation, that the growth and development of truss 1 was improved. It was suggested that this was due to this change producing an increase in shoot dry matter content, which made more assimilate available to the developing truss under mid winter conditions. Brouwer (1968) has reported similar changes taking place in maize plants exposed to a fall in temperature. The question was therefore posed in 2.4.4 as to whether some of the increase in yield, due to the exposure of young tomato plants to low temperature, might be due to the change in temperature level per se as well as to the effect of low temperature on flower number.

It was decided that this possibility could be examined by combining high and low temperatures factorially in a manner similar to that used for the nitrogen treatments of the previous investigation. The change in temperature levels in the present experiment occurred prior to flower initiation, whereas in the nitrogen investigation it occurred at flower initiation. The time of flower initiation was determined by the examination of spare plants. Plants that produced single and double inflorescences, when propagated under identical environmental conditions, were also included in the experiment in an attempt to study the effect of fruit number, unaffected by temperature, on yield. This was done by exposing these plants during the treatment period to temperature conditions somewhere between the high and low temperatures of the factorial treatments.

The treatments making up this experiment differed only in the temperature regimes they received during the treatment period. This was in fact a period of 23 days commencing at cotyledon expansion. The plants were grown as single-truss plants as the literature published on the effects of low temperature on the yield of truss 1, as distinct from the effects on flower number, refers mainly to single-truss plants (Lake, 1967; Hurd and Cooper, 1970).

3.2 Materials and methods

3.2.1 General

Seed of cv Eurocross BB was sown on 5th May 1972 and germinated at 21°C. An even line of seedlings was pricked out at cotyledon expansion on 15th May into 8 cm plastic pots containing U.C. compost (Appendix 21). 200 seedlings were allocated at random to a 'warm' glasshouse and 60 to a 'natural' glasshouse. The two 6m x 6m glasshouses used were adjacent to each other and of identical design and orientation.

The 'warm' glasshouse maintained a minimum temperature of 16°C with fan ventilation coming into operation at 22°C. The 'natural' glasshouse had no control over its minimum temperature and fan ventilation came into operation at 22°C. The environments in the two glasshouses differed therefore only with respect to the minimum temperature. The treatments were applied from the night 15th May to the night 7th June. On 8th June the plants from the 'natural' glasshouse were shifted into the 'warm' house and from this date until the end of the experiment all plants received the temperature regime of the latter house. The mean maximum and minimum temperatures recorded in the two glasshouses during the treatment period are presented in Table 3.1

Table 3.1 Temperatures in glasshouses during treatment period.

Temperature °C	'Warm' gh	'Natural' gh
Mean day (max.)	20.1	19.9
* Mean night (min.)	16.1	10.3

* recorded under black polythene cover.

3.2.2 Treatments

3.2.2.1 Warm glasshouse

Warm and cold night temperatures were combined in factorial combination early and late during the propagation stage. The early stage (15th - 23rd May) consisted of 9 nights starting at cotyledon expansion and finishing prior to flower initiation and the late stage (24th May - 7th June) consisted of the next 14 nights. By day all the plants were kept in the glasshouse, while at night the plants receiving a warm treatment stayed in the glasshouse, whereas those receiving a cold treatment were removed to a cold room kept at 4°C. While the plants were in the cold room the warm plants were covered with black polythene with the dark period averaging 15 hours per night.

Fifty plants were allocated at random to each of the four treatments and on 3 occasions during the application of the treatments 5 plant samples were taken from each treatment and their fresh and dry weights recorded.

3.2.2.2 Natural glasshouse

No control of minimum glasshouse temperature was maintained in this glasshouse in the hope that the mean daily temperature would be such that both single and double inflorescences would be initiated. Any differences in yield between these two types of plant could not therefore be due to temperature effects. The plants in this house were placed under black polythene covers at the same time as the plants in the warm house.

On 8th June the plants from this house were removed to the warm glasshouse and by 7th July it was possible to determine what type of inflorescence each plant from the natural house was to have. 22 had single inflorescences and 38 double inflorescences and they were referred to as the single and double treatments.

3.2.3 Post treatment stage

All treatments ceased on 8th June and from then on all plants received the same temperature regime as previously outlined (3.2.1). The six treatments are presented in Table 3.2.

Table 3.2 Treatments applied to study the effects of temperature during propagation on the yield of single-truss tomatoes.

Treatment	Code	Glasshouse
warm temperature early and late	W/W	warm
warm temperature early cold temperature late	W/C	warm
cold temperature early warm temperature late	C/W	warm
cold temperature early and late	C/C	warm
single inflorescence	1	natural
double inflorescence	2	natural

At the buds visible stage each treatment was planted into 9 litre black polythene bags containing a 50:50 peat sand compost plus a complete fertilizer mix (Appendix 22), which required watering only. On 7th July, when the single and double plants could be identified, 15 plants were selected at random from the remaining plants of each treatment and allocated at random to a different block. From this date till the end of the experiment (6th October) a randomized block design of 15 blocks each containing 1 plant per treatment was used. The spacing used provided an area of 0.2 m^2 per plant.

From the start of the experiment until 7th July each treatment was kept on a separate mobile bench and these were shifted to a different position in the glasshouse each day to minimize positional effects.

Harvesting of the fruit commenced on 28th August and was completed by 6th October. The fresh weight and number of fruit was recorded at each harvest. On the final harvest date the above ground parts of the plant were removed and divided into leaves and stems and oven dried at 100°C and the dry weights recorded.

3.3 Results

3.3.1 Introduction

The data were analysed in a number of ways. The results of the four treatments from the warm glasshouse were analysed, where applicable, as a 2 x 2 factorial experiment. Where the results of the 6 treatments were examined together, then either an analysis of variance was used or significant relationships between the various parameters were sought. The t test was used to calculate significant differences where two means were compared and Tukey's w procedure was used where more than two means were involved.

3.3.2 Effect of temperature level at different stages during propagation on yield, number and mean weight of fruit.

The results of the analysis of variance carried out on the relevant data are presented in Table 3.3 (Appendices 23-25).

Table 3.3 Effect of temperature level at different stages during propagation on yield, number and mean weight of fruit.

Early		Late		*Significant differences	
W	C	W	C	P 0.05	P 0.01
	Yield (g)				
558	787	640	735	51.4	68.7
	Fruit Number				
7.5	11.2	8.6	10.2	0.78	1.04
	Mean fruit weight (g)				
79.5	71.2	77.8	72.9	4.36	5.83

* Significant differences for comparing either early or late means.

The cold treatment early or late significantly increased ($P < 0.01$) yield and number of fruit and significantly decreased mean fruit weight. Cold treatment early produced the greater response in each case. There were no significant interactions.

3.3.3 Treatment effects on fruit yield.

The results of the analysis of variance carried out on the relevant data are presented in summarized form in Table 3.4 (Appendix 28).

Table 3.4 Treatment effects on fruit yield.

Treatment	W/W	W/C	C/W	C/C	1	2	Significant differences	
							P 0.05	P 0.01
Yield (g)	541	635	739	834	576	818	106.7	127.7

The W/W and 1 treatments had a significantly ($P < 0.01$) lower yield than the C/W, C/C and 2 treatments, while the W/C treatment had a significantly ($P < 0.01$) lower yield than the C/C and 2 treatments.

3.3.4 Relationship between yield and fruit number per plant.

There was a significant ($P < 0.01$) correlation ($r = 0.97$) between yield and fruit number per plant for the 6 treatments (Fig. 3.1).

3.3.5 Relationship between mean weight and number of fruit per plant.

There was a significant ($P < 0.05$) negative relationship ($r = -0.88$) between mean weight and number of fruit per plant for the 6 treatments (Fig. 3.2).

3.3.6 Shoot dry matter content of young plants.

The mean shoot dry matter contents ($\frac{\text{dry wt}}{\text{fresh wt}} \times \frac{100}{1}$) of 5 plants at 3 harvest dates for each of the 4 treatments grown in the warm glasshouse are presented in Table 3.5. The 3 harvest dates included 1 prior to the change in temperature levels and 2 after the change. The period prior to the change was designated the early stage and that after the change the late stage.

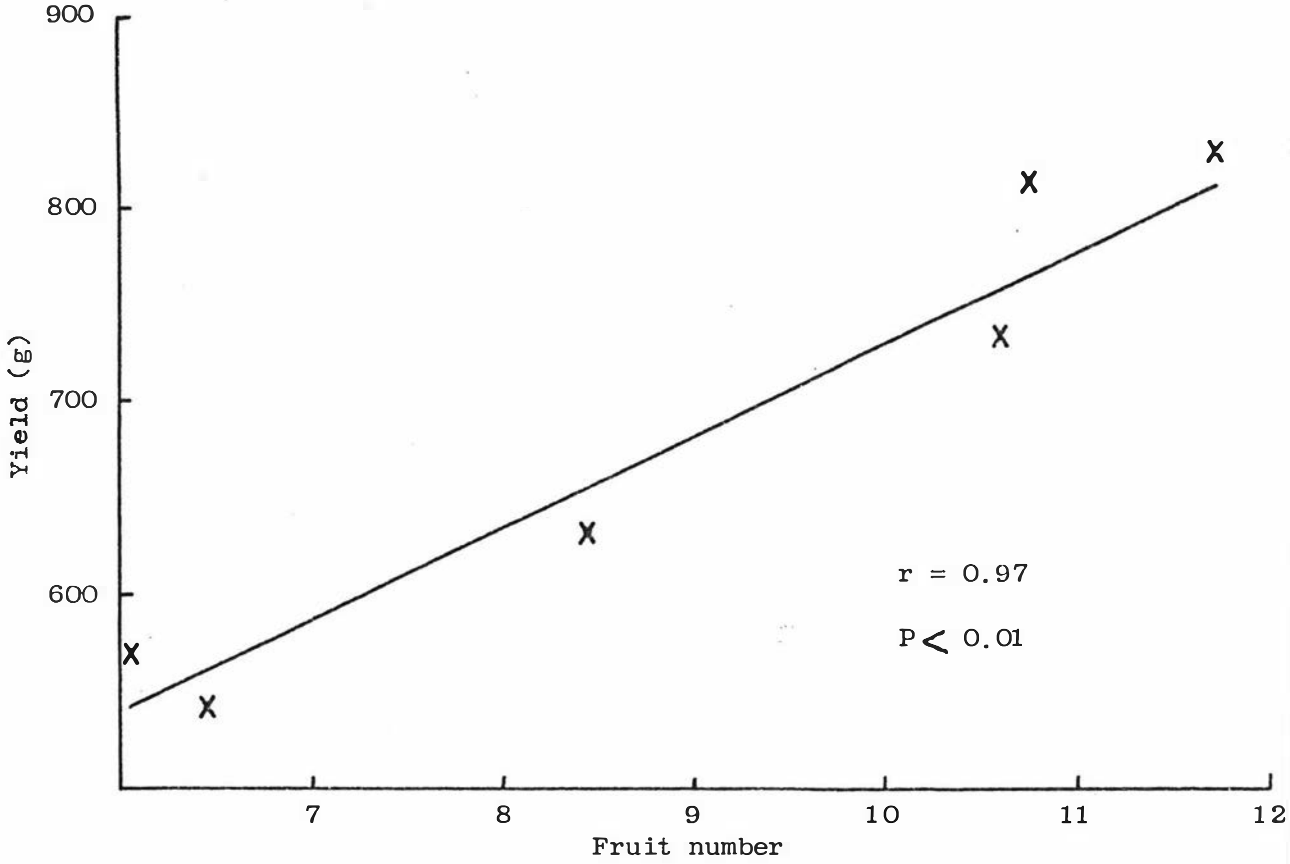


Fig. 3.1. Relation between yield and fruit number.

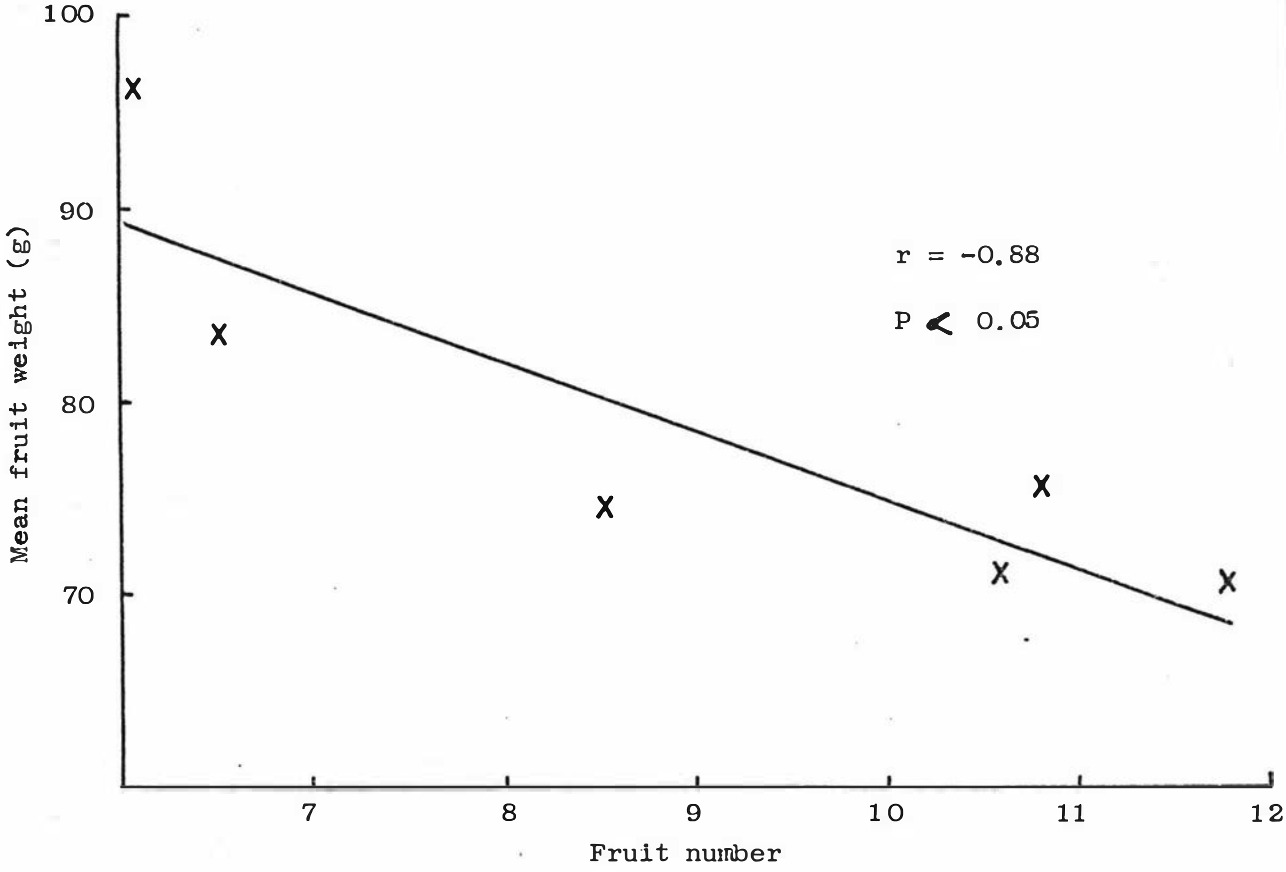


Fig. 3.2. Relation between mean weight and number of fruit.

Table 3.5 Shoot dry matter content of young plants

Date	Comments	Treatment			
		W	W/C	C/W	C
23/5	Early stage -1 night before change	7.9	7.9	11.0	10.9
30/5	Late stage	6.5	8.8	6.6	8.9
6/6	Late stage -1 night of treatment left	7.0	10.7	6.5	10.9

The shoot dry matter content was highest with those treatments receiving the cold treatment at the time of harvest.

3.3.7 Effect of temperature level at different stages during propagation on dry weight of plant top.

The results of the analysis of variance carried out on the relevant data are presented in summerized form in Table 3.6 (Appendix 27).

Table 3.6 Effect of temperature level at different stages during propagation on dry weight of plant top.

Treatment means (g)		Late		Significant differences	
		W	C	P 0.05	P 0.01
Early	W	40.0	26.6	4.93	5.75
	C	34.5	32.6		

There was a significant ($P < 0.01$) interaction between temperature level applied early and late with respect to dry weight of plant top. If cold was applied early then the dry weight of plant top was not effected by the temperature level late. If however warm temperatures were applied early, then the dry weight of plant top was high if combined with warm temperatures late and extremely low if combined with cold temperatures late.

3.3.8 Relationship between dry weight of plant top and fruit yield.

If the W/C treatment is deleted then a significant ($P < 0.05$) negative correlation ($r = -0.96$) was shown to exist between dry weight of plant top and fruit yield for the remaining 5 treatments (Fig. 3.3).

3.3.9 Relationship between percent total shoot dry weight in leaves and fruit yield.

There was a significant ($P < 0.05$) negative relationship ($r = -0.89$) between the percent total shoot dry weight in the leaves and fruit yield for the 6 treatments (Fig. 3.4).

