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EFFECTS OF ENVIRONMENT ON FLOWERING AND FRUIT SET IN SWEET PEPPER *{Capsicum annuum* L.)

by

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To my late parents,

Chief Enisin and Mrs Onaolapo Olarewaju

Abbreviations

Chap.	Chapter
Exp.	Experiment
(F)	Warm-white fluorescent lamps
Fig.	Figures
GA_3	Gibberellic acid
h	hours
NOA	Beta-naphthoxyacetic acid
ppm	parts per million
(T)	Tungsten-filament lamps
Tween 20	Polyoxyethylene sorbitan mon-oleate
W	Watts

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ABSTRACT

Effects of environment on flowering and fruit set in sweet pepper *{Capsicum annuum* L.)

A study was made of factors affecting flowering and fruit set in pepper plants grown from seed. The duration of the initial vegetative phase of growth was prolonged when radiant exposures were low, as in the winter or when shading was used in the summer. The change from vegetative to reproductive development was also delayed by a reduction in night temperatures from 20°C to 13°C. It is suggested that radiant exposure and night temperature affected flower initiation through effects on the rate of growth and development of the whole plant rather than on processes specific to the control of flowering.

In experiments designed to examine responses to long and short photoperiods, results varied with the source of illumination used in providing the long-day treatments. Extension of an 8h day to 18h by the use of low intensity illumination from tungsten-filament lamps delayed flower initiation by a few days but when warm-white fluorescent lamps were used to extend the day the time to flower initiation was unaffected.

A proportion of the flowers initiated stopped growing in the bud stage and aborted. Conditions found to be conducive to flower abortion were low radiant exposures, high night temperatures, long-day treatments produced by the use of tungsten filament lamps and infrequent watering.

Pollination and fertilization were not prerequisites

for fruit set since parthenocarpic fruit development could occur. The incidence of parthenocarpy was high when night temperatures were low. Low radiant exposures, high night temperatures and infrequent watering were unfavourable to fruit set and led to increases in the proportion of flowers that were shed after opening. Under some conditions the proportion of open flowers that set fruits could be increased by pruning the plants to reduce the number of leading shoots or by spraying with B-naphthoxyacetic acid.

Chapter 1

Introduction

Pepper is an important vegetable in Nigeria and up to 1970 peppers were exported to supply world markets. Since then the volume of export trade has been considerably reduced due to a rising domestic demand. In Nigeria sweet pepper is cultivated outdoors as either a rainfed or irrigation crop, mainly in northern States. The area of land devoted to the crop is not known; production has been mainly limited to peasant farmers and statistics on the crop are difficult to collect. The long-term objective of research on peppers in Nigeria will be the production of crops sufficient to meet domestic demand and also to restore the export trade.

In the United Kingdom over the past few years, sweet pepper has gained in popularity with the British public both as a cooked vegetable and for use in salads. The area devoted to sweet pepper in England and Wales in 1978 was 40 hectares while tomatoes, the most important of the protected crop on an area basis, occupied 868 hectares (Ministry of Agriculture, Fisheries and Food, 1978). In the United Kingdom peppers are grown under glass or film plastics. Cropping programmes and practices are based on those developed for tomatoes, because the two crops have similar life cycles and general requirements. The amount of experimental work that has been carried out on effects of environment on growth and development is much less for peppers than for tomatoes.

The developmental sequences that lead to the formation of fruits in sweet pepper plants may be described in terms of the whole plant and also in terms of the individual flowers. After germination of the seed there is a vegetative stage during which a primary shoot bearing a number of leaves is produced. The initiation of leaves on the shoot ceases with the initiation of flowers at the apex. From this stage the stem system develops as a sympodium with the production of successive orders of lateral shoots. The time to initiation of the first flowers at the apex of the primary shoot varies with the environment as also does the number of leaves formed on the shoot before the flowers are initiated.

After the first flowers have been initiated, further flowers are initiated terminally on the lateral shoots. The rate at which these flowers are initiated may vary with the rate of formation and growth of the shoots but in morphological terms the initiation of the flowers on the branches is regular and predictable (see Chapter 3).

Not all flowers initiated during the life cycle of the plant develop into fruits. Some are abscised in the bud stage before opening; the term "flower abortion" will be used to describe failure of flower development at this stage. Some flowers are abscised shortly after opening; the term "post-anthesis shedding" will be used to describe this. At a later stage premature fruit drop reflect failure of fruit set; a fruit is said to have "set" if it can be expected to develop to maturity.

The object of the present investigation was to study all

stages of reproductive development but particular interest was attached to factors influencing the post-initiation development of flowers and fruit set.

Failure of fruit set is a potential cause of reductions in fruit yield and has been observed in a number of different environments (Gopalaratnam, 1933; Nagarathnam and Rajamani, 1963; Mote et al. 1973 and Park and Jeong, 1976). In Nigeria, seasonal reduction in yields of sweet pepper often appear to be associated with the failure of a major proportion of flowers to set fruit. Thus it appeared possible that information on factors affecting fruit set might provide a basis for the development of techniques to increase fruit yields.

1.1 Flower initiation; onset of reproductive phase and growth

The influence of the environment on the change from vegetative to reproductive development in pepper has generally been assessed in terms of effects on the number of leaves formed below the first flower, the time taken from the first flower bud to become macroscopically visible or the time taken for the first flower to open. Cochran (1938 and 1942), Deli and Tiessen (1969) and Munting (1974) studied the time of initiation of the first flowers by dissection of the shoot apices.

Cochran (1936) reported that temperature had a marked effect on flower initiation. He used a hand lens to detect early stages of flower development in "World beater" variety of pepper (*Capsicum frutescens* L.). Within a range of temperature treatments, from about 13^{o}C to 35^{o}C, Cochran found that the higher the temperature, the earlier flower formation

occurred. Time from sowing to opening of first flower was similarly affected by temperature. Deli and Tiessen (1969) worked on sweet pepper, variety "California Wonder" grown at night temperatures of 12°C and 18°C. They found that flowering occurred earlier in the plants grown at the higher night temperature. More recently, Rylski (1972) using the same variety of sweet pepper "California Wonder" found that the number of days to appearance of the first flower bud and to anthesis decreased with an increase in night temperature from 10°C to 30°C

Flowering in peppers has been reported to be influenced in different ways when plants are subjected to low night temperature for a limited period at the seedling stage. Deli and Tiessen (1969) found that the effect of a night temperature of 12°C applied for 25 days in the early stage of growth was to reduce the number of leaves formed below the first flower, while Rylski (1972) reported that the effect of a night temperature of 10°C applied from the time of expansion of the cotyledons was to increase leaf number to flower. This discrepancy may be explained if it is supposed that in Deli and Tiessen's experiments, the rate of leaf formation was reduced by the low temperature treatments and that in Rylski's experiments the rate of leaf formation was not affected.

There have been relatively few reports of experiments concerned with the influence of total radiation on flowering in peppers. Auchter and Harley (1924) reported that time to appearance of the first flower buds and to first opening of the flowers was not affected by shading to reduce normal light intensities by about 60 percent in Maryland in the United States

of America during the summer. Deli and Tiessen (1969) found that growing pepper seedlings in low light intensity of 17,200 lux delayed anthesis for about 5 days.

Peppers were classified as day-neutral plants by Salisbury (1963). Auchter and Harley (1924) reported that extending natural long days of summer in Maryland by the use of filament lamps to 24h, caused small delays in times to appearance of flower buds and opening of the first flower. When Cochran (1936) lengthened the natural day length to 22h by the use of tungsten-filament lamps, he found that the appearance of first flower bud and anthesis were delayed by 9 and 11 days respectively. The experiments were carried out in New York from December to April when the natural day length from sunrise to sunset was between 10h and 14h. In 1942, using a different variety of pepper "Perfection Pimiento" Cochran again reported that flowering might be delayed by the long day treatment. He estimated time of flower initiation by dissection and found that long days delayed initiation by 5 days.

Rylski (1972) observed no effect of photoperiodic treatments on time of first flower opening in sweet pepper in Israel during winter. However, she found that plants grown in short days consisting of 7h of natural light developed more leaves below the first flower than those grown in long days. Long days consisted of 7h of natural day light extended by 10h of artificial illumination from a fluorescent and a 200W incandescent lamp together creating a light intensity of 2,700 lux.

There is evidence that the moisture content of the soil

may influence flower initiation and the time to flower opening in peppers. Cochran (1936) maintained plants with three watering regimes. He found that frequent watering reduced the time from sowing to initiation of the first flowers and time to anthesis of the first flower.

1.2 *Flower formation and flower abortion*

After the first flowers have been initiated, further flowers are initiated regularly on the branches that develop. The environment of the plants can influence the rate at which flowers are formed by influencing the rate of development and growth of the branches. The number of flowers that open in a given time will depend on the rate of flower formation, the rate of development of the individual flowers after their initiation and on the number that abort before anthesis is reached. Workers have not always distinguished between these possible effects of environment on flowering.