3.4 Discussion

3.4.1 Fruit yield

Cold applied early and late increased yield and number of fruit and decreased mean weight of fruit (3.3.2). Data presented by Hussey (1963b) showed that at low temperatures the apex was larger at the time of flower initiation. His studies were not however carried past the time of flower

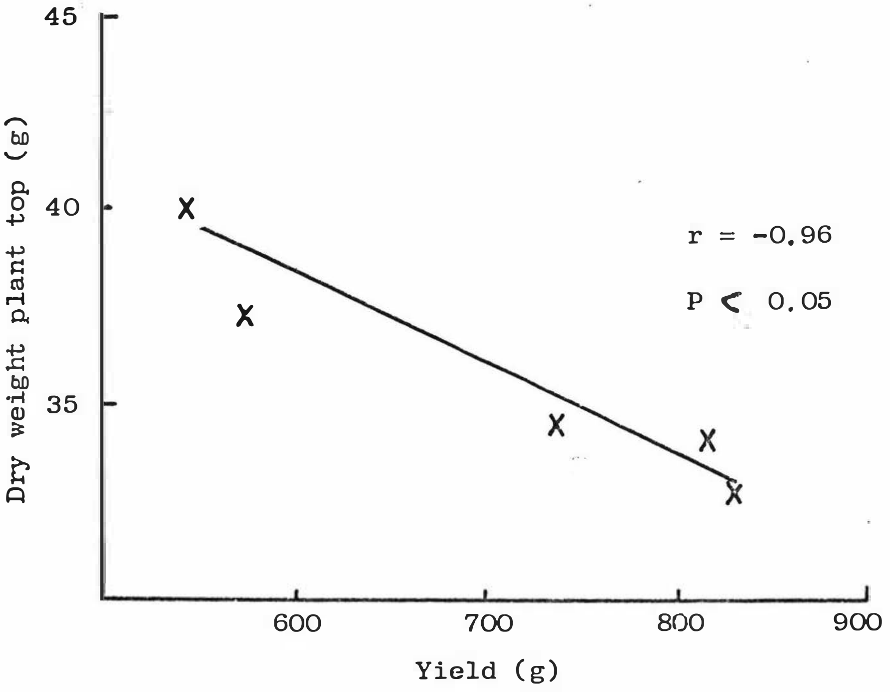


Fig. 3.3. Relation between dry weight of plant top and yield.

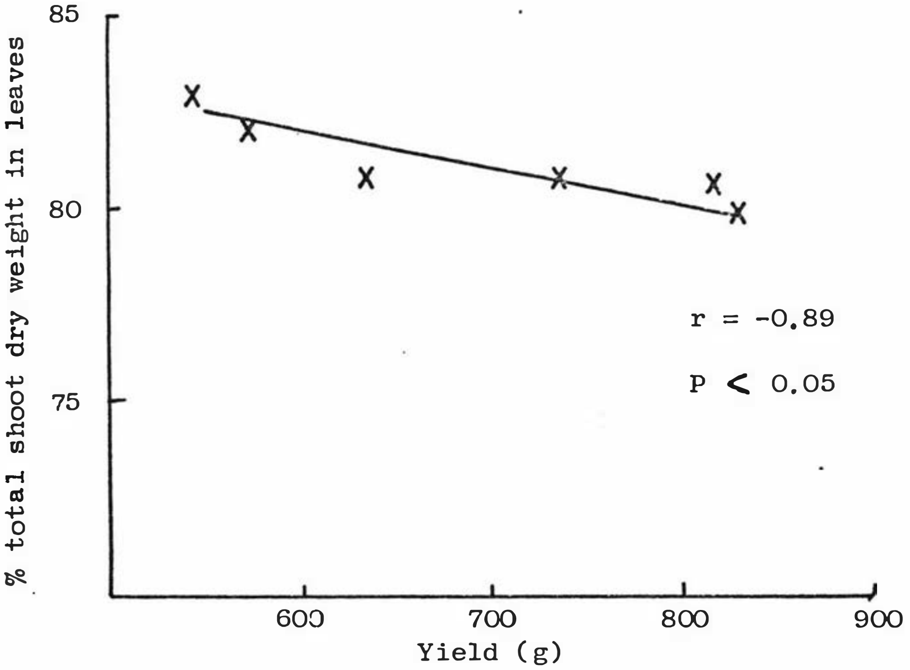


Fig. 3.4. Relation between percent total shoot dry weight in leaves and yield.

initiation. It would seem reasonable to suggest that the larger the apex at flower initiation, then the greater the number of flowers that will be initiated. Lake (1967) found that low temperatures prior to flower initiation increased flower number and the response of the plants in the present experiment to low temperature early supports such a conclusion. The present results in fact indicate that early treatment might be the most effective.

The cold treatment during the late stage commenced just prior to flower initiation and therefore included the time of flower initiation. This has been the most common period of treatment to increase flower number (Lewis, 1953; Calvert, 1957; Hurd and Cooper, 1967) and fruit yield (Hurd and Cooper, 1970).

That the increase in fruit yield was due primarily to an increase in fruit number is clearly demonstrated by the data. Thus a close relationship was shown to exist between yield and fruit number for all six treatments (Fig. 3.1). The work of Lake (1967) and Hurd and Cooper (1970) has demonstrated that the increase in fruit number brought about by cold treatment was accompanied by a decrease in fruit size. Results of a similar nature were obtained in the present study, where a negative relationship was shown to exist between mean weight and number of fruit (Fig. 3.2).

Treatments 1 and 2 differed only in that one had a single truss and the other a double truss, the temperature regimes they experienced were identical. The yields of these two treatments were similar to that of the equivalent treatment from the warm house - the W/W and C/C treatments (3.3.3). This suggests that truss size is determining yield and that exposure to low temperatures benefits yield solely due to its effect on fruit number. The close relationship between fruit number and yield obtained with the 6 treatments was a further indication that the effect of temperature on fruit number was the determining factor.

The data on shoot dry matter content (3.3.6) indicates, that with the temperature treatments applied in this investigation, that cold temperatures were associated with the accumulation of dry matter, rather than the change from warm to cold temperatures. The effect of temperature here, differed therefore from that of nitrogen, where a change from high to low nitrogen was necessary to accumulate carbohydrate and carbohydrate did not accumulate with low nitrogen alone (2.4.4). The explanation offered in 2.4.4 as to why a change from a high to low temperature, under low light conditions, favours truss development during the post initiation stage is still acceptable. For in the work under review (Calvert, 1969) in that instance, the low level of temperature used was not particularly low (15.6°C). Under such circumstances it is considered likely that a change in temperature level would be required to accumulate carbohydrates.

It is suggested here, that the accumulation of carbohydrate which is brought about by low temperature is the major contributing factor to the increase in flower number associated with low temperature. It is in fact possible that some of the increase in fruit number due to low temperatures late in the present experiment, could have been due to improved assimilate supply enhancing the development of initiated flowers.

The importance of assimilate is also implicated by the work of Hussey (1963a,b) on the effects of temperature on the competition between leaves and the apex for assimilate and by the investigation of Hurd and Cooper (1967), where under summer light conditions (where assimilate supply is less likely to be limiting), unchilled control plants produced some truss branching. This later response is often observed with commercial crops sown during the summer months. It is not intended to imply that assimilate supply is the only factor affecting flower number as work with growth substances, (Wittwer and Bukovac, 1962) clearly demonstrate that this is not so. Rather it is suggested that in many commercial situations an increased availability of carbohydrates to the apex immediately prior to and during flower initiation would increase flower number.

Further work involving growth analysis of plants receiving cold treatments of varying durations before, during and after initiation is required so that the effect of low temperature in increasing flower number can be more precisely understood.

3.4.2 Dry weight of plant top and percent total shoot dry weight in the leaves.

No explanation can be offered for the interaction between temperature level early and late with respect to dry weight of plant top (3.3.7). One might have expected the order of dry weights for the treatment means to have been such that the longer the period during treatment that the plant received warm temperatures the greater would have been the plant dry weight.

If the treatments are ranked with respect to the length of time they received warm temperatures, then the following was the order from the longest to the shortest - W/W, C/W, W/C, C/C. The treatment means were in this order with the exception of the W/C treatment which had the lowest dry weight.

Close negative relationships were shown to exist between dry weight of plant top and fruit yield (Fig. 3.3) and percent total shoot dry weight in the leaves and fruit yield (Fig. 3.4). The W/C treatment was deleted when the first of these relationships was determined. This was done because it did not fit this relationship, presumably due to the unexplained interaction discussed above. It was considered this was justifiable as it was then possible to demonstrate the general relationship, which existed in this experiment, between vegetative growth and fruit yield. All six treatments were included however in determining the latter of the above relationships.

These relationships demonstrate that competition occurs between the shoot and fruit for assimilates. The results emphasize that it is the leaves and fruit in particular that are in competition. A negative relationship between vegetative growth and fruit yield has previously been reported by Salter (1958) and Cooper (1964c), while the data of Cooper (1972a) suggest the existence of competition between leaves and fruit. Aspects of this relationship are discussed in Chapter Four.

3.5 Summary

Cold treatment prior to flower initiation (9 nights) or for a subsequent period (14 nights) which included flower initiation increased yield and number of fruit and decreased mean weight of fruit of single-truss tomatoes. The early treatment was the most effective.

Yield was closely related to fruit number and it was suggested that the exposure of plants to low temperatures produced an enhanced supply of assimilates to the apex, which then initiated more flowers. No direct effect of low temperature on yield could be demonstrated.

Shoot growth was reduced as fruit yield increased and it was suggested that competition occurs for assimilates between the leaves and fruit.

CHAPTER FOUR

EFFECT OF THE AMOUNT AND POSITION OF LEAF TISSUE ON THE YIELD OF SINGLE-TRUSS TOMATOES.

4.1 Introduction

The relationship between vegetative growth and yield is essentially the relationship between the leaves as the source of assimilates and the fruit which is the major sink (Khan and Sagar, 1969b) present on the plant. The work of Drollinger (1957) and Khan and Sagar (1966) indicates that although fruit obtain most of their assimilates from the leaves closest to them this is not an absolute relationship.

The present investigation was designed to study whether groups of leaves could completely or only partially replace each other as suppliers of assimilate to a particular truss. It was decided that this would be carried out by applying leaf removal treatments to single-truss tomato plants. The treatments used supplied information on the effects of the amount and position of leaf tissue on fruit yield.

4.2 Materials and methods

Seed of the cultivar Eurocross BB was sown on 10th February 1971 in a U.C. compost (Appendix 21). At cotyledon expansion an even line of 100 seedlings was pricked out into the nitrate-type nutrient solution described by Hewitt (1966). The nutrient solution was continuously circulated along PVC guttering the top of which was covered with rigid

PVC sheets painted silver on the outside. The plants were placed in gaps between the PVC sheets. Initially the cotyledons and later the leaves supported the plants on the PVC sheets, but for most of the experiment strings attached to overhead wires were used.

The nutrient solution was aerated as it cascaded from return pipes into a central storage tank from which it was pumped back to the guttering. The plants were grown in a 6m x 6m glasshouse which maintained a minimum air temperature of 16°C via the heating system with fan ventilation coming into operation at 22°C.

Plants were selected having single inflorescences and 7 leaves below this inflorescence. All plants were stopped 2 leaves above the first inflorescence giving a total of 9 leaves. Anthesis of the first flower occurred from 22nd to 26th March.

Plants were allocated at random to treatments and blocks on 26th March and all the remaining plants removed. This gave 1.8 litres of nutrient solution per plant in each gutter. The treatments were applied on this date by removing leaves to provide different leaf numbers at varying positions on the stem. The leaves were numbered from the base upwards and the treatments are presented in Table 4.1.

Table 4.1 Number and position of leaves retained.

Treatment	Number of leaves retained	Position of leaves retained
1	2	8,9
2	2	6,7
3	3	7-9
4	3	4-6
5	3	1-3
6	6	1,2,4,6,8,9
7	6	1,3,4,6,7,8
8(control)	9	1-9

There were six randomized blocks each containing one plant per treatment. A block consisted of two rows of plants 90 cm apart with plants 60 cm apart in the row. Inter plant shading was therefore minimal.

Harvesting of the fruit commenced on 10th May and was completed by 10th June when the plants were harvested and divided into roots, stems, leaves and inflorescence, dried at 90°C and weighed. Fresh and dry weights of fruits were also recorded.

4.3 Results and discussion

4.3.1 Relationship between fresh weight of fruit and leaf dry weight.

There was a significant ($P < 0.001$) linear relationship between fresh weight of fruit and leaf dry weight (Fig. 4.1). The data suggest that it would have benefited yield to have allowed more leaves to have developed on

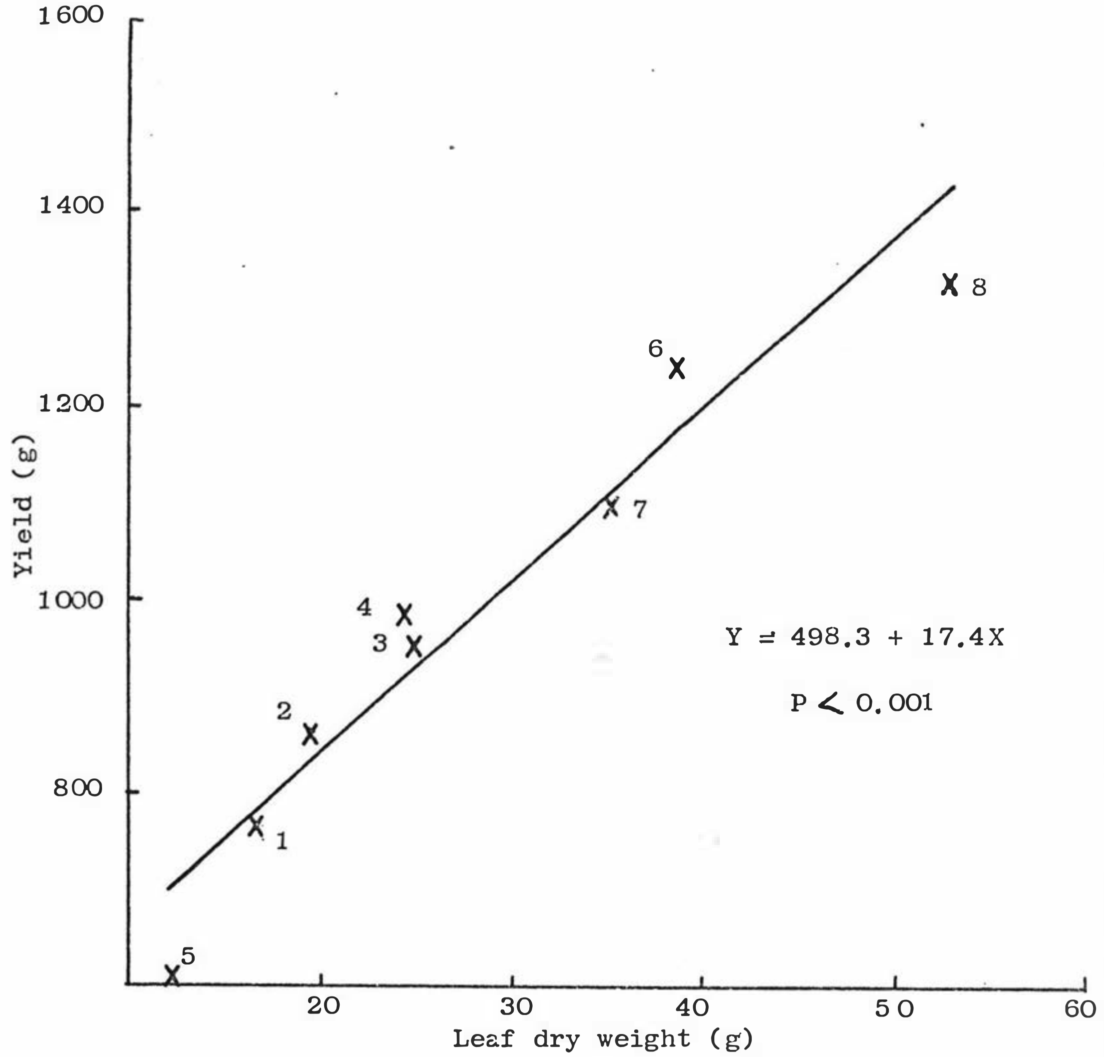


Fig. 4.1. Relation between yield and leaf dry weight.

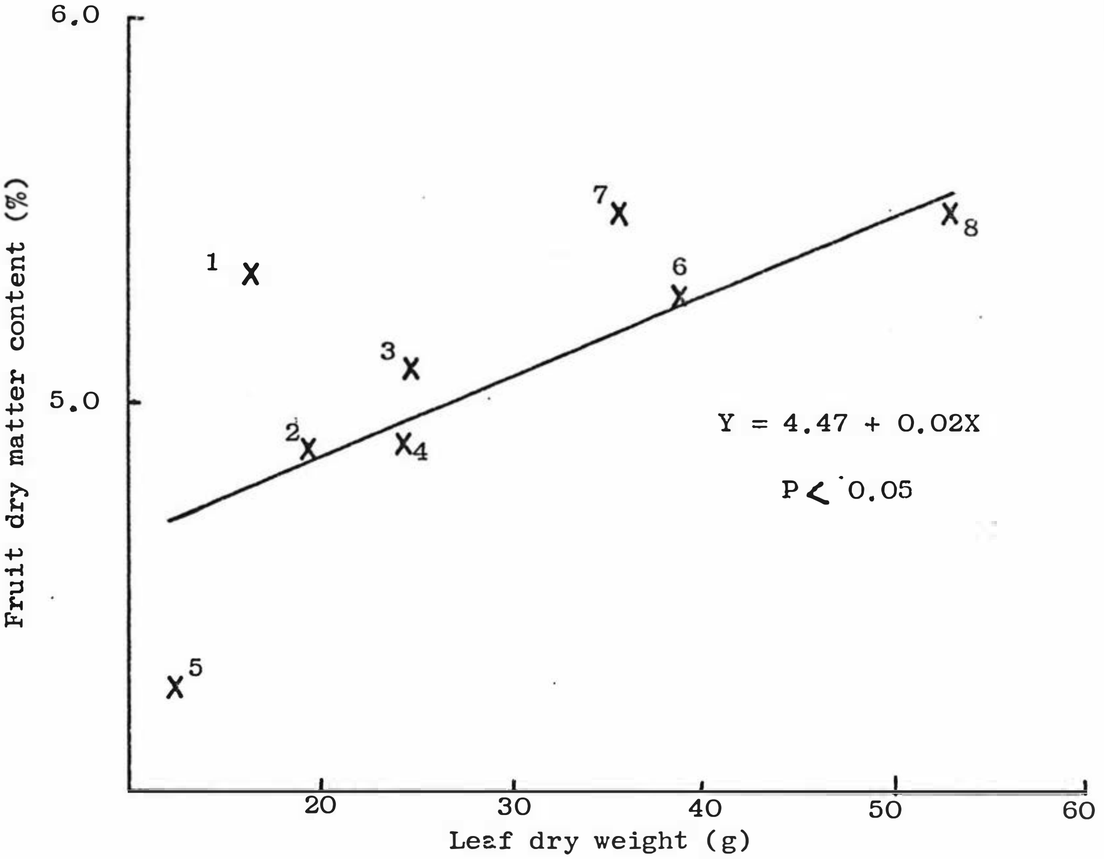


Fig. 4.2. Relation between fruit dry matter content and leaf dry weight.

the control plants. This was an experiment where the plants were widely spaced and whether stopping closely spaced single-truss plants at a higher leaf number would increase fruit yield would depend on how close the leaf area index was to the optimum.