For three consecutive years, Cochran (1936) grew pepper plants in glasshouses at four different temperatures of 13°, 20°, 25° and 35°C respectively. The treatments commenced when the plants were 6 weeks old. He found that the highest number of flower buds was formed in plants grown at 25°C followed by those at 20° and 35°C respectively; at 13°C development was markedly retarded and no flowers opened. Similarly Dorland and Went (1947) obtained more flowers at 30°C night temperature than at lower night temperatures in Chilli peppers. Both Cochran (1936) and Dorland and Went (1947) reported that many of the flowers formed at the higher temperatures were aborted

whereas most formed at the lower temperatures opened. Dorland and Went observed that the longer the plants were grown, the lower was the optimum night temperature for flowering and after 23 weeks most open flowers occurred on plants grown at a night temperature of 8.5°C.

Deli and Tiessen (1969) reported that plants of sweet pepper subjected to low night temperatures of 12°C for 25 nights branched more profusely than those grown at night temperature of 18°C throughout. Associated with the increased number of branches, more flowers were produced.

There is evidence that high day temperatures may lead to increased flower abortion in sweet pepper. Rylski and Halevy (1974) claimed that high day temperatures between 30° and 40°C promoted flower abortion in Israel when light intensities were low.

There have been few investigations on effects of radiant exposure on flower abortion in pepper. Rylski and Halevy (1974) obtained up to 100 percent abortion when 30 percent shade was provided at flower bud developmental stages in sweet pepper. Park and Jeong (1976) studied the effect of shading on flower abscission in the hot pepper in Korea. They shaded plants to cut out 60 percent and 25 percent of the natural radiation in the glasshouse. They found that shading promoted abortion. Similarly Song et al. (1976) reported that reduction of light intensity promoted flower abortion in Korea.

Flower abortion has been reported to be influenced by photoperiod. Deats (1925) and Cochran (1936) claimed that extension of natural day length to 22 hours increased flower

abortion in peppers. However, Song et al. (1976) working with hot peppers in Korea, claimed that shott day treatments increased the incidence of flower abortion.

1.3 Fruit set; post-anthesis shedding

Many of the flowers formed in pepper plants do not develop into fruits. In India Warade and Singh (1977) reported that only 5 percent of flowers formed set fruit. Mote et al. (1975) also working in India estimated that up to 11 percent of the flowers formed set fruit in pepper. How far failure of fruit development was due to flower abortion before flower opening or to failure of fruit set after flower opening as a result of flower shedding was not indicated. In pepper, fruit set is not necessarily an indication that pollination and fertilisation of the ovules has occurred; there are a number of reports of the occurrence of parthenocarpic (seedless) fruits.

Plant growth substances are known to promote fruit set in a number of crops. Gibberellins and some auxins have been used to achieve fruit set in some Solanaceous crops, namely tomato (Kepcka, 1966) and eggplant (Nothmann and Koller, 1975). Relatively little is known concerning effects of growth substances on fruit set in peppers. Rylski (1974) reported that application of 100 ppm of GA_3 to emasculated flowers of sweet pepper increased fruit set in Israel. El-Maguid (1965) observed increased fruit set in peppers as a result of applying beta-naphthoxyacetic acid (NOA). NOA promoted parthenocarpy in fruits.

Effects of temperature on fruit set in many species have

been reported by Nitsch (1965). Temperature, especially at night time has been reported to influence fruit set in peppers. When Cochran (1936) grew pepper plants at 35°C, he could not obtain fruit set due to post-anthesis shedding. However, when he transferred some plants from pre-anthesis temperature of 35°C to post-anthesis temperature of 13°C, he was able to improve fruit set from 0 percent to 99.3 percent. Cochran's results suggest that a high pre-anthesis followed by a low post-anthesis temperature may increase fruit set in pepper. Similar results have been obtained by workers who carried out experiments on effects of night temperature on fruit set in sweet pepper (Tiessen, 1962; Wells, 1966; Hamadeh, 1967 and Rylski, 1973). Rylski and Halevy (1974) recommend a pre-anthesis night temperature of 20°C followed by a post-anthesis of 8-10°C night temperature as a prerequisite for optimum fruit set in sweet pepper in Israel.

There are several reports of effects of solar radiation on fruit set in the pepper plant. An increase in fruit set in sweet pepper when shading was provided to reduce solar radiation reaching plants by 45 percent was reported from the Carribean area (Schoch, 1972). Similarly Quagliotti (1976) found that shading pepper plants with a black plastic net to provide a 30 percent reduction in solar radiation increased fruit set in Italy; whereas 50 percent shading reduced fruit set.

Cochran (1936) suggested that fruit set in peppers could be increased by shading plants with slatted frames. Cochran attributed the effect of shading to the reduced temperatures that resulted. He did not indicate the percentage reduction in

solar radiation due to the shading applied. A decrease in fruit set was obtained by Park and Jeong (1976) in Korea due mainly to flower shedding, when they shaded hot pepper plants to give a reduction of 60 percent or 25 percent of total solar radiation. Post-anthesis shedding accounted for 83 percent of the failure of fruit set.

There are two reports of effects of photoperiod on fruit set in pepper. Deats (1925) could not obtain fruit set in plants grown in short days of 6.5h day light. He obtained an increase in fruit set in plants grown in normal day length of 12h natural day light as compared with plants grown in 18h days consisting 12h of natural day light extended with artificial illumination from tungsten filament lamps for 6h. These findings were supported by those of Cochran (1936) who obtained 5.6 percent increase in fruit set in plants grown in normal day length (12h day light) over those grown in long days (12h day light + 10h artificial illumination from tungsten filament lamps.

Cochran (1936) reported that moisture content of soil could influence fruit set in the pepper. In his experiments where he maintained pepper plants at three watering regimes, he obtained an increase in fruit set in plants receiving most frequent watering. More recently Chmela and Vlcek (1974) reported that an increase in fruit set in pepper was obtained when plants were grown at high irrigation rate.

The number of fruits developed on pepper plants has been found to influence subsequent fruit set just as reported for tomato. Cochran (1936), Wells (1966), Kato and Tanaka (1971) and Song and Park (1976) have found that fruiting in the pepper

plant is cyclic. As number of fruits set is increased, percentage fruit set rapidly decreases until it reaches the lowest value at the time the highest number of fruits is set.

There is evidence that fruit growth in pepper is influenced by the night temperature at which the plants are grown. Wells (1966), Hamadeh (1967), Rylski (1972) and Rylski and Halevy (1974) reported that when sweet pepper plants were grown in a low temperature throughout, the fruits were elongated and pointed at the stylar end, in contrast to the more blocky type fruit developed at a high post-anthesis night temperature. Rylski (1973) further reported that fruits set at a low night temperature were parthenocarpic. She also associated the promotion of fruit growth at a higher post-anthesis night temperature to the seeds contained in the fruits. She obtained a high correlation between seed number and fruit size.

There is evidence from the investigations previously discussed that certain environmental factors may influence flowering and fruit set in sweet pepper. The primary objective of the present investigation was to make a systematic study of effects of radiant exposure, photoperiod, night temperature and water stress on flowering and fruit set in sweet pepper. Interest was attached to factors controlling the change from vegetative to reproductive growth with the initiation of flowers particularly on the primary shoot to rates of flower formation and to the incidence of flower abortion before the flowers opened. Experiments were designed to examine factors that might limit fruit set and to determine how far these limitations might be removed by application of growth substances.

Chapter 2

Materials and Methods

The materials and methods described in this section are those which were generally used. Methods which were specific to an individual experiment or group of experiments are described in the appropriate chapters.

2.1 Seeds and composts

One cultivar of sweet pepper (*Capsicum annuum* L.) was used throughout. This was the F_1 hybrid cultivar, "Bellboy".

The seed compost used was based on recommendation by the Glasshouse Crops Research Institute (Bunt, 1976). It was a loamless compost with the bulk constituents of 50 percent by volume peat and 50 percent by volume sand. Base fertilizers added were as follows:

Fertilizers	kg m^{-3}
Superphosphate of lime	0.75
Potassium nitrate	0.4
Ground limestone	3.0

Seeds were sown in the compost in seed trays and were germinated in a room maintained at 25°C ± 1°C until seedling emergence when they were moved into a glasshouse with a minimum temperature of 18°C. Seedlings were pricked out when the cotyledons had fully expanded, usually 13 to 15 days after sowing the seed.

Seedlings were first planted in 10.8 cm diameter plastic

pots. In some experiments, larger pot sizes were used, in which case plants were potted-on into them. The following pot sizes were used in the experiments to be described here:

Pot size (cm)	Volume of compost (cm^3)
10.8	628.0
12.7	1312.0
15.2	1949.0
20.3	3622.0

Potting composts used were a proprietary peat-sand compost, "Levington Universal" or John Innes potting compost No. 2 (Bunt, 1976).

The composition of John Innes No. 2 potting compost was as follows: 70 percent by volume sterilized loam, 30 percent by volume peat, 20 percent by volume grit. To these bulk constituents the following base fertilizers were added:

Fertilizers	kg m^{-3}
Hoof and horn	1.186
Superphosphate of lime	1.186
Sulphate of potash	0.593
Calcium carbonate	0.593

The composition of G.C.R.I. potting compost was as follows: 75 percent by volume peat, 25 percent by volume sand with the following base fertilizers added:

Fertilizers	kg m^{-3}
Urea formaldehyde	1.0
Superphosphate of lime	1.5
Potassium nitrate	0.75
Ground limestone	2.25
Fritted trace elements consisting B, Cu, Fe, Mn, Mo and Zn	0.375

2.2 Plant management

When plants had four visible foliage leaves they were fed with the solution of a proprietary fertilizer containing nitrogen, phosphorus and potassium. Liquid feed was applied once or twice a week.