The results of this experiment suggest that source strength was limiting yield. This is somewhat surprising as the plants had single trusses, so that sink strength could not have been great, and as the plants were widely spaced their leaves should have been fairly active photosynthetically. In Chapter Three it appeared that it was sink strength that was limiting yield as yield increased with increasing fruit number (3.4.1). In the present investigation it is not unreasonable to have expected yield to have increased if larger inflorescences had been initiated. If this is so then it would mean that both lack of source and sink strength would have been limiting economic yield at the same time. That this can occur has been established for potato (Nösberger and Humphries, 1965) and wheat (Thorne, Ford and Watson, 1968). The possibility of such a situation existing in the tomato plant is referred to later (5.3.4, 6.3.5).

It should be noted that in the above discussion the term yield used with reference to the previous and present studies refers to fresh weight not dry weight of fruit. In the present work fruit dry matter content increased with increasing leaf dry weight ($P < 0.05$) (Fig. 4.2) so that fruit dry weight would also have increased. In the previous experiment it is not certain whether the fruit dry matter content changed as fruit number increased. It is possible that it may have decreased so that there may not have been any difference in total fruit dry weight between, for example, single and double truss plants. This is not considered likely as the dry weight of plant top was lower with plants with double compared to single trusses (3.4.2). This would have been due to the diversion of assimilates to the fruit.

As the treatments used in the present study were applied just after anthesis of the first flower, the treatment differences were due to effects on fruit growth and development and not inflorescence growth and development.

4.3.2 Relationship between percent total plant dry weight in reproductive tissues and percent total plant dry weight in leaves.

There was a significant ($P < 0.01$) negative relationship ($r = -.92$) between the proportion of dry matter going to reproductive tissues (inflorescence and fruit) and the leaves (Fig. 4.3). Results of a similar nature have been reported by Cooper (1972a) with unstopped plants. He found with a February sowing once ovary swelling began then a corresponding rapid decline in the proportion of the absolute growth rate was found in the stem and leaves. However with an October sowing when the growth of the reproductive tissue was checked the proportion of the absolute growth rate of the whole plant found in the stem still fell, but that of the leaves was not greatly affected. This would suggest a competitive relationship between reproductive tissue and leaf growth.

Cooper (1972b) studied the effects of container volume on dry matter partitioning and suggested that improved inflorescence development produced by the commercial technique of "root restriction" was at the expense of

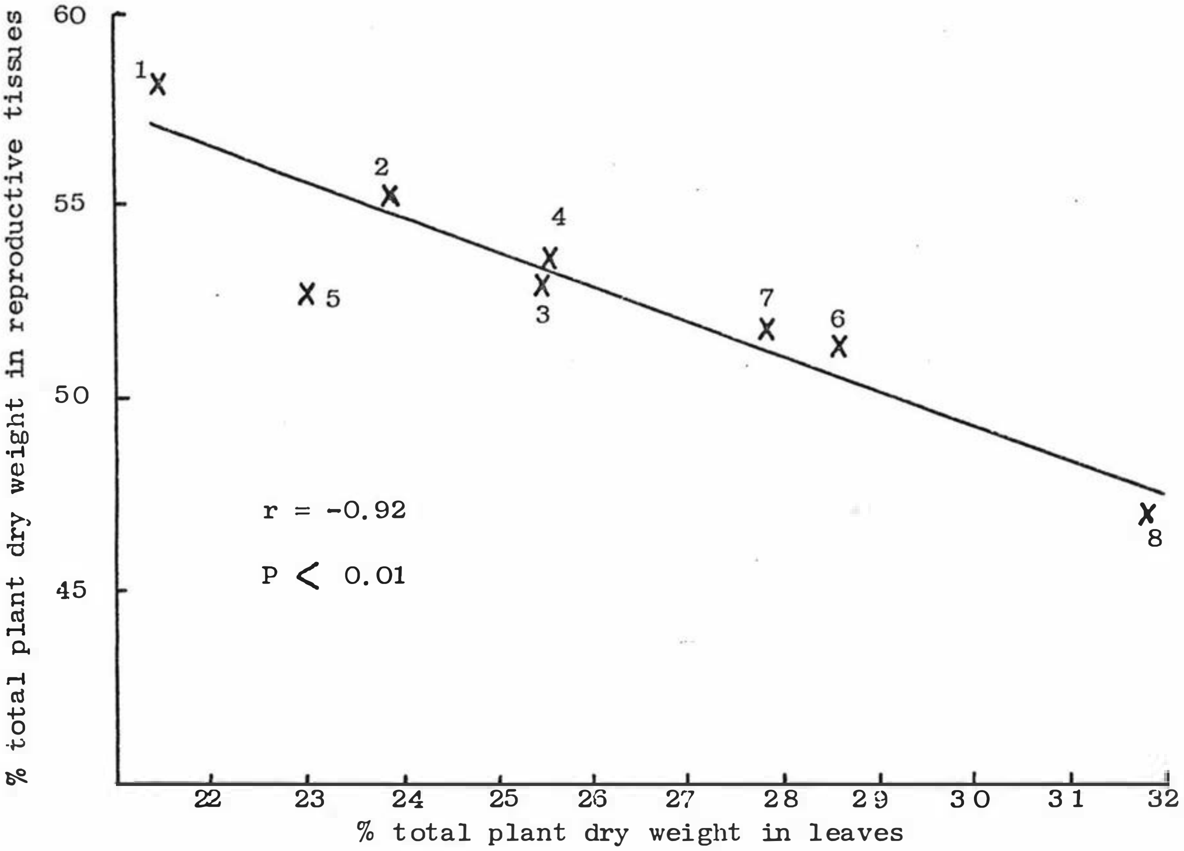


Fig. 4.3. Relation between % total plant dry weight in reproductive tissues and leaves.

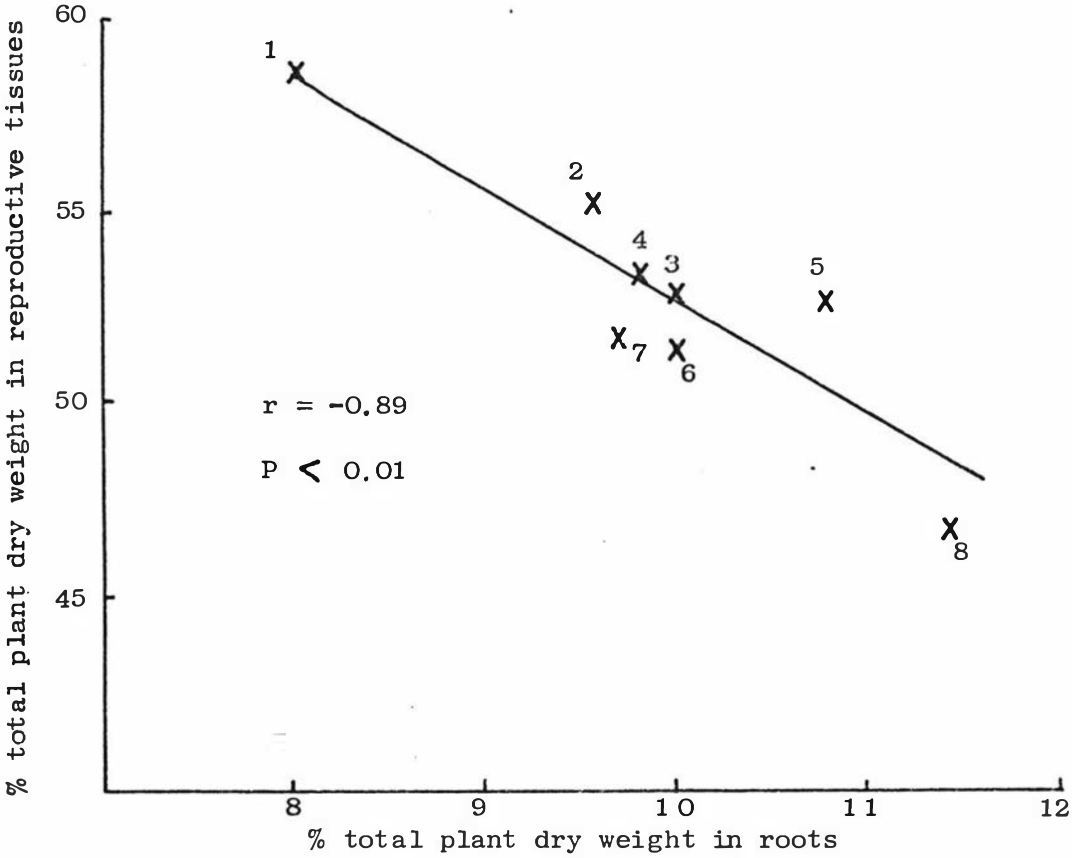


Fig. 4.4. Relation between % total plant dry weight in reproductive tissues and roots.

leaves and not at the expense of roots as commonly thought. Here again the data support the existence of a competitive relationship between reproductive and leaf tissues.

The percent total plant dry weight in reproductive tissues is equivalent to the harvest index (H) defined by Donald (1962). The results of the present study (4.3.1) imply that to increase yield the optimal leaf area index should occur at flowering and be maintained for as long as possible after this. Presumably once the optimal leaf area index is achieved attempts should be made, with single truss tomatoes or high density direct sown outdoor crops, to increase H. Prior to this point however any increase in H will be at the expense of leaf tissue and therefore yield.

4.3.3 Relationship between percent total plant dry weight in reproductive tissues and percent total plant dry weight in roots.

There was a significant ($P < 0.01$) negative relationship ($r = -0.89$) between the proportion of dry matter going to the reproductive tissues and that going to the roots (Fig. 4.4).

The data published (Fig. 2 lower) by Cooper (1972a) are not at variance with this result. Here with an October sowing, where fruit swelling was restricted, the proportion of the absolute growth rate of the whole plant found in the roots was maintained at a higher level than with sowing dates where fruit swelling occurred.

4.3.4 Importance of leaf position.

As there was a close linear relationship between yield and leaf dry weight (Fig. 4.1), with treatments covering a range of leaf positions, it is considered that with single-truss tomatoes it is the amount rather than the position of leaves that is important. The work of Drollinger (1957) and Khan and Sagar (1967) indicates that with a multitruss crop that leaves can compensate for each other. How complete this is with a multitruss crop is not certain.

The data in Figures 4.1 and 4.2 indicate that treatment 5 tended not to be as closely associated with the general trend as did the other treatments. This could be due to the leaves of this treatment being older and further away from the first truss than with the leaves of the other treatments. These leaves may also have had a special function to supply the roots.

4.4 Summary

Immediately after first anthesis leaf removal produced treatments consisting of varying amounts of leaf tissue at different positions on the stem of widely spaced single-truss tomato plants.

A close positive relationship was established between leaf dry weight and fruit yield, while leaf position did not appear to be important. The leaf and root were shown to be in competition with reproductive tissues for dry matter.

CHAPTER FIVE

COMPETITION EFFECTS BETWEEN FRUIT TRUSSES.

5.1 Introduction

The data presented in the nitrogen investigation indicated that a compensation mechanism exists in the tomato plant. In that experiment high fruit yields in truss 1 were compensated for by reduced fruit size in later trusses and despite differences in early yield between treatments no differences were detected in final yield (2.4.2-3). The existence of such a mechanism has been suggested by Cooper (1964c) and Cooper and Hurd (1968a).

As it was considered that such effects were brought about by competition between trusses for assimilates it was decided to design an experiment to demonstrate the existence of competition between trusses and to determine whether it was restricted to adjacent or widely separated trusses. It was considered that this could be achieved by allowing plants to develop different number of trusses and then examine the effects of these treatments on the yield of a particular truss. Two series of plants were studied. One where the plants were stopped at the required truss number and another where vegetative growth was allowed to continue to be stopped later.

5.2 Materials and methods

Seed of the cultivar Eurocross BB was sown on 14th July 1971 in U.C. compost (Appendix 21) and germinated at 21°C. At cotyledon expansion

(23rd July) the plants were pricked out into 8 cm plastic pots containing U.C. compost and grown on in a 6m x 6m glasshouse where minimum temperatures of 16°C were maintained via the heating system with fan ventilation coming into operation at 22°C.

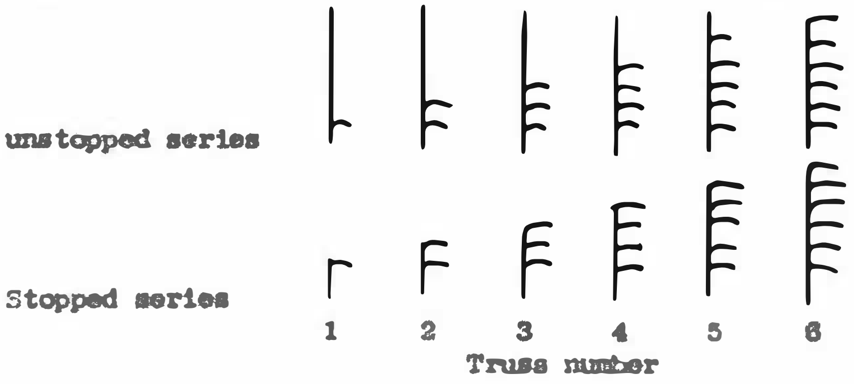
On 21st August an even line of 72 plants was selected and planted into 9 litre black polythene bags and then allocated at random to the treatments and then to the blocks. The bags contained a 50/50 peat sand compost plus a complete fertilizer mixture (Appendix 28) which required watering only. A randomized block design was used consisting of 6 blocks containing 1 plant per treatment. The 12 treatments consisted of two series each containing 6 treatments and were as follows.

Unstopped series. Plants stopped 2 leaves above inflorescence 6 and then inflorescences removed as necessary to give 1,2,3,4,5 and 6 truss plants.

Stopped series. Plants stopped 2 leaves above the last truss to give 1,2,3,4,5 and 6 truss plants.

The treatments are represented diagramatically in Figure 5.1, the last treatment in each series being identical.

Fig. 5.1 Diagramatic representation of treatments applied.



There were 3 double rows of plants ($\frac{1}{2}$ double row per block) with guard plants at the end of each row and along the glasshouse walls near the outer blocks. Plants were spaced 32 cm apart in the row, 40 cms between rows with 90 cm paths between the double rows. It was considered that the shorter plants of the stopped series were not significantly shaded by adjacent plants. This was considered to be so due to the good light transmission characteristics of the glasshouse, the plant spacing and the time of the year.

The plants were hose watered as required. This was as frequent as twice daily near the end of the experiment. The plants were trained up strings according to the normal commercial practice and the plants were damped down daily to aid fruit setting. No regular disease and pest control programme was followed. On one occasion Dibrom (naled) was applied to control white fly (Trialeurodes vaporariorum Westw.).

Harvesting of fruit commenced on 18th November 1971 and the final harvest was made on 14th January 1972. The fresh weight and number of fruit per truss were recorded and on the final harvest date the plant tops were removed and oven dried at 90°C and the dry weight of plant top determined.

5.3 Results and discussion

5.3.1 Analysis of results

Analyses of variance were carried out on the relevant data and the method of orthogonal polynomials was used to determine the best fit for possible regression lines (Appendices 29-42).

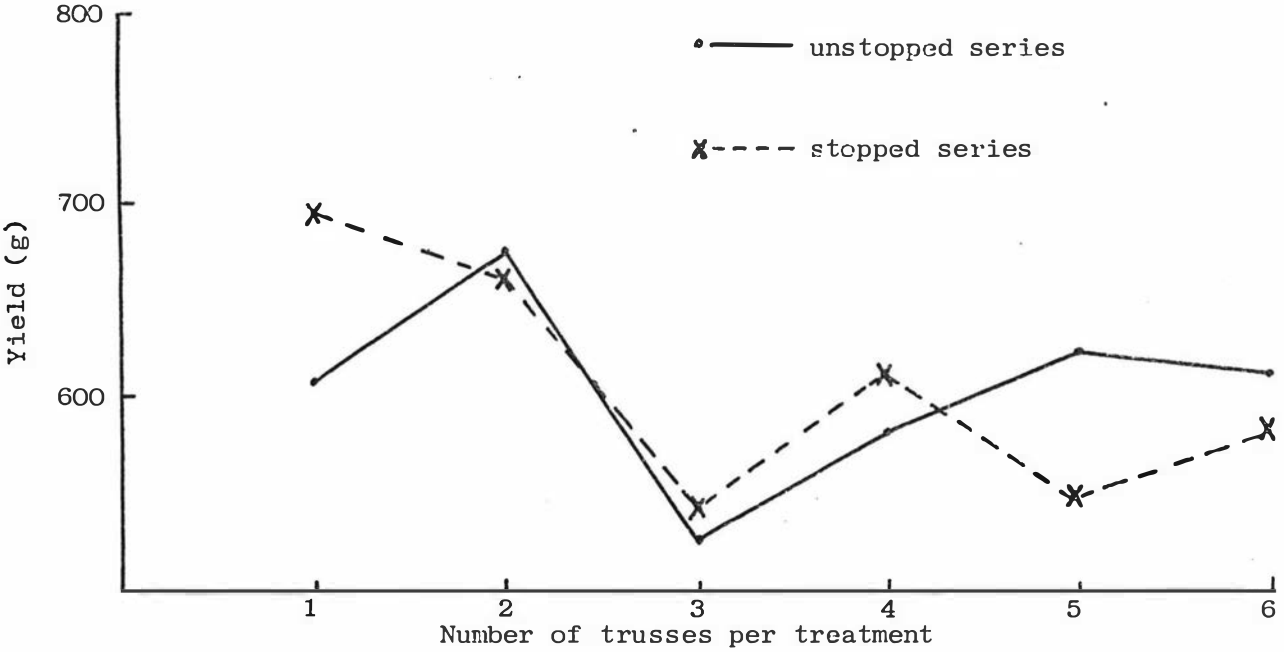


Fig. 5.2 Relation between yield truss 1 and truss number.