Plants were raised in the glasshouse with the thermostat set to give a minimum air temperature of 20°C during the day and ventilators were opened when temperature exceeded 23°C. During the night a minimum temperature of 16°-18°C was maintained.

2.3 Control of photoperiod

Plants were placed on trolleys which stood in the glasshouse for 8h (9.00h to 17.00h) during the day and were pushed into light-tight compartments during the night. "Short days" comprised 8h day light in the glasshouse followed by 16h of darkness. "Long days" comprised 8h of day light in the glasshouse followed by 10h of artificial illumination from tungsten or fluorescent lamps and 6h of darkness.

Two 40W tungsten filament lamps were used in each

compartment to light a bench area of 1 m^2 formed by two trolleys. Illuminance at plant height as measured with a megatron type C cosine-corrected light meter was about 150 to 170 lux. The lamps were suspended at about 100 cm above the plants. Where "warm white" fluorescent lamps were used 80W lamp was used in each compartment to give an illuminance of 360 lux at plant height as measured with a megatron type C cosine-corrected light meter. For this treatment two layers of muslin were used as a neutral filter around each lamp.

Further light measurements were made with quantum sensor made by Lambda Company to determine rate of energy received by plants. Light energy at plant height from tungsten lamps was 3.2 micro einsteins m^{-2} sec^{-1} and 4.3 micro einsteins m^{-2} sec^{-1} from a fluorescent lamp.

2.4 Supplementary illumination and shading during the day

In some experiments, daily radiant exposure was varied by the use of artificial lighting with 400W high pressure mercury fluorescent lamps (MBFU) suspended about 100 cm above the plants for 8h (9.00h to 17.00h) during the day. The lamps were fitted with reflectors and when they were the sole light source produced an illuminance of about 3000 lux at plant height as measured with a megatron type C cosine-corrected light meter. One lamp was used to light a bench area of about 1 m^2 formed by two trolleys.

In other experiments shading treatments were effected by the use of a layer of green plastic netting, "netlon" which covered the tops and sides of the trolleys on which the plants

were placed. Similar trolleys without netlon were used for the unshaded plants. The shading reduced solar radiation by 50 to 60 percent. The percentage reduction was in the higher part of the range during dull weather and in the lower part during bright weather.

2.5 Methods of flower emasculation

The whole corolla with anthers intact was carefully removed (with sterilized forceps) taking care not to damage ovary and stigma, two or three days before flower opening (anthesis). The forceps were dipped in alcohol after each emasculation. This method of emasculation was recommended by Pickersgill (personal communication). Shaking plants was avoided to prevent cross pollination.

2.6 Records and measurements

Shoot height (cm) was measured from soil level to the uppermost shoot tip which carried a visible flower bud. Internode length (cm), unless indicated otherwise, represents the mean length of the internodes of the primary shoot below the first flower after their elongation had been completed. The number of leaves below the first flower where recorded did not include the two or three leaves originally subtending the first lateral shoots that were carried upon these shoots as they grew (see Chapter 3). Leaf area was determined using a photo-electric planimeter and all leaves greater than 2 cm in length were measured. Plant material was dried in a forced draught oven at 80^{o}C for 48 hours.

Plate 1 : Macroscopic stages of flower development

Stage 1

Flower bud is macroscopically visible to unaided eye;
Sepals are tightly closed, pedicels short and erected.

Stage 2

Sepals begin to open, petals are just visible;
Pedicel is elongated and erect.
Mean bud size is 5.0 mm.

Stage 3

Petal lobes are visible, petal is green.
Stalk is more elongated and curved;
Bud is drooping on pedicel;
Mean bud size is 13.0 mm.

Stage 4

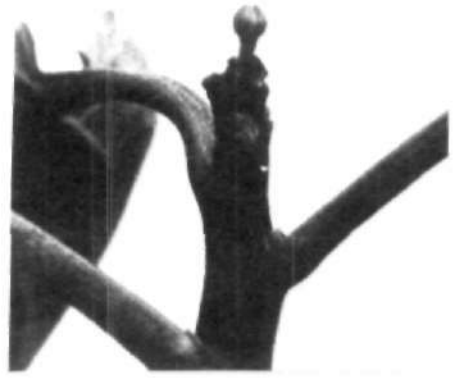
Petals, 5-6 lobed. Lobes become distinct and protrude from calyx, but remain unopen;
Petals are turning white in colour.
Pedicel greatly elongated and curved;
2 or 3 days before anthesis.
Mean size of bud is 23.0 mm.