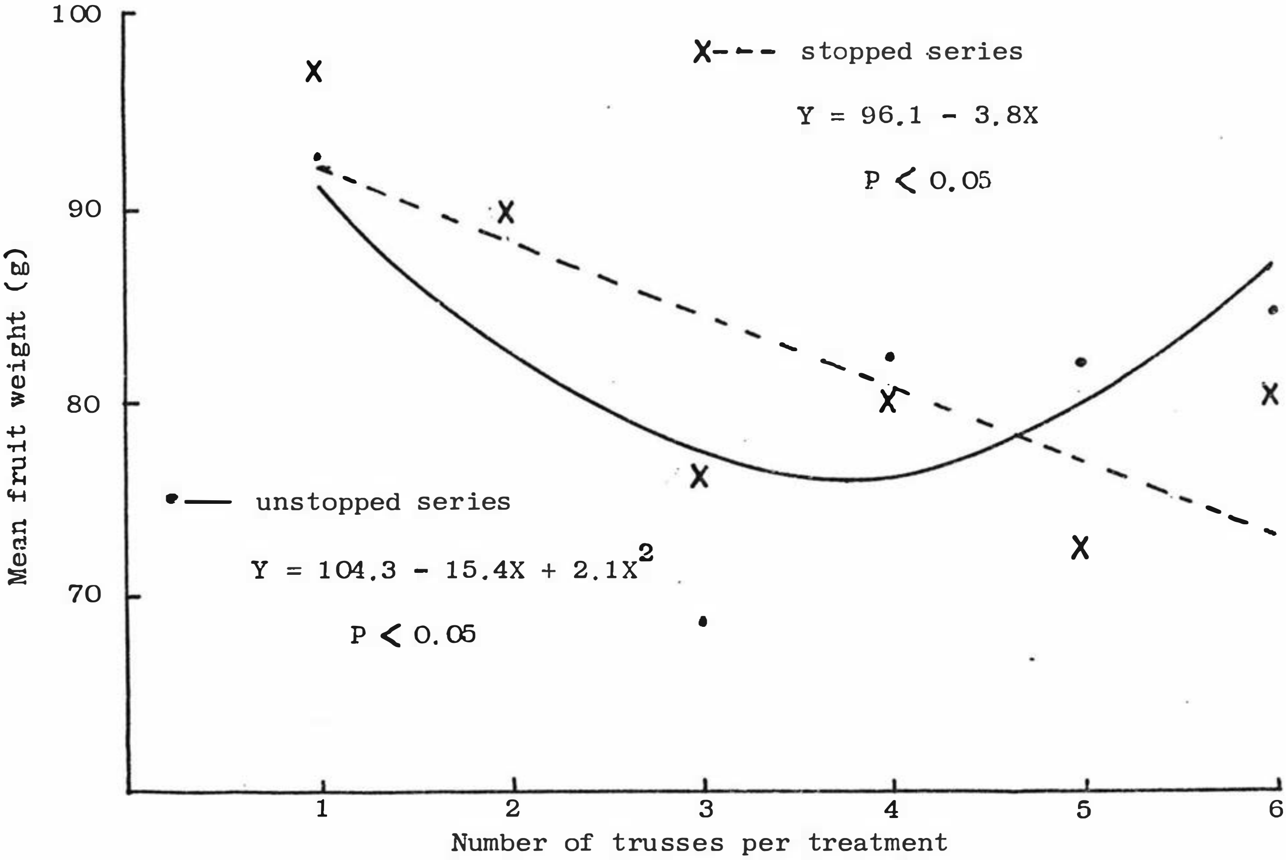


Fig. 5.3. Relation between mean fruit weight truss 1 and truss number.

5.3.2 Fruit yield

5.3.2.1 Yield truss 1

No relationship between the yield of truss 1 and the number of trusses carried above it could be established. Examination of Figure 5.2 suggests however that it is possible to discern a decreasing trend in yield as the number of trusses per treatment increases.

The mean fruit weight in truss 1 decreased with the stopped series ($P < 0.05$) as the number of trusses per treatment increased, while a curvilinear relationship ($P < 0.05$) existed with the unstopped series (Fig. 5.3). It is suggested that the data on mean fruit weight obtained from the stopped series indicate that the apparent decreasing trend in yield with increasing truss number noted above, was probably real. The curvilinear relationship obtained for the unstopped series cannot be explained and is not thought to be meaningful physiologically. No significant treatment effects on fruit number were found, which is in keeping with the apparent lack of treatment effects on fruit yield.

Khan and Sagar (1967) have shown that during the early life of the crop the first truss is a major sink for assimilates for all leaves. It is possible that the lack of any treatment effect could have been due to the sink strength of truss 1 being so great that it was unaffected by the presence of other trusses. However, it is considered more likely that the marked fluctuations in yields, which are apparent in Figure 5.2, indicates that some other factor was disguising treatment effects. Such a factor could have been the level of natural pollination, which despite the damping down could have been variable in this truss. These possibilities are examined in Chapter Six.

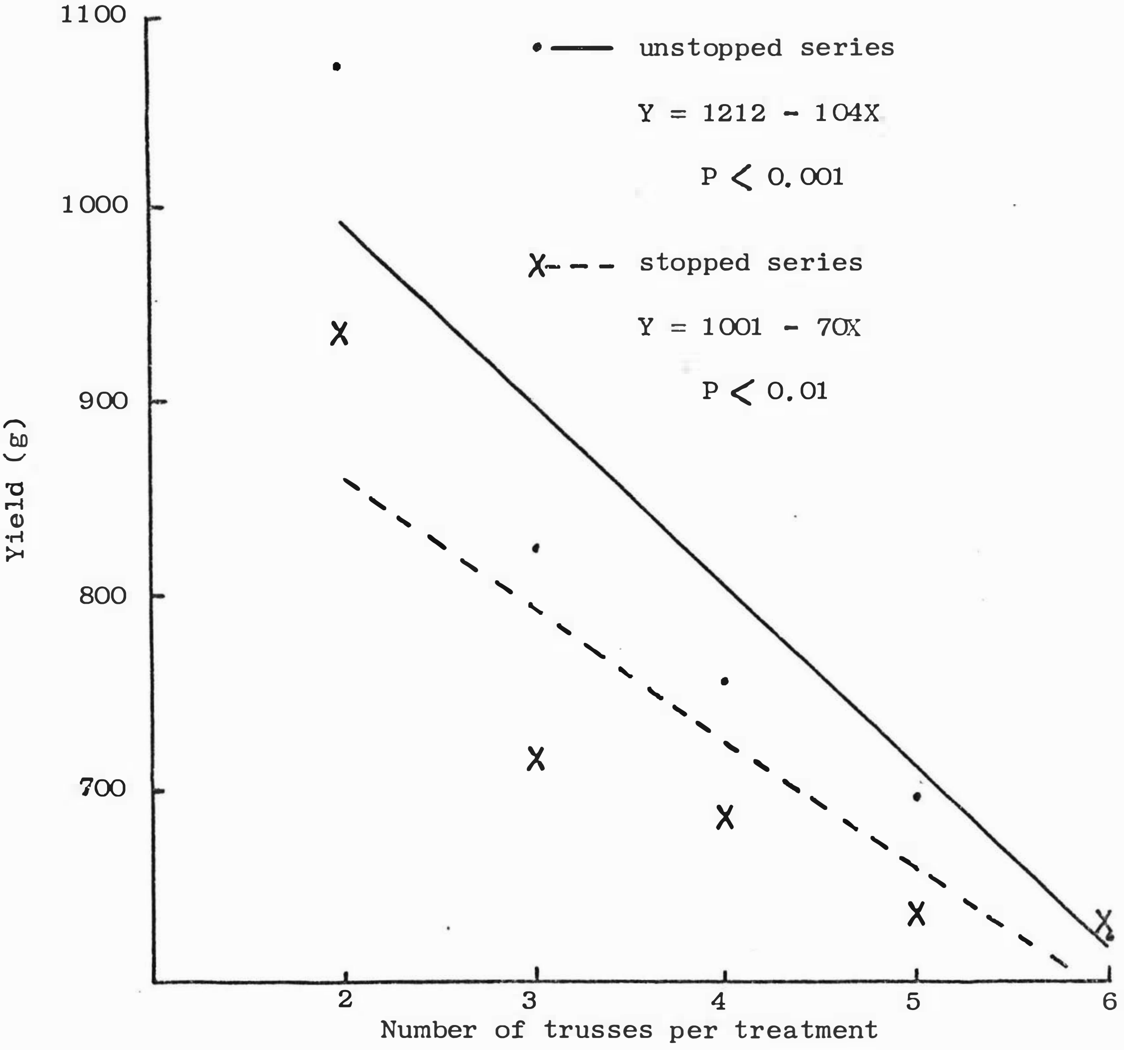


Fig. 5.4. Relation between yield truss 2 and truss number

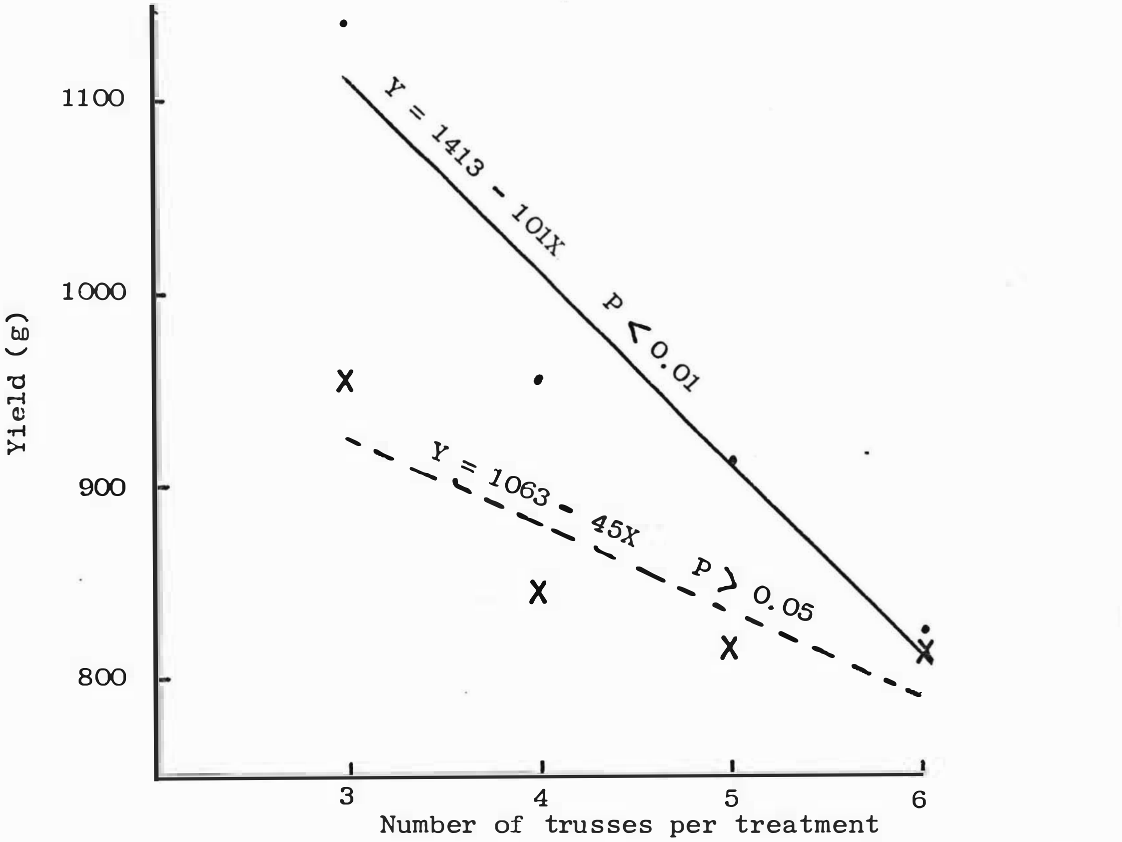


Fig. 5.5. Relation between yield truss 3 and truss number.

5.3.2.2 Yield trusses 2-5

With the unstopped series with trusses 2-4 (Fig. 5.4-6) there were significant linear relationships between the yield of a particular truss and the number of trusses above. The greater the number of trusses carried the smaller the yield of a particular truss. The same trend was apparent with the stopped series, but the linear relationship was only significant ($P < 0.01$) with truss 2. The presence of truss 6 significantly ($P < 0.05$) depressed the yield of truss 5 in the unstopped series, but no significant effects were obtained with the stopped series (Table 5.1).

Table 5.1 Yield truss 5.

Number trusses per plant	Treatment means 5	 6	Significant differences		
Yield truss 5 unstopped (g)	994	719	P 0.05	=	272
Yield truss 5 stopped (g)	894	701	P 0.01	=	350

Significant linear relationships existed for the unstopped series between fruit number for trusses 2 and 3 and the number of trusses above (Fig. 5.7) and between mean fruit weight for trusses 2 and 4 and the number of trusses above (Fig. 5.8). This implies that the reduction in yield of a particular truss due to the presence of subsequent trusses is due to reductions in both number and size of fruit. Cooper and Hurd (1968a) have reported compensation effects between trusses on fruit number and the results of the nitrogen investigation indicated that they may also occur with respect to mean fruit weight (2.4.2).

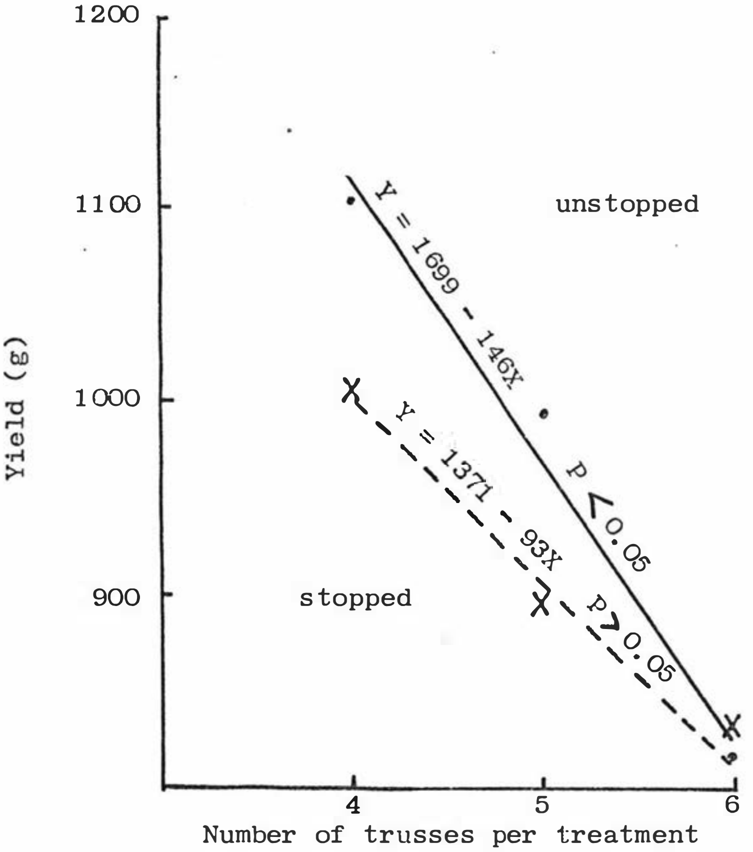


Fig. 5.6. Relation between yield truss 4 and truss number.

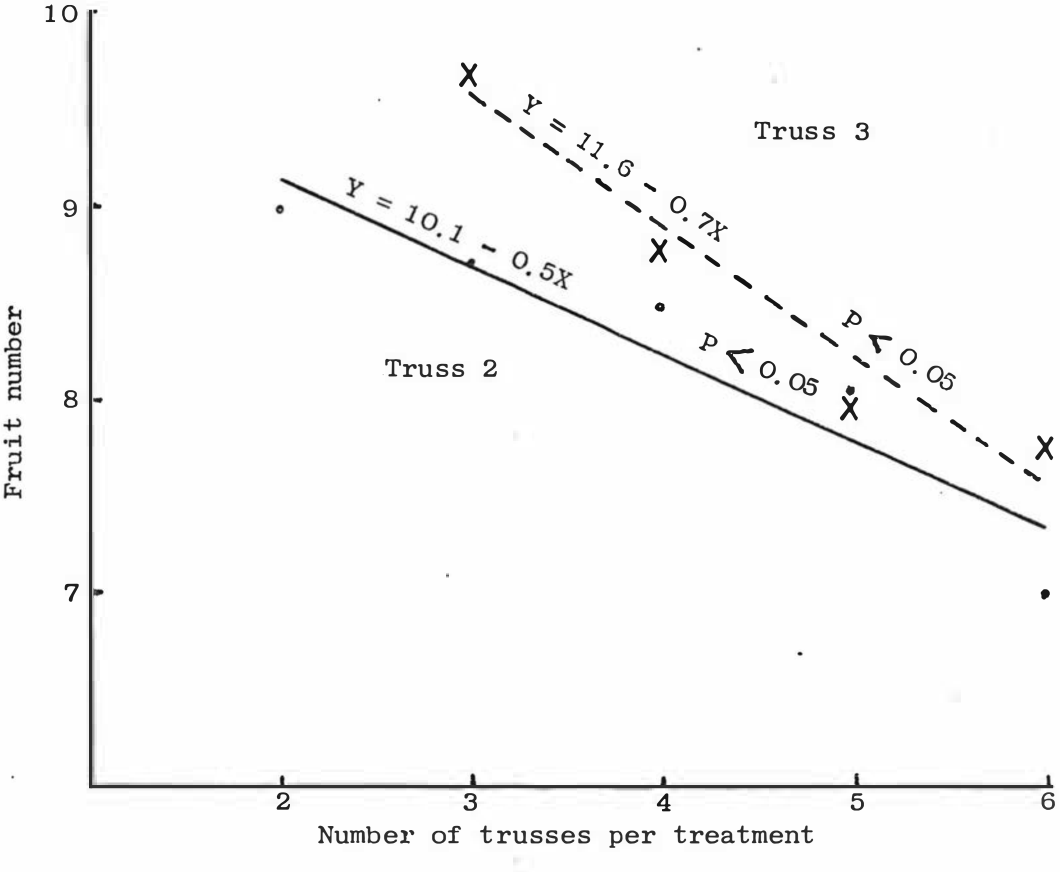


Fig. 5.7. Relation between fruit number trusses 2 and 3 unstopped series and truss number.