Stage 5

Anthesis: Petals completely open and somewhat reflected.
Anthers dehisce and pollination may take place;
Flower drooping on pedicel. Elongation of pedicel ceased;
Style is short, straight and club-shaped.

Stage 6

Fruit set: 15 days after anthesis;
Petals, stamens dihisce;
Calyx and style persist;
Ovary size about 23-30 mm in diameter;
Fruit expected to be retained and to grow to maturity.



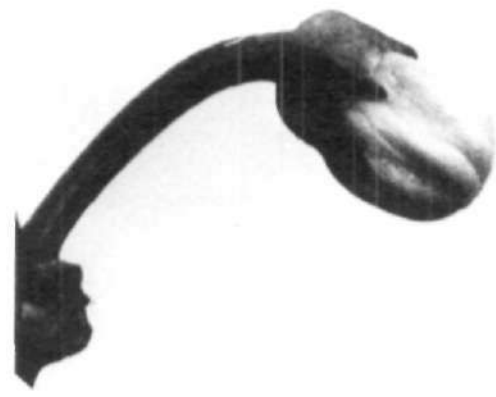
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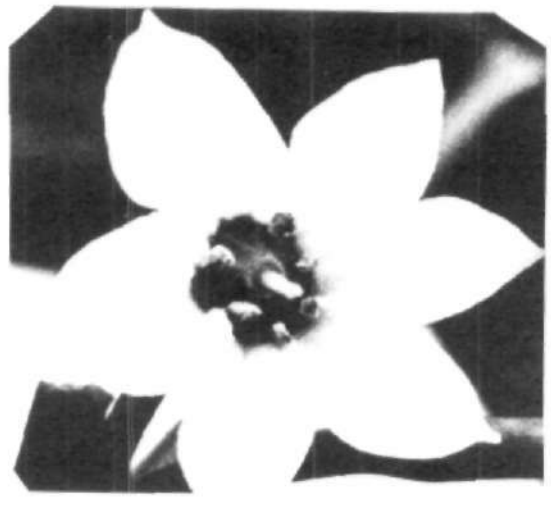
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3



4



5



6

In some experiments the shoot apices were dissected, using a binocular microscope in order to detect whether flower initiation had occurred. In most experiments, the time that first flower bud became visible "first flower bud visibility stage" was recorded. This was taken as the time a bud could be seen without the aid of dissection or a microscope. Stages of flower development were determined as described in Chapter 3 (see Plate 1).

The number of days from sowing to opening of the first flower was recorded as "days from sowing to first anthesis". A flower was said to have reached anthesis when the petals had fully opened.

2.7 Flower abortion and shedding

Flowers that stopped growing and failed to reach anthesis were recorded as "aborted" (see Plate 2a). When flowers were abscised after anthesis this was termed "post-anthesis shedding" (see Plate 2b).

2.8 Fruit set, growth and development

A fruit was said to have "set" when it could be expected to complete normal development in the plant. Observations suggested that fruits remaining on the plant 15 days after anthesis generally met this requirement; such fruits were regarded as "set".

In some experiments fruit volume was determined by water displacement.



(a)



(b)

2.9 Experimental design and analysis of results

The majority of experiments were of a factorial design with randomised blocks. Some of them were of split-plot design. They were designed to enable a test of the significance of treatment effects to be made using an analysis of variance. In a few experiments, it was not possible to replicate temperature treatments due to limitations in the facilities available. In these cases it was not valid to test the significance of such treatments since their effects would be confounded with positional effects. However, it was possible to test the significance of their interactions with other factors. Some experiments were replicated in time as a means of checking results.

Positional effect in the glasshouse was minimised by re-randomising position of plants and trolleys at weekly intervals wherever possible.