The above effects on yield, mean weight and number of fruit on a particular truss by subsequent trusses it is suggested was due to competition for available assimilates. The term competition is considered to be synonymous with the term compensation which has been used by other workers (Cooper, 1964c; Cooper and Hurd, 1968a). The existence of such competition effects, demonstrates that yield is being limited by assimilate supply (source strength).

Although the use of the method of orthogonal polynomials established the existence of significant linear relationships only, examination of the figures for truss 2 (Fig. 5.4) and truss 3 (Fig. 5.5) indicates that the biggest decrease in yield may occur due to competition from the truss immediately above the truss under consideration. Figure 5.4 also shows that a truss as distant as truss 6 still had a competitive role to ply with respect to truss 2.

5.3.2.3 Total yield

There was a significant ($P < 0.001$) linear relationship between total yield and the number of trusses carried for both series (Fig. 5.9). Similar relationships ($P < 0.001$) existed between total fruit number and the number of trusses carried for the two series (Fig. 5.10). This was only to be expected as the increase in yield was due to the increase in fruit number associated with the addition of each truss.

With respect to the unstopped series the use of the method of orthogonal polynomials also showed the quadratic component was significant ($P < 0.001$). This implies that the tendancy for yield to level off with

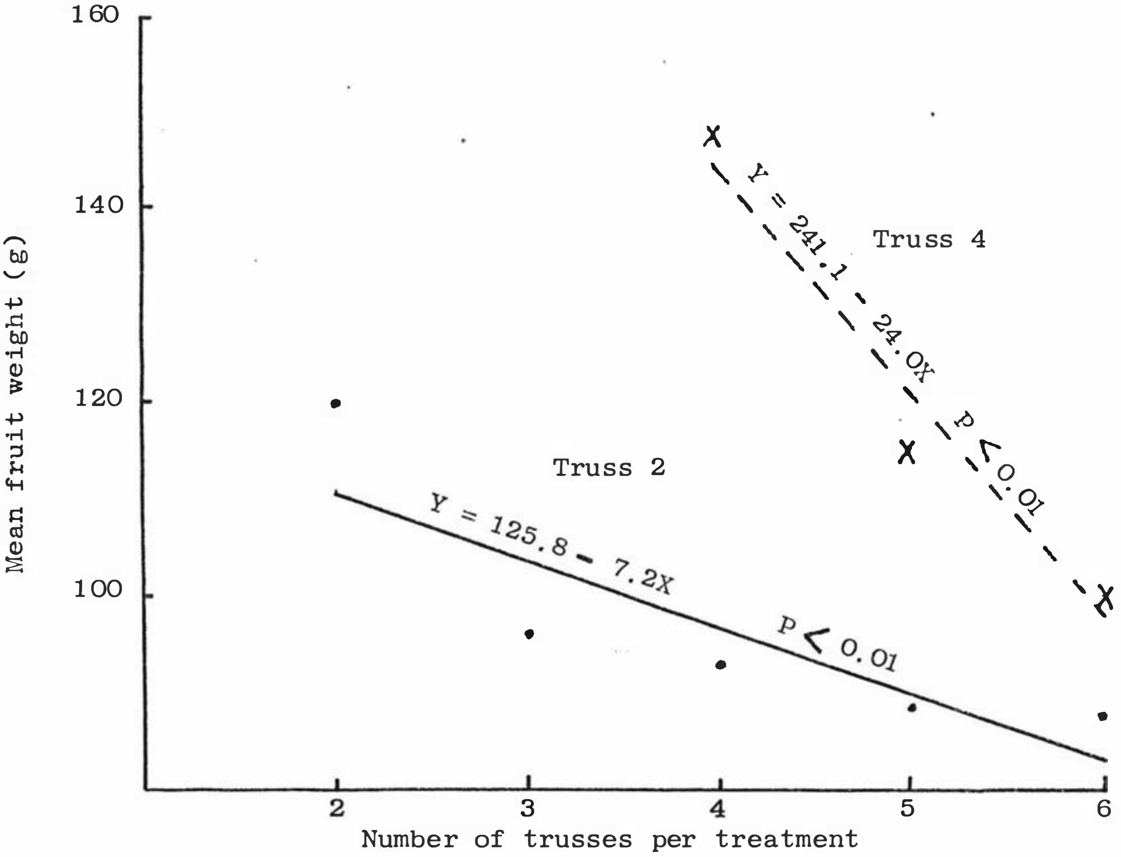


Fig. 5.8. Relation between mean fruit weight trusses 2 and 4 unstopped series and truss number.

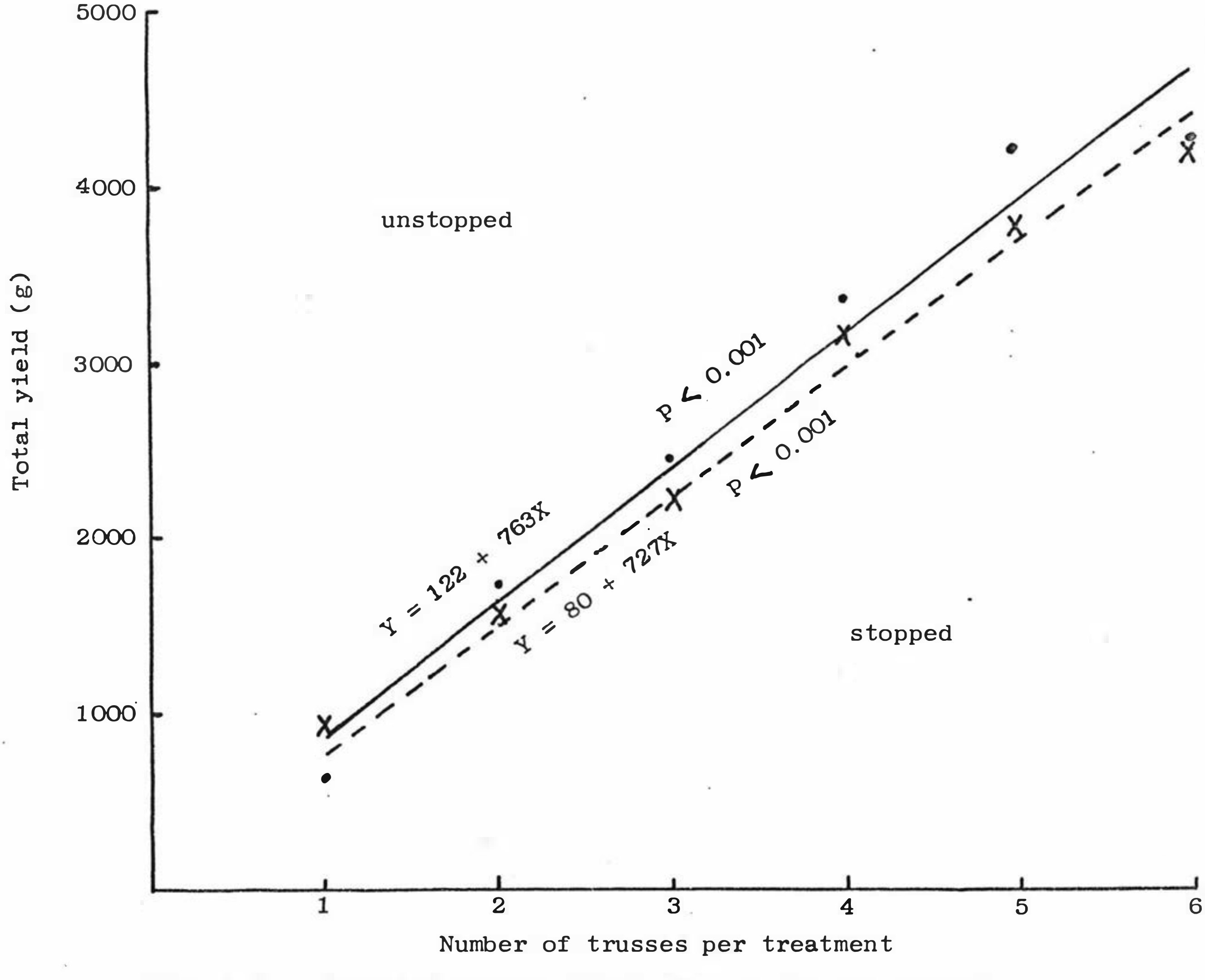


Fig. 5.9. Relation between total yield and truss number.

the addition of truss 6 was a real trend (Fig. 5.9). In this series trusses were added to a fixed number of total leaves so that a fall off in the rate of yield increase with the addition of the last truss was not unexpected. With the stopped series the addition of each truss meant the addition of 3 leaves.

5.3.3 Dry weight of plant top

With the unstopped series the maximum size of the source (leaf area) was limited by the stopping of the plants 2 leaves above inflorescence 6. The actual size was determined by the number of trusses present, with the decrease in dry weight of plant top resulting from the addition of trusses being linear (Fig. 5.11). There was a significant ($P < 0.01$) negative correlation ($r = -0.93$) between fruit fresh weight and dry weight of plant top (Fig. 5.12). A similar relationship between vegetative growth and yield has been reported by Salter (1958) and Cooper (1964c).

In the above series the addition of each truss resulted in increasing the strength of the total economic sinks (trusses), which then obtained assimilate from a source which was decreasing in size. An increase in truss number would therefore be expected to result in a reduction of yield per truss (5.3.2.2).

With the stopped series the dry weight of plant top increased linearly with the addition of each truss (Fig. 5.11). An increase was to be expected as the addition of each truss involved the addition of 3 leaves and the appropriate amount of stem. The significant ($P < 0.001$) correlation ($r = 0.99$) that was found to exist between fruit fresh weight and dry weight of plant top (Fig. 5.12) suggests that the additional leaves were sufficient to meet the extra demands for assimilate that each added truss made.

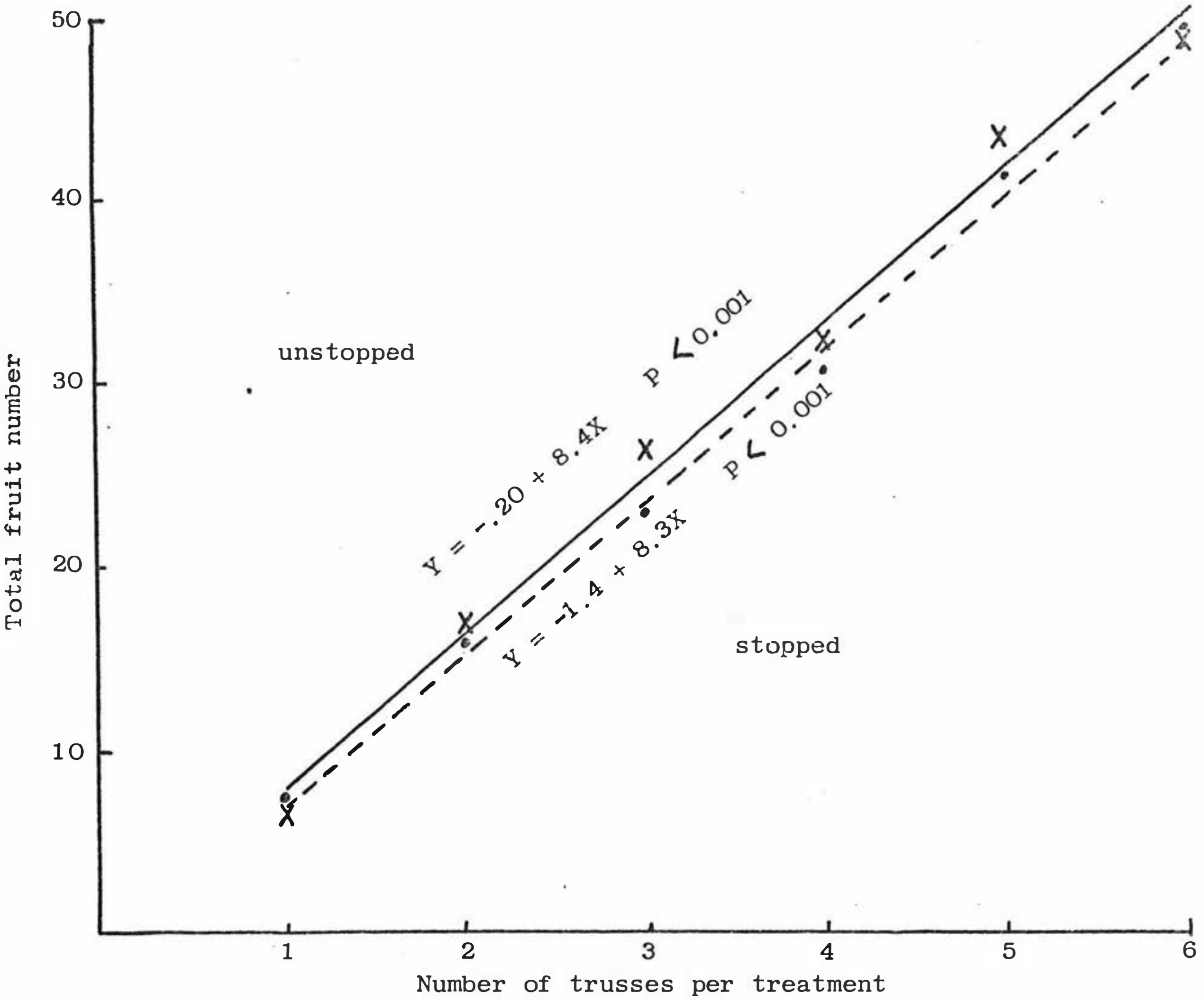


Fig. 5.10. Relation between total fruit number and truss number.

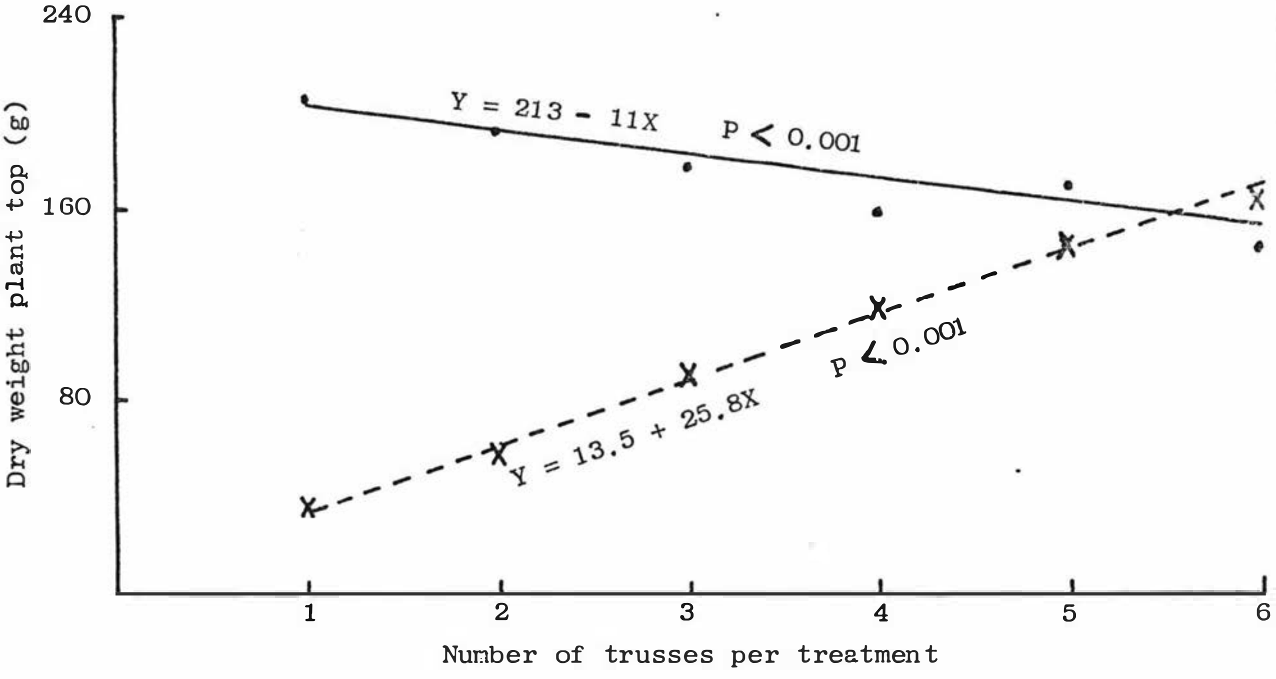


Fig. 5.11. Relation between dry weight of plant top and truss number.

Although no significant differences could be shown to exist between the yield of individual trusses or total yield for the two series, the unstopped series always had the higher yield. This suggests that the extra leaves were of some benefit. In the following section (5.3.4) evidence is presented to suggest that the net assimilation rate in the leaves of the unstopped series was depressed which could be one reason why the differences in yield between the two series was not significant.

5.3.4 Effect of truss number on net assimilation rate of the unstopped series.

A significant ($P < 0.001$) linear relationship was shown to exist between total dry weight of the above ground parts of the plant and the number of trusses present (Fig. 5.13) for the unstopped series. As only fresh fruit weight was determined the contribution that the fruit made to the total dry weight could only be estimated. This was done by assuming that the fruit from all treatments had a dry matter content of 5%. The results of the study on the effect of the amount of leaf tissue on the yield of single-truss tomatoes would suggest that this would not have been so, as there, the dry matter content of the fruit increased as the amount of leaf tissue per truss increased (4.3.1). This would have the effect of increasing the total dry weight in Figure 5.13 for the treatments with the smaller number of trusses, but the effect of any increases would not have been great - at the most 10-12 grams dry weight.

Root dry weight was not included as the relevant data were not collected. It is not considered that this would have varied greatly between treatments and it is likely to have been greatest with plants with the fewer trusses (4.3.3).

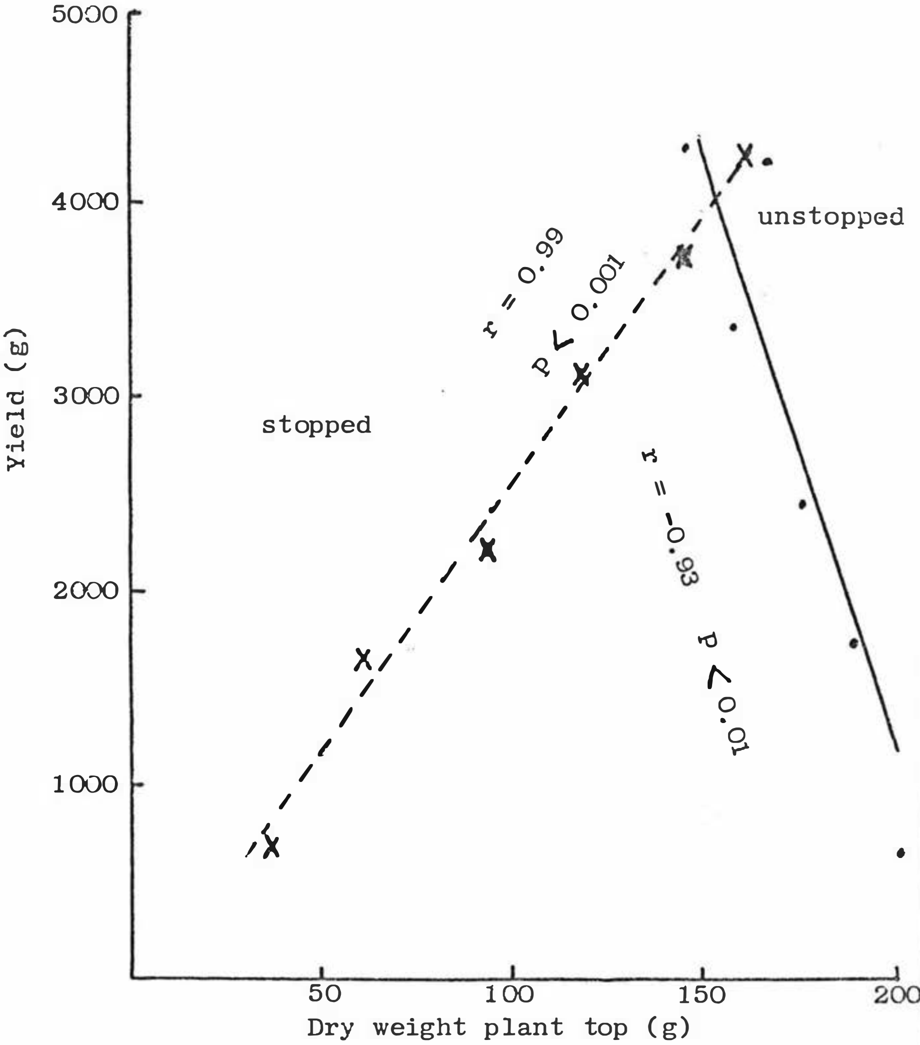


Fig. 5.12. Relation between yield and dry weight of plant top.

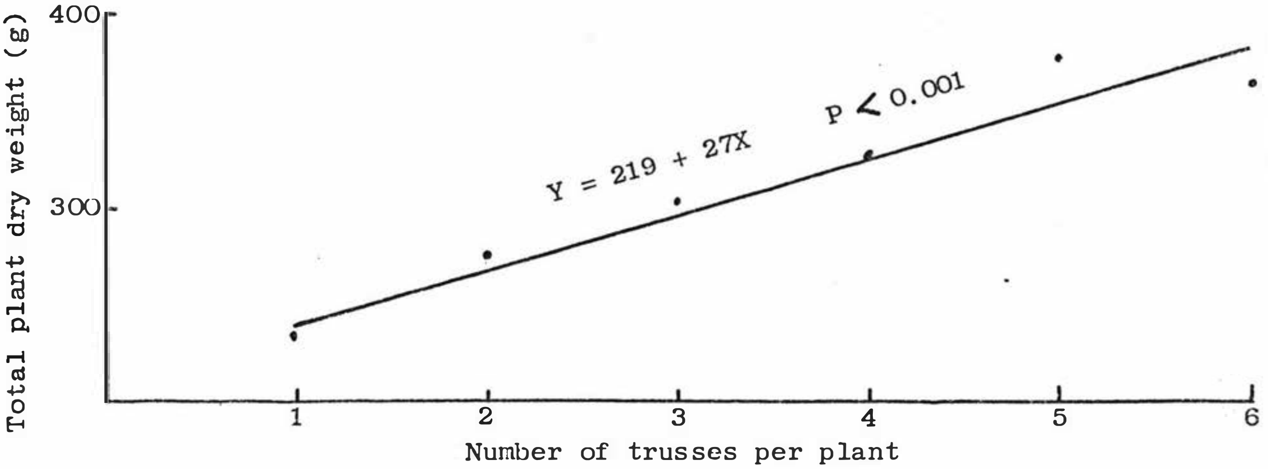


Fig. 5.13. Relation between total plant dry weight (above ground parts unstopped series and truss number.

As total plant dry weight of the above ground parts of the plant increased with increasing truss number this implies that as the strength of the economic sinks increased total dry matter production increased. It is suggested that this could only have been due to the net assimilation rate increasing as sink strength increased. Although leaf area was not measured this would have decreased along with the rest of the shoot as fruit load increased.

An increase in net assimilation rate with increasing economic sink strength suggests that lack of sink strength was limiting economic yield. The increase in yield with the addition of trusses also demonstrates that yield was being limited by lack of sink strength. The existence of competition between adjacent trusses, as demonstrated with plants of the same series (5.3.2.2), can only mean that source and sink strength were simultaneously limiting yield of the unstopped series. It was suggested in Chapter Four that this may occur in the tomato plant (4.3.1) and reference was made to a similar response being reported with both potato (Nöseberger and Humphries, 1965) and wheat (Thorne, Ford and Watson, 1968).

It should be noted that with the exception of the last plant (6 trusses) of this series the various treatments were not typical of commercially grown plants. This could mean that the depression in net assimilation rate reported may not be so apparent with plants where fruit are allowed to develop at each truss.

5.4 Summary

Two series of plants were grown. There were 6 treatments in each series covering the range from 1-6 trusses per plant. In the stopped series plants were stopped 2 leaves above the last truss of each treatment, while in the unstopped series plants were stopped 2 leaves above inflorescence 6 and inflorescences were removed as necessary to produce the 6 treatments.

The yield of trusses 2-5 in the unstopped and the yield of truss 2 in the stopped series were reduced by the presence of trusses subsequent to them. Similar but not significant trends were apparent with trusses 3-5 of the stopped series. It was suggested that the reduction in yield was due to competition between trusses for assimilates resulting in smaller and/or fewer fruit per truss. The dry weight of plant top decreased as trusses were added with the unstopped series and increased with the stopped series. In the later case this was due to the addition of more leaves and stem.

Evidence is presented that the net assimilation rate in the tomato plant can be reduced due to lack of economic sinks and that economic yield can be limited simultaneously by lack of both sink and source strength.

CHAPTER SIX

EFFECTS OF LEAF LEVEL, POLLINATION LEVEL AND TRUSS NUMBER ON GROWTH AND DEVELOPMENT.

6.1 Introduction

The results reported in Chapter Five failed to demonstrate any effects of inter-truss competition on the yield of truss 1. It was suggested that this may have been due to natural pollination varying from plant to plant such that any treatment effects were masked. Also if pollination was generally at a low level in truss 1 then competition effects would be small and hard to detect due to the total economic sink (trusses) strength being low. An alternative explanation was that truss 1 was such a dominant sink that it was unaffected by the presence of other trusses.

It was considered that this problem could be examined by using a low and high level of pollination of truss 1 and study how this effected the response of this truss to the presence of other trusses. Once the decision was made to use 2 pollination levels and 3 truss numbers it became logical to combine these treatments in factorial combination with 3 leaf levels to gain further information on the relationship between source (leaf level) and sink (truss number and pollination level) in the tomato plant.

6.2 Materials and methods

Seed of cv. Eurocross BB was sown on 23rd February 1973 in a U.C. compost (Appendix 21) and germinated at 21°C. At cotyledon expansion the seedlings were pricked out into 13 cm plastic pots containing U.C. compost and grown on in a 6m x 6m glasshouse where a minimum temperature of 16°C was maintained via the heating system and fan ventilation came into operation at 22°C. These temperature settings were maintained throughout the experiment.

On 28th March 1972 72 plants were selected and planted into 9 litre black polythene bags and then allocated at random to the 18 treatments and to the 4 blocks. A randomized block design was used consisting of single plant plots. The treatments consisted of 3 leaf levels, 2 pollination levels and 3 truss numbers combined together in factorial combination.

The plants were stopped 2 leaves above truss 3 and the leaves of the plants were divided into groups of three successive leaves. The leaf levels were obtained by removing leaves as required from each group of 3 starting from the base upwards. Thus leaf level 3 had no leaves removed and levels 2 and 1 had 1 and 2 leaves removed respectively from each group of leaves. The leaves up to truss 1 were removed where necessary at anthesis of truss 1, those up to truss 2 at anthesis of truss 2 and the remaining leaves at anthesis of truss 3.

The pollination levels consisted of natural pollination (-), where pollination took place without any form of assistance, and extra pollination (+) where daily treatment with a battery operated truss vibrator took place of all trusses that had flowers open. Damping down was not carried out as it would have aided the naturally pollinated plants.

The three truss numbers were achieved by leaving all the inflorescences on T_3 plants, removing inflorescence 3 on T_2 plants and inflorescences 3 and 2 on T_1 plants. All the trusses remaining on the plants had flowers removed to ensure that only 6 fruit developed per truss, because it was considered that each truss should have potentially the same sink size. This meant that data were not produced on the effects of the treatments on fruit number and effects on fruit size were not reported as they would not have differed from effects on fruit yield.

The spacing provided an area of $0.25m^2$ per plant and the plants were trained up strings according to standard commercial practice. The 9 litre bags contained a complete fertilize mixture (Appendix 43) which required hose watering only.

The harvesting of fruit commenced on 29th May 1973 and finished on 8th July. The fresh weight of fruit from each truss was recorded and on the final harvest date the plant tops were divided into leaves and stems and dried at 90°C and their dry weights determined.

6.3 Results and discussion

6.3.1 Introduction

The relevant data were analysed as 3 x 3 x 2 factorial experiment. The results of the analyses of variance carried out on these data are presented in Tables 6.1-3, 6.5-6 (Appendices 44-49). The t test was used to calculate significant differences where two means were compared and Tukey's w procedure was used where more than two means were involved.

6.3.2 Yield truss 1 (Table 6.1)

Fruit yield increased as the amount of leaf tissue increased, although the difference between the L_2 and L_3 levels was not significant.

Table 6.1 Treatment effects on yield truss 1.

Treatment		Yield (g)		Significant differences	
				0.05	0.01
Leaf level	L_1	L_2	L_3		
	544	644	677	60.9	78.9
Truss number x pollination interaction	T_1	T_2	T_3		
	- 547	501	508	105.6	127.0
	+ 830	722	646		

There was a significant interaction between truss number and pollination level on yield. Extra pollination increased yield at each level of truss number, but the presence of trusses above truss 1 only produced significant reductions in yield of this truss with extra pollination. Here the yield of truss 1 of plants with 2 or 3 trusses was significantly lower than with plants with only 1 truss. This indicates that competition between truss 1 and the trusses above will only occur when the sink strength of truss 1 has reached a high enough level. If this is low then the yield of this truss will not be greatly affected by the presence of other trusses. In this experiment the truss vibrator was used on all trusses of an extra pollinated plant so that the competition effects between truss 1 and trusses 2 and 3 would have been intensified not only by the pollination of truss 1, but also by the pollination of the later trusses.

This offers an explanation as to why in Chapter Five (5.3.2.1) no such effects were observed with truss 1. It is considered likely that the natural pollination and hence sink strength of truss 1 in that experiment varied from plant to plant independant of treatment, such that it was not possible to establish the existence of any inter truss competition. The above result emphasizes the need for adequate pollination of truss 1 to ensure adequate early yields.

The data presented in this section suggests that the yield of a particular truss can be restricted due to lack of both source and sink strength simultaneously. The following example using treatment means (truss 1) demonstrates this response.

$$\begin{tikzcd}[row sep=large]
\begin{matrix} L_1T_1\ - \\ 491 \end{matrix} \arrow[r, "\text{Sink}", "\text{strength}"'] \arrow[d, "\text{source}"', "\text{strength}"] & \begin{matrix} L_1T_1\ + \\ 762 \end{matrix} \\
\begin{matrix} L_2T_1\ - \\ 549 \end{matrix} \arrow[d, "\text{source}"', "\text{strength}"] & \\
\begin{matrix} L_3T_1\ - \\ 601 \end{matrix} &
\end{tikzcd}$$

Yield of truss 1 in grams.

This subject is discussed with respect to total yield in section 6.3.5.

6.3.3 Yield truss 2 (Table 6.2)

Table 6.2 Treatment effects truss 2.

Treatment		Yield (g)			Significant differences	
					0.05	0.01
Truss number		T_2	T_3			
		510	420		52.1	70.2
Leaf x pollination		L_1	L_2	L_3		
interaction	-	481	444	387	133.6	162.3
	+	362	533	582		

The competitive effect of truss 3 was apparent as the yield of truss 2 of plants carrying 3 trusses was significantly less then with plants where only 2 trusses were carried. This was true of both pollination levels. Thus given time sink strength will build up such that competition occurs between trusses at the lower pollination level. The existence of competition between truss 2 and later trusses was demonstrated in Chapter Five (5.3.2.2).

There was an interaction between leaf level and pollination level on yield. Extra pollination increased yield at the high leaf level (L_3) only, indicating that adequate assimilatory tissue was necessary in this truss to bring out the effect of extra pollination. This is in contrast to truss 1 where extra pollination increased yield at all leaf levels.

This indicates that as the sink strength increases the response to extra pollination will be determined by the source strength. Yield increased as the amount of leaf tissue increased from L_1 with extra pollination. Here the converse of the above is implied. That is the response to additional leaf will be determined by the sink strength. There was no indication in this truss that yield was limited by source and sink considerations simultaneously.

An unusual trend (not significant) was apparent in the naturally pollinated series where yield appeared to fall with increasing leaf level. It is hard to find a satisfactory explanation, but it could possibly demonstrate again that where pollination is not controlled in an experiment then plant to plant variation increases.

6.3.4 Yield truss 3.

No significant treatment effects on the yield of truss 3 were obtained.

6.3.5 Total yield (Table 6.3)

There was a significant interaction between leaf level, truss number and pollination level on total yield. The only significant increase in total yield in response to an increase in leaf level occurred with the plants having the highest sink strength. That is 3 trusses and extra pollination. Here levels L_3 and L_2 produced significantly greater yields than the L_1 level. A similar interaction occurred with respect to the yield of truss 2 (6.3.3). This result is in agreement with the work of Verkerk (1963) who found that intense pollination was necessary if a marked response was to be obtained from additional leaves.

Table 6.3 Treatment effects on total yield.

		Yield (g)		
Truss number	Pollination level	Leaf level		
		1	2	3
1	-	491	549	601
	+	762	848	881
2	-	995	1055	849
	+	1107	1324	1394
3	-	1313	1359	1338
	+	1195	1632	1830
Significant differences		P 0.05 = 336.2,	P 0.01 = 388.1	

With respect to total yield, increases in sink strength were brought about by the addition of trusses and by extra pollination. There was no significant difference in yield between the T_1 and T_2 plants of the naturally pollinated series at the high leaf level (L_3). Otherwise all the differences between the appropriate comparisons (pollination level) in the T_1 and T_2 series were significant as were the differences between the T_2 and T_3 series at the high leaf level (L_3). Differences in yield between the T_1 and T_3 series were all significant and this was only to be expected as the T_3 series represented a further increase in sink strength on the T_2 series. Significant increases due to extra pollination occurred only at the high leaf level (L_3) with the T_2 and T_3 series.

These results imply that total yield will be increased due to increases in sink strength where there is sufficient assimilatory tissue present. This was true of comparisons at the high leaf level (L_3) or comparisons involving truss 1 where the sink strength would be relatively low.

White (1970) reported results which could be interpreted in a similar way. He found no significant effect of pollination on total yield with an autumn crop and reported raw data for a spring crop which indicate that total yield was increased. In the first instance source strength would have been decreasing with time, whereas in the latter case it would have been on the increase during the time that fruit load was building up. The data of Cooper's (1961a) on seasonal effects on leaf length and fruit volume production are in accordance with such a variation in source strength.

The data for truss 1 showed a significant increase in yield occurred both due to extra pollination and to increases in leaf level above the lowest level (6.3.2). Thus the trends apparent in Table 6.3 with respect to truss 1 are real. If this is so then it could be expected that at higher levels of sink strength (T_2 or T_3) increases in yield due to increases in leaf level would be even more likely. This trend is apparent in every instance where leaf level is increased from L_1 to L_2, but is not apparent with naturally pollinated plants as leaf level is increased from L_2 to L_3. This could be due to the vagaries of natural pollination. With respect to extra pollination there was only one comparison (L_3T_3- versus L_3T_3+) where the trend did not imply an increase in yield.