Chapter 3

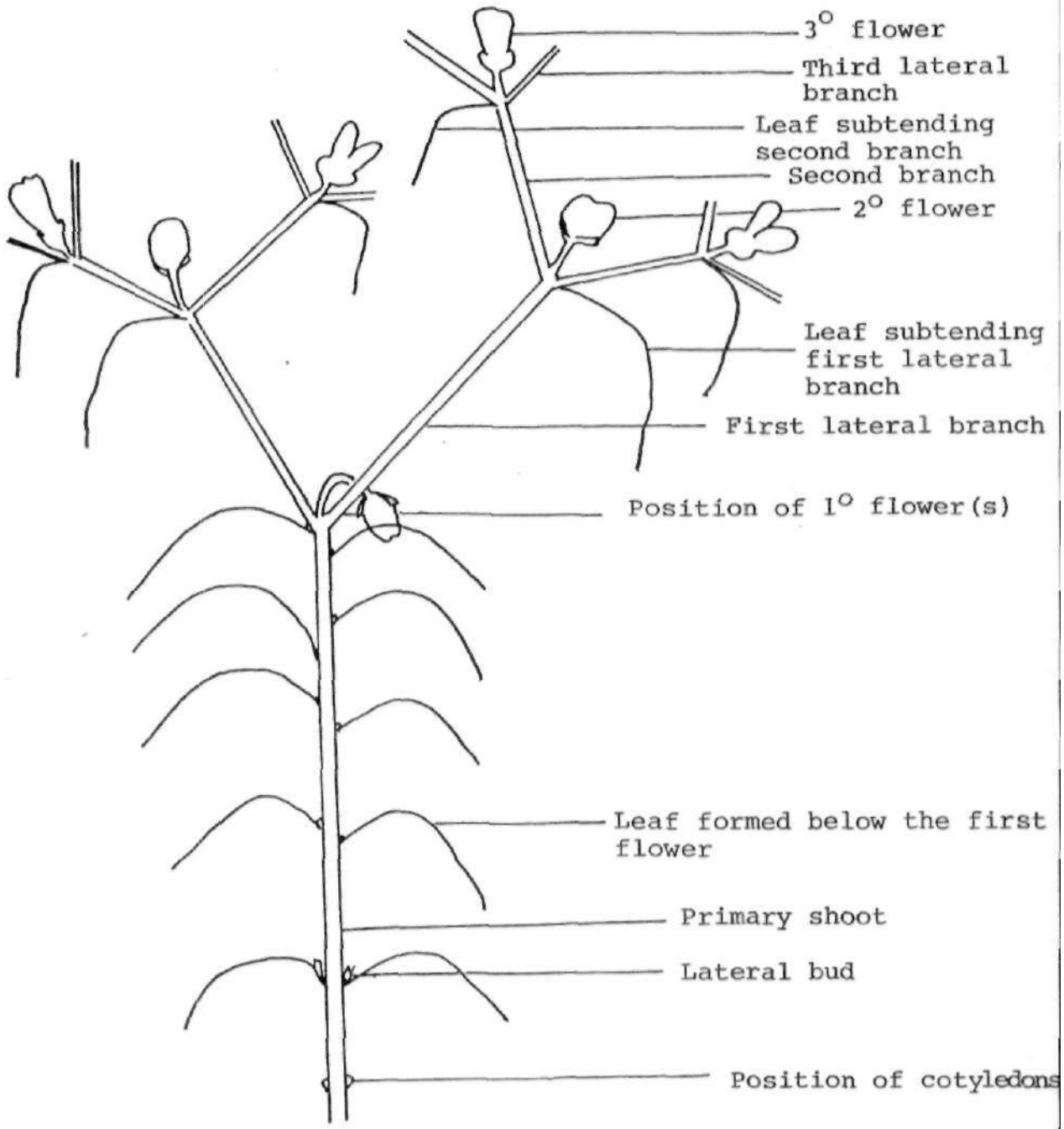
Morphology of the Plant

The common cultivated varieties of pepper grown in temperate regions are regarded as belonging to the species *Capsicum annuum* L.; they vary mainly in the size of the plant and in the shape, size and pungency of the fruit.

The nomenclature of Capsicum is confused. Initially colour and shape of the fruit were the main characteristics on which species were classified. Whereas Shaw and Khan (1928) used the characteristics of the flower to classify Capsicum in India, leaf and calyx shape were used as means of classification in America (Erwin, 1929).

It appears that different species names have been used to denote the same varieties of Capsicum. Terpo (1966) made the same observation. To overcome this, Heiser and Pickersgill (1969) made a detailed study of herbarium material in which they tried to find as many flower and fruit characteristics as possible. They distinguished five cultivated species which are generally accepted today. Rosengarten (1970) adhered to the classification made by Heisser and Pickersgill in his book on species. Sweet peppers fall into classification made by Heisser and Pickersgill and they are accepted as belonging to *Capsicum annuum* L., although Deli and Tiessen (1969) classified them as *Capsicum frutescens*.

The description of morphology that follows is based on observation made on plants of sweet pepper cultivar Bell Boy.


3° flower
Third lateral branch
Leaf subtending second branch
Second branch
2° flower
Leaf subtending first lateral branch
First lateral branch
Position of 1° flower(s)
Leaf formed below the first flower
Primary shoot
Lateral bud
Position of cotyledons

The plant grows as a single primary stem until a number of leaves have been formed and then a terminal inflorescence is initiated on the primary shoot.

The branch system with the possible exception of the stem below the first formed flowers is apparently dichotomous. A flower, or group of flowers is formed terminally on the primary shoot and either two or three laterals continue the growth of the shoot (Fig. 1). The leaves subtending these laterals are carried up on the shoots so that their points of attachment come to be on the laterals that they originally subtend (Fig. 2). Growth of each lateral is terminated by the formation of one or two flowers while two sub laterals grow out and again the subtending leaves are carried up on the shoots as they grow. After the completion of elongation in growth each lateral carries one leaf, representing the leaf that originally subtended it and one or occasionally two terminal flower buds.