The results of the present study with truss 1 (6.3.2), of the single-truss plants of Chapter Four (4.3.1) and with the unstopped series of the investigation into competition effects between trusses all demonstrated that source and sink considerations could limit yield simultaneously. Similar trends were apparent with respect to total yield here (Table 6.3), but the response was not great. This may indicate that in the tomato this type of response is only marked where sink strength is low. The limiting of yield simultaneously by source and sink considerations has been reported with potato (Nösberger and Humphries, 1965) and wheat (Thorne, Ford and Watson, 1968).

If it is assumed that significant increases in total yield occurred in the present experiment where yield was being limited to a marked extent by lack of source or sink strength, and that the trends apparent in Table 6.3 were generally real and indicative that only small increases in yield were likely as source and sink strengths were close to balance, then the following offers a possible explanation of the results. It is suggested that total yield can only be increased substantially by increases in source strength where sink strength is relatively strong and vice versa. Between these two situations both source and sink are close to balance for those particular environmental conditions and small increases in yield may occur due to increases in either source or sink strength. Presumably in this situation significant increases in yield would only occur where both source and sink strength are raised together.

Source strength would be limited by leaf area and the level of such factors as light intensity and carbon dioxide concentration and sink strength by the number of trusses present, their size and the level of pollination.

Once a sufficient number of trusses are carried on a plant and provided fruit set is satisfactory it is most likely that sink strength is not markedly limiting yield but rather source strength. Thus attempts to increase total yield are most likely to be successful if based on improving conditions for photosynthesis.

6.3.6 Seed number per fruit (Table 6.4).

The seed number per fruit from a sample of similar sized fruit (10 from each pollination level) harvested from truss 1 (18th June) showed that the number was greater in the vibrated than in naturally pollinated fruit. Verkerk (1963) reported a similar finding with the difference being greater in higher trusses and was less when the plants had more leaves. The available evidence suggests that increases in yield due to additional pollination is related to the increase in seed number per fruit.

Table 6.4 Effect of pollination level on seed number per fruit

	Pollination level	
	-	+
mean weight of fruit (g)	110	112
weight of seed/fruit (g)	0.40	0.50
Number of seed/fruit	116	153

6.3.7 Dry weight of plant top (Table 6.5)

The increase in dry weight of plant top with increasing leaf level was only to be expected. The 3 truss series had a significantly lower dry weight than the 1 truss series, while extra pollination significantly reduced the dry weight of plant top. Thus increases in sink strength brought about decreases in vegetative growth. This has been reported previously by Salter (1958) and Cooper (1964c). The decrease in dry weight of plant top must have been due to the diversion of assimilates to fruit production.

It is suggested that in the 1 truss series that the net assimilation rate had been depressed due to lack of sink strength. The evidence presented to support this is that the dry weight of plant top decreased by an average of 9 grams per plant from the 1 truss to the 3 truss series, while the dry weight of fruit increased by an estimated 38 grams per plant. This is an average increase in total plant dry weight of 31 grams due to the addition of sinks T_2 and T_3. It was assumed that any change in dry weight of root was small and as only fresh weights of fruit were recorded the above figure for dry weight of fruit was calculated on the basis that the fruits averaged 5% dry matter content. The results of the previous investigation with the unstopped series also indicated that net assimilation rates can be depressed by lack of sink strength (5.3.4). In both these experiments the evidence was gained from plants some of which were trained to a form not grown commercially.

Table 6.5 Treatment effects on dry weight of plant top.

Treatment	Dry weight (g)			Significant differences	
				0.05	0.01
Leaf level	L_1	L_2	L_3		
	56.9	83.8	112.2	8.56	10.82
Truss number	T_1	T_2	T_3		
	88.8	84.2	79.9	8.56	10.82
Pollination level	-		+		
	89.4		79.2	5.82	7.76

6.3.8 Ratio of dry weight of leaf to dry weight of plant top (Table 6.6)

The ratio of dry weight of leaf to dry weight of plant top was remarkably constant over the wide range of treatments applied. Only one significant difference was observed and this took the form of an interaction between leaf level and pollination level. This interaction was brought about by the plants at the high leaf level (L_3) and low pollination level having a lower ratio. A possible explanation of this is that of the 6 combinations in Table 6.6 this combination would have the largest surplus of assimilates due to the amount of leaf tissue present and the low sink strength. Thus more assimilates could have been used for stem growth or stored in the stem. The constancy of this ratio demonstrates the ability of the tomato plant to maintain a balance between leaf and shoot growth despite the leaf and truss removal treatments.

Table 6.6 Interaction of leaf level and pollination level on ratio of dry weight of leaf to dry weight of plant top.

Ratio $\frac{\text{dry wt leaf}}{\text{dry wt plant top}}$

Pollination level	Leaf level			Significant differences	
	L_1	L_2	L_3	0.05	0.01
-	0.63	0.63	0.59	0.035	0.042
+	0.62	0.63	0.63		

6.4 Summary

The effects of 3 leaf levels, 3 truss numbers and 2 pollination levels in factorial combination on the yield and growth of tomato plants stopped 2 leaves above truss 3 were investigated. The leaf and truss treatments were achieved by removing leaves or trusses and the pollination levels by the use of a truss vibrator.

The yield of truss 1 was increased by an increase in leaf level and by extra pollination. Thus yield was limited simultaneously by lack of source and sink strength. It was considered that if this type of response occurred in later trusses or in total yield then it was only of a minor nature. The yield of the extra pollinated level in truss 1 and both pollination levels in truss 2 was reduced by the presence of subsequent trusses. This suggested that the degree of competition between trusses was influenced by the level of sink strength. Extra pollination increased the yield of truss 2 only at the high leaf level.

Total yield was increased by increases in leaf level when sink strength was high and by additional trusses or extra pollination when the amount of leaf tissue was adequate. The dry weight of plant top decreased as sink strength increased and evidence is presented that suggests that the net assimilation rate in the tomato may be depressed when the sink strength is low. The ratio of dry weight of leaf to dry weight of plant top varied very little with the treatments used.

CHAPTER SEVEN

THE SOURCE ECONOMIC SINK RELATIONSHIP

The following discussion attempts to use the results of the last two experiments and published data to examine certain aspects of the source economic sink relationship in the tomato.

Here the term economic sink strength is used to refer to the individual fruits of a truss and trusses of a plant. Warren Wilson (1972) has defined sink strength as equal to sink size x sink activity, or in terms of total dry matter,

$$\underset{(\mathrm{g\ day^{-1}})}{\text{absolute growth rate}} = \underset{(\mathrm{g})}{\text{dry wt}} \times \underset{(\mathrm{g\ g^{-1}\ day^{-1}})}{\text{relative growth rate}}$$

The total economic sink strength (TESS) at any one point in time will be determined by the sum of the sink strengths at that point in time for each truss. The existence of competition between trusses demonstrates that these trusses are operating below their potential. It is suggested that their potential is determined by the number of flowers present (potential sink size) and the level of pollination (potential sink activity). The factor causing the TESS to be below its potential must be the strength of the source. Source strength has been defined by Warren Wilson (1972) as equal to source size x source activity or,

rate of assimilation per plant (g plant^{-1} day^{-1}) = leaf area per plant (m^2 plant^{-1}) x rate of assimilation per unit leaf area (g m^{-2} day^{-1}).

The growth of fruit has been studied by Salter (1958) and Cooper (1959). They reported that most fruits have a maturity period of 60-70 days so that the maturity period of a truss would be somewhat longer. The maturity period would of course be influenced by the environmental conditions, particularly the temperature regime. This would represent the period when the truss was an active sink and therefore competing with other trusses for assimilates. The above workers reported that the growth rate of individual fruit reached a peak and then fell. Cooper (1959) found that with most fruit 50-60% of the growth occurred in the first half of the maturity period.

Thus the absolute growth rate of a truss must rise to a peak and then fall. As sink strength = absolute growth rate (Warren Wilson, 1972) the variation in sink strength of the truss will be the same. A pattern emerges therefore where the sink strength of each truss rises to a peak and then falls in sequence up the stem. Whenever the maturity periods of these trusses overlap then competition for assimilates may occur. Information on the nature of the absolute growth rates for individual trusses and what their absolute growth rates are at any point in time would aid in the understanding of assimilate distribution in the tomato plant.

The fact that the competitive effect of extra trusses on the yield of an individual truss was explained satisfactorily by a linear relationship (Figs 5.4-6) suggests that the trusses compete on a fairly equal basis when considering the whole growth period of the truss under study. At a particular point however, the contribution that the trusses higher up the plant make towards the competition for assimilates will presumably depend on at what point they are at on their respective growth curves. The data presented in Chapters Five and Six on competition for assimilates between trusses (5.3.2.2; 6.3.2-5) referred only to the effect of trusses above rather than below the truss under examination. That the yield of a truss is affected by the presence of trusses below is demonstrated by the results of the nitrogen experiment. Here the plants that produced a heavy yield early did not produce a heavy yield late (2.4.3).

In the study of competition effects between trusses the yield of truss 2 was limited by the presence of trusses 3-6 (Fig. 5.4), while in the final experiment competition for assimilates reduced the yield of truss 1 when pollination was adequate (6.3.2). The evidence suggests therefore that competition for assimilates can start to limit fruit yield at a very early stage in the life of the tomato crop. Data on absolute growth rates of trusses would again have been useful to establish when competition became important in the growth of truss 2 in 5.3.2.2 and truss 1 in 6.3.2.

Presumably assimilates will be apportioned to trusses with respect to the amount available and their individual sink strengths at that point in time. The transport system and the source may modify this concept by giving some preferential treatment to certain trusses. Thus leaves may favour trusses nearest them (Khan and Sagar, 1966). It is also possible that the position of the truss with respect to the area of most active assimilation may affect its competitive status. Thus leaves higher up the plant are often more active photosynthetically (Wiebe, 1969) so that the lower trusses, which at any point in time will be the more mature, will always be further removed from the site of active photosynthesis. This may affect their competitive status.

It is considered that the evidence available on the source economic sink relationship is not at variance with the proposal of Cooper (1964c) "that the amount of fruit a given tomato plant is able to produce in a given environment is a fixed quantity." In essence this means that for a given variety grown under a given set of environmental conditions that the source economic sink relationship is fixed such that total yield will not vary. There may be plant to plant variations in the yield of a particular truss, but competition effects between trusses operate such that an increase in yield of a particular truss will be compensated for by a reduction in yield in other trusses. Thus the TESS at any point in time is unaffected. The results of the nitrogen experiment with respect to a total yield are in accordance with this possibility (2.4.3).

Cooper's (1961a, 1963) data on seasonal effects on fruit volume production per week must also indicate the variation in maximum TESS per week brought about by seasonal changes in light conditions. These observations plus the relationships reported between the pattern of leaf and fruit growth (Cooper, 1961a) throughout the season are in accordance with Cooper's (1964c) fixed fruit load concept. They are as such a description of the effect of changing light conditions on the source economic sink relationship and although this information is of considerable value it does not offer an explanation of the mechanism of control.

It seems reasonable to conclude that fruit yield in the tomato is initially limited by lack of economic sink strength. However the results presented in Chapters Four (4.3.1), Five (5.3.4) and Six (6.3.2) indicate that yield in the tomato can be limited simultaneously by lack of source and sink strength. It was suggested in Chapter Six (6.3.5) that this type of response appeared to be of significance with plants carrying few trusses such as single truss plants or the yield of truss 1 rather than of total yield of multitruss plants. After this initial stage the plant enters a phase where source and sink strength are near balance and increases in either will produce small increases in yield and it is suggested that the most likely way to increase yield during this phase would be to increase both source and sink strength together (6.3.5). As sink strength builds up then source strength will start to limit yield and the provision of conditions favouring improved photosynthesis should increase yield (6.3.5).

It is important to note that the results from the last two experiments, upon which the above postulations are based, were obtained from plants which had leaf and truss removal treatments applied and were therefore not typical of a commercial type of plant. Also in some instances conclusions were based on trends where the differences were small and it could therefore be questioned as to whether the evidence was strong enough to establish them as real trends with any degree of certainty.

Finally it is suggested that the source economic sink relationship in the tomato is an area of research worthy of greater attention as it should aid our understanding of the relationship between vegetative and reproductive growth and development and help to highlight factor(s) that are limiting yield. Such studies should include at least some work with plants typical of the commercial situation.

LIST OF APPENDICES

Appendix 1

Analysis of variance of flower number truss 1.

Source	SS	df	MS	F	Result
Blocks	2.0	8	0.25	0.46	n.s.
After	11.1	1	11.10	20.56	***
Before	0.1	1	0.10	0.19	n.s.
A x B	0.1	1	0.10	0.19	n.s.
Error	12.7	24	0.54		
Total	26.0	35			

Appendix 2

Analysis of variance of flower number truss 2.

Source	SS	df	MS	F	Result
Blocks	26.1	8	3.26	0.45	n.s.
After	38.0	1	38.00	5.20	*
Before	0.2	1	0.20	0.03	n.s.
A x B	6.3	1	6.30	0.86	n.s.
Error	175.4	24	7.31		
Total	246.0	35			

Appendix 3

Analysis of variance of days to flowering truss 1

Source	SS	df	MS	F	Result
Blocks	67	8	8.38	4.28	**
After	187	1	187.00	95.41	***
Before	196	1	196.00	100.00	***
A x B	93	1	93.00	47.45	***
Error	47	24	1.96		
Total	590	35			

Appendix 4

Analysis of variance of days to flowering truss 2.

Source	SS	df	MS	F	Result
Blocks	70	8	8.76	2.15	n.s.
After	100	1	100.00	35.51	***
Before	2	1	2.00	0.49	n.s.
A x B	2	1	2.00	0.49	n.s.
Error	98	24	4.08		
Total	272	35			

Appendix 5

Analysis of variance of days to flowering truss 3.

Source	SS	df	MS	F	Result
Blocks	11	8	1,37	0.62	n.s.
After	21	1	21.00	9.50	**
Before	3	1	3.00	1.36	n s.
A x B	13	1	13.00	5.88	*
Error	53	24	2.21		
Total	101	35			

Appendix 6

Analysis of variance of days to flowering truss 4.

Source	SS	df	MS	F	Result
Blocks	6	8	0.75	0.33	n.s.
After	4	1	4.00	1.75	n.s.
Before	9	1	9.00	3.93	n.s.
A x B	4	1	4.00	1.75	n.s.
Error	55	24	2.29		
Total	78	35			

Appendix 7

Analysis of variance of days to flowering truss 5.

Source	SS	df	MS	F	Result
Blocks	21.7	8	2.71	1.75	n.s.
After	18.8	1	18.80	12.13	n.s.
Before	0.1	1	0.10	0.06	n.s.
A x B	0.4	1	0.40	0.26	n.s.
Error	37.2	24	1.55		
Total	78.2	35			

Appendix 8

Analysis of variance of shoot dry weight (8 weeks)

Source	SS	df	MS	F	Result
Blocks	13.6	8	1.70	4.03	**
After	138.0	1	138.00	328.57	***
Before	11.0	1	11.00	26.13	***
A x B	5.1	1	5.10	12.11	**
Error	10.1	24	0.42		
Total	177.8	35			

Appendix 9

Analysis of variance of final dry weight.

Source	SS	df	MS	F	Result
Blocks	12 ,570	8	1,571	2.61	*
After	54	1	54	0.09	n.s.
Before	1,067	1	1,067	1.78	n.s.
A x B	802	1	802	1.33	n.s.
Error	14,423	24	601		
Total	28,916	35			

Appendix 10

Analysis of variance of yield truss 1.

Source	SS	df	MS	F	Result
Blocks	187,048	8	23,381	1.11	n.s.
After	33,550	1	33,550	1.59	n.s.
Before	205,662	1	205,662	9.72	**
A x B	1,922	1	1,922	0.09	n.s.
Error	507,785	24	21,158		
Total	935,967	35			

Appendix 11

Analysis of variance of early crop.

Source	SS	df	MS	F	Result
Blocks	1,271,684	8	158,961	2.08	n.s.
After	3,054,921	1	3,054,921	40.06	***
Before	979,110	1	979,110	12.84	**
A x B	572,797	1	572,797	7.51	*
Error	1,830,109	24	76,255		
Total	7,708,621	35			

Appendix 12

Analysis of variance of final crop.

Source	SS	df	MS	F	Result
Blocks	2,438,402	8	304,800	1.63	n.s.
After	72,003	1	72,003	0.39	n.s.
Before	363,609	1	363,609	1.95	n.s.
A x B	3,600	1	3,600	0.02	n.s.
Error	4,483,058	24	186,794		
Total	7,360,672	35			

Appendix 13

Analysis of variance of mean fruit weight truss 1.

Source	SS	df	MS	F	Result
Blocks	929	8	116	0.28	n.s.
After	76	1	76	0.18	n.s.
Before	3,006	1	3,006	7.21	*
A x B	118	1	118	0.28	n.s.
Error	10,003	24	417		
Total	14,134	35			

Appendix 14

Analysis of variance of mean fruit weight truss 2.

Source	SS	df	MS	F	Result
Blocks	1,538	8	193	1.05	n.s.
After	1,272	1	1,272	6.91	*
Before	676	1	676	3.67	n.s.
A x B	427	1	427	2.32	n.s.
Error	4,420	24	184		
Total	8,333	35			

Appendix 15

Analysis of variance of mean fruit weight truss 3.

Source	SS	df	MS	F	Result
Blocks	3,980	8	498	3.23	*
After	192	1	192	1.25	n.s.
Before	1,237	1	1,237	8.03	**
A x B	12	1	12	0.08	n.s.
Error	3,693	24	154		
Total	9,114	35			

Appendix 16

Analysis of variance of mean fruit weight early crop.

Source	SS	df	MS	F	Result
Blocks	1,423	8	178	0.62	n.s.
After	1,345	1	1,345	4.69	*
Before	1,444	1	1,444	5.03	*
A x B	608	1	608	2.12	n.s.
Error	6,878	24	287		
Total	11,698	35			

Appendix 17

Analysis of variance of mean fruit weight final crop.

Source	SS	df	MS	F	Result
Blocks	799	8	100	1.07	n.s.
After	324	1	324	3.48	n.s.
Before	87	1	87	0.94	n.s.
A x B	1	1	1	0.01	n.s.
Error	2,229	24	93		
Total	3,440	35			

Appendix 18

Analysis of variance of fruit number early crop.

Source	SS	df	MS	F	Result
Blocks	144	8	18	1.38	n.s.
After	289	1	289	22.23	***
Before	88	1	88	6.77	*
A x B	53	1	53	4.08	n.s.
Error	309	24	13		
Total	883	35			

Appendix 19

Analysis of variance of leaf area per unit shoot dry weight.

Source	SS	df	MS	F	Result
Blocks	.0456	8	.0057	1.06	n.s.
After	.0032	1	.0032	0.59	n.s.
Before	.1296	1	.1296	24.00	***
A x B	.1547	1	.1547	28.65	***
Error	.1298	24	.0054		
Total	.4629	35			

Appendix 20

Analysis of variance of shoot dry matter content.

Source	SS	df	MS	F	Result
Blocks	2.10	8	0.263	4.24	**
After	2.87	1	2.870	46.29	***
Before	0.28	1	0.280	4.52	*
A x B	1.38	1	1.380	22.26	***
Error	1.48	24	0.062		
Total	8.11	35			

Appendix 21

U.C. Compost

Fertilizer mixture added to 50/50 peat sand compost.

Fertilizer	$g\ m^{-3}$
Uramite	889
potassium nitrate	148
potassium sulphate	148
superphosphate	1483
dolomite lime	1483
ground lime	1483

The above is a modification of the IIc mixture recommended by the University of California.

Appendix 22

Fertilizer mixture added to 50/50 peat sand compost and then used for growing plants in the investigation of temperature effects during propagation on the yield of single-truss tomatoes. This fertilized compost was applied at the rate of 9,000 cm^3 $plant^{-1}$.

Fertilizer	$Kg\ m^{-3}$
osmocote 18. 3.9. 7.5	3.09
potassium sulphate	1.33
superphosphate	1.48
dolomite lime	4.12
ground lime	1.48
chelated iron	0.04

	N	P	K
g $plant^{-1}$	5.0	2.3	6.8

Appendix 23

Analysis of variance of yield.

Source	SS	df	MS	F	Result
Blocks	138,565	14	9,898	1.02	n.s.
After	133,671	1	133,671	13.77	***
Before	590,042	1	590,042	60.80	***
A x B	6	1	6	-	n.s.
Error	407,547	42	9,704		
Total	1,269,831	59			

Appendix 24

Analysis of variance of fruit number.

Source	SS	df	MS	F	Result
Blocks	40	14	2.86	1.29	n.s.
After	40	1	40.00	18.09	***
Before	206	1	206.00	93.21	***
A x B	3	1	3.00	1.36	
Error	93	42	2.21		
Total	382	59			

Appendix 25

Analysis of variance of mean fruit weight.

Source	SS	df	MS	F	Result
Blocks	1,897	14	136	1.94	n.s.
After	363	1	363	5.19	*
Before	1,044	1	1,044	14.91	***
A x B	254	1	254	3.63	n.s.
Error	2,942	42	70		
Total	6,500	59			

Appendix 26

Analysis of variance of yield (6 treatments)

Source	SS	df	MS	F	Result
Block	89,266	14	6,376	0.64	n.s.
Treatment	1,161,855	5	232,371	23.44	***
Error	693,899	70	9,913		
Total	1,945,020	89			

Appendix 27

Analysis of variance of dry weight plant top.

Source	SS	df	MS	F	Result
Blocks	218	14	16	1.14	n.s.
After	870	1	870	62.14	***
Before	1	1	1	0.07	n.s.
A x B	499	1	499	35.64	***
Error	587	42	14		
Total	2,175	59			

Appendix 28

Fertilizer mixture added to 50/50 peat sand compost and then used for growing plants in the study of competition effects between trusses. This fertilized compost was applied at the rate of 9,000 cm^3 $plant^{-1}$.

Fertilizer	$Kg\ m^{-3}$
osmocote 18. 2.6. 10	8.82
osmocote 12. 0. 34.8	1.48
superphosphate	1.48
dolomite lime	4.42
ground lime	1.48
chelated iron	0.04

		N	P	K
g	$plant^{-1}$	15.9	3.3	12.6
*Kg	ha^{-1}	588	121	465

* based on 37,000 plants ha^{-1}

Appendix 29

Analysis of variance of yield truss 1.

Source	SS	df	MS	F	Result
Blocks	60,336	5	12,067	0.65	n.s.
Treatments	185,036	11	16,821	0.90	n.s.
Unstopped:					
linear	1,180	1	1,180	0.06	n.s.
quadratic	8,592	1	8,592	0.46	n.s.
cubic	686	1	686	0.04	n.s.
quartic	44,851	1	44,851	2.41	n.s.
quintic	14,954	1	14,954	0.80	n.s.
Stopped:					
linear	62,001	1	62,001	3.33	n.s.
quadratic	24,598	1	24,598	1.32	n.s.
cubic	59	1	59	0.003	n.s.
quartic	444	1	444	0.02	n.s.
quintic	27,370	1	27,370	1.47	n.s.
Between	300	1			
Error	1,024,511	55	18,627		
Total	1,269,883	71			

Appendix 30

Analysis of variance of mean fruit weight truss 1.

Source	SS	df	MS	F	Result
Blocks	1,050	5	210	0.95	n.s.
Treatments	4,344	11	395	1.79	n.s.
Unstopped:					
linear	60	1	60	0.27	n.s.
quadratic	975	1	975	4.41	*
cubic	300	1	300	1.36	n.s.
quartic	39	1	39	0.18	n.s.
quintic	420	1	420	1.90	n.s.
Stopped:					
linear	1,531	1	1,531	6.93	*
quadratic	712	1	712	3.22	n.s.
cubic	16	1	16	0.07	n.s.
quartic	2	1	2	0.01	n.s.
quintic	282	1	282	1.28	n.s.
Between	6	1			
Error	12,142	55	221		
Total	17,536	71			

Appendix 31

Analysis of variance of yield truss 2.

Source	SS	df	MS	F	Result
Blocks	122,187	5	24,437	0.82	n.s.
Treatments	1,194,215	9	132,691	4.45	***
Unstopped:					
linear	652,510	1	652,501	21.88	***
quadratic	51,257	1	51,257	1.72	n.s.
cubic	24,442	1	24,442	0.82	n.s.
quartic	1,644	1	1,644	0.06	n.s.
Stopped:					
linear	293,300	1	293,300	9.83	**
quadratic	70,586	1	70,586	2.37	n.s.
cubic	12,470	1	12,470	0.42	n.s.
quartic	7,200	1	7,200	0.24	n.s.
Between	80,813	1			
Error	1,342,048	45	29,823		
Total	2,658,450	59			

Appendix 32

Analysis of variance of yield truss 3.

Source	SS	df	MS	F	Result
Blocks	91,230	5	18,246	0.49	n.s.
Treatments	526,999	7	75,286	2.03	n.s.
Unstopped:					
linear	306,535	1	306,535	8.26	**
quadratic	15,060	1	15,060	0.41	n.s.
cubic	10,175	1	10,175	0.27	n.s.
Stopped:					
linear	61,427	1	61,427	1.66	n.s.
quadratic	17,767	1	17,767	0.48	n.s.
cubic	992	1	992	0.03	n.s.
Between	115,062	1			
Error	1,298,516	35	37,100		
Total	1,916,745	47			

Appendix 33

Analysis of variance of yield truss 4.

Source	SS	df	MS	F	Result
Blocks	117,133	5	23,427	0.66	n.s.
Treatments	395,900	5	79,180	2.23	n.s.
Unstopped:					
linear	253,171	1	253,171	7.13	*
quadratic	3,948	1	3,948	0.11	n.s.
Stopped:					
linear	103,045	1	103,045	2.90	n.s.
quadratic	642	1	642	0.02	n.s.
Between	35,094	1			
Error	887,745	25	35,510		
Total	1,400,778	35			

Appendix 34

Analysis of variance of yield truss 5.

Source	SS	df	MS	F	Result
Blocks	130,321	5	26,064	0.98	n.s.
Treatments	359,842	3	119,947	4.50	*
Error	400,129	15	26,675		
Total	890,292	23			

Appendix 35

Analysis of variance of fruit number truss 2.

Source	SS	df	MS	F	Result
Blocks	14.1	5	2.8	1.00	n.s.
Treatments	48.0	9	5.3	1.89	n.s.
Unstopped:					
linear	13.1	1	13.1	4.68	*
quadratic	1.2	1	1.2	0.43	n.s.
cubic	0.3	1	0.3	0.11	n.s.
quartic	0.0	1	0.0	0.00	n.s.
Stopped:					
linear	7.4	1	7.4	2.64	n.s.
quadratic	2.7	1	2.7	0.96	n.s.
cubic	8.8	1	8.8	3.14	n.s.
quartic	0.7	1	0.7	0.25	n.s.
Between	14.0	1			
Error	125.1	45	2.8		
Total	187.2	59			

Appendix 36

Analysis of variance of fruit number truss 3.

Source	SS	df	MS	F	Result
Blocks	4.80	5	0.96	0.28	n.s.
Treatments	21.30	7	3.04	0.90	n.s.
Unstopped:					
linear	14.01	1	14.01	4.16	*
quadratic	0.38	1	0.38	0.11	n.s.
cubic	0.08	1	0.08	0.02	n.s.
Stopped:					
linear	0.21	1	0.21	0.06	n.s.
quadratic	1.04	1	1.04	0.31	n.s.
cubic	5.21	1	5.21	1.55	n.s.
Between	0.33	1			
Error	117.90	35	3.37		
Total	144.00	47			

Appendix 37

Analysis of variance of mean fruit weight truss 2.

Source	SS	df	MS	F	Result
Blocks	1,167	5	233	0.53	n.s.
Treatments	7,169	9	797	1.83	n.s.
Unstopped:					
linear	3,197	1	3,197	7.33	**
quadratic	920	1	920	2.11	n.s.
cubic	163	1	163	0.37	n.s.
quartic	66	1	66	0.15	n.s.
Stopped:					
linear	960	1	960	2.20	n.s.
quadratic	76	1	76	0.17	n.s.
cubic	882	1	882	2.02	n.s.
quartic	600	1	600	1.38	n.s.
Between	304	1			
Error	19,599	45	436		
Total	27,935	59			

Appendix 38

Analysis of variance of mean fruit weight truss 4.

Source	SS	df	MS	F	Result
Blocks	4,659	5	932	1.40	n.s.
Treatments	10,938	5	2,188	3.28	*
Unstopped:					
linear	6,912	1	6,912	10.36	**
quadratic	245	1	245	0.37	n.s.
Stopped:					
linear	1,344	1	1,344	2.01	n.s.
quadratic	51	1	51	0.08	n.s.
Between	2,385	1			
Error	16,666	25	667		
Total	32,263	35			

Appendix 39

Analysis of variance of total yield.

Source	SS	df	MS	F	Result
Blocks	152,196	5	30,439	0.32	n.s.
Treatments	119,955,620	11	10,905,056	115.15	***
Unstopped:					
linear	61,172,007	1	61,172,007	645.93	***
quadratic	1,823,060	1	1,823,060	19.25	***
cubic	202,596	1	202,596	2.14	n.s.
quartic	309,944	1	309,944	3,27	n.s.
quintic	3,213	1	3,213	0.03	n.s.
Stopped:					
linear	55,472,283	1	55,472,283	585.74	***
quadratic	275,755	1	275,756	2.91	n.s.
cubic	46,506	1	46,506	0.49	n.s.
quartic	47,706	1	47,706	0.50	n.s.
quintic	83,720	1	83,720	0.88	n.s.
Between	518,841	1			
Error	5,208,727	55	94,704		
Total	125,316,543	71			

Appendix 40

Analysis of variance of total fruit number.

Source	SS	df	MS	F	Result
Blocks	43	5	9	0.69	n.s.
Treatments	14,772	11	1,343	103.31	***
Unstopped:					
linear	7,367	1	7,367	566.69	***
quadratic	38	1	38	2.92	n.s.
cubic	1	1	1	0.08	n.s.
quartic	24	1	24	1.85	n.s.
quintic	17	1	17	1.31	n.s.
Stopped:					
linear	7,267	1	7,267	559.00	***
cubic	5	1	5	0.38	n.s.
quadratic	0	1	0	0	n.s.
quartic	19	1	19	1.46	n.s.
quintic	2	1	2	0.15	n.s.
Between	32	1			
Error	688	55	13		
Total	15,503	71			

Appendix 41

Analysis of variance of dry weight plant top.

Source	SS	df	MS	F	Result
Blocks	1,978	5	396	1.26	n.s.
Treatments	174,641	11	15,876	50.56	***
Unstopped:					
linear	12,410	1	12,410	39.52	***
quadratic	210	1	210	0.67	n.s.
cubic	74	1	74	0.24	n.s.
quartic	750	1	750	2.39	n.s.
quintic	535	1	535	1.70	n.s.
Stopped:					
linear	69,737	1	69,737	222.09	***
quadratic	203	1	203	0.65	n.s.
cubic	147	1	147	0.47	n.s.
quartic	7	1	7	0.02	n.s.
quintic	43	1	43	0.14	n.s.
Between	90,525	1			
Error	17,268	55	314		
Total	193,885	71			

Appendix 42

Analysis of variance of total plant dry weight (above ground parts) - unstopped series.

Source	SS	df	MS	F	Result
Blocks	6,122	5	1,224	1.83	n.s.
Treatments	85,423	5	17,085	25.50	***
linear	78,201	1	78,201	116.72	***
quadratic	2,791	1	2,791	4.17	n.s.
cubic	952	1	952	1.42	n.s.
quartic	3,062	1	3,062	4.56	*
quintic	428	1	428	0.64	n.s.
Error	16,761	25	670		
Total	108,306	35			

Appendix 43

Fertilizer mixture added to 50/50 peat sand compost and then used for growing plants in the study of the effects of leaf level, pollination level and truss number on growth and development. This fertilized compost was applied at the rate of 9,000 cm^3 $plant^{-1}$.

Fertilizer	$Kg\ m^{-3}$
osmocote 18. 2.6. 10	5.88
osmocote 12.0. 34.8	1.18
potassium sulphate	1.48
superphosphate	1.48
dolomite lime	4.42
ground lime	1.48

Trace elements	$g\ m^{-3}$
borax	13.8
copper sulphate	25.2
iron sulphate	41.4
iron chelate	41.4
manganese sulphate	16.8
zinc sulphate	16.8
sodium molybdate	2.8

	N	P	K
$g\ plant^{-1}$	10.8	2.6	14.2
$Kg\ ha^{-1}$	399	95	524

Appendix 44

Analysis of variance of yield truss 1.

Source	SS	df	MS	F	Result
Blocks	21,811	3	7,270	0.95	n.s.
Leaf	194,384	2	97,192	12.74	***
Truss	162,285	2	81,143	10.63	***
Pollination	840,024	1	840,024	110.07	***
LT	25,766	4	6,442	0.84	n.s.
LP	28,789	2	14,395	1.89	n.s.
TP	59,342	2	29,671	3.89	*
LTP	24,690	4	6,173	0.81	n.s.
Error	389,206	51	7,632		
Total	1,746,296	71			

Appendix 45

Analysis of variance of yield truss 2.

Source	SS	df	MS	F	Result
Blocks	9,967	3	3,322	0,43	n.s.
Leaf	45,053	2	22,527	2.88	n.s.
Truss	97,560	1	97,560	12.49	**
Pollination	36,300	1	36,300	4.65	*
LT	40,377	2	20,189	2.59	n.s.
LP	202,767	2	101,384	12.96	**
TP	12,741	1	12,741	1.63	n.s.
LTP	6,864	2	3,432	0.44	n.s.
Error	257,685	33	7,809		
Total	700,314	47			

Appendix 46

Analysis of variance of yield truss 3.

Source	SS	df	MS	F	Result
Blocks	46,981	3	15,660	3.27	n.s.
Leaf	9,706	2	4,853	1.01	n.s.
Pollination	15,352	1	15,352	3.21	n.s.
LP	20,695	2	10,348	2.16	n.s.
Error	71,730	15	4,782		
Total	164,464	23			

Appendix 47

Analysis of variance of total yield.

Source	SS	df	MS	F	Result
Blocks	21,169	3	7,056	0.42	n.s.
Leaf	421,564	2	210,782	12.58	***
Truss	6,909,111	2	3,454,556	206.11	***
Pollination	1,306,526	1	1,306,526	77.95	***
LT	176,229	4	44,057	2.63	*
LP	370,384	2	185,192	11.05	***
TP	27,695	2	13,848	0.83	n.s.
LTP	205,354	4	51,339	3.06	*
Error	854,797	51	16,761		
Total	10,292,829	71			

Appendix 48

Analysis of variance of dry weight plant top.

Source	SS	df	MS	F	Result
Blocks	5,343	3	1,781	11.79	***
Leaf	36,639	2	18,320	121.32	***
Truss	963	2	482	3.19	*
Pollination	1,860	1	1,860	12.32	**
LT	100	4	25	0.17	n.s.
LP	657	2	329	2.18	n.s.
TP	664	2	332	2.20	n.s.
LTP	1,274	4	319	2.11	n.s.
Error	7,719	51	151		
Total	55,219	71			

Appendix 49

Analysis of variance of leaf dry weight to dry weight of plant top.

Source	SS	df	MS	F	Result
Blocks	.0019	3	.00063	0.74	n.s.
Leaf	.0040	2	.00200	2.35	n.s.
Truss	.0001	2	.00005	0.06	n.s.
Pollination	.0027	1	.00270	3.17	n.s.
LT	.0009	4	.000225	0.26	n.s.
LP	.0074	2	.00370	4.35	*
TP	.0003	2	.000150	0.18	n.s.
LTP	.0044	4	.001100	1.29	n.s.
Error	.0434	51	.000851		
Total	.0651	71			

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