The growth of the shoots are never equal - one is greater in diameter and longer than the other(s) while its subtending leaf is larger. One possibility is that the longer lateral always has its origin in the axil of the leaf immediately below the terminal flower and that the smaller branch arises in the axil of the leaf initiated below this. The inequality of the branches becomes more apparent with the growth of the plant and a shoot may finally appear as a single main axis, made up of the successive larger branches from which lateral shoots (the smaller of the pairs) arise. When plants are grown for relatively long periods further branches may arise from the

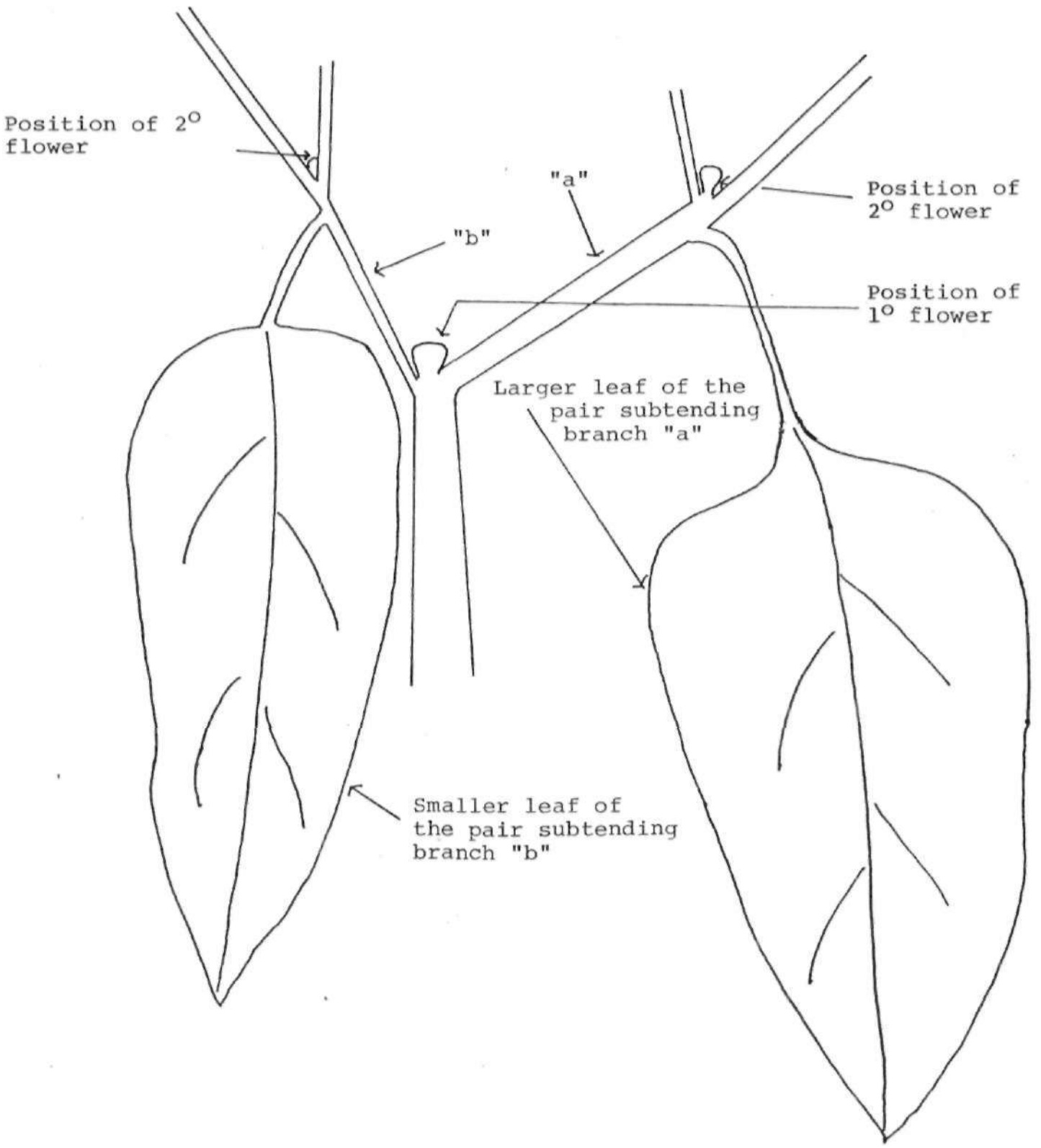
axils of lower leaves on the primary shoot.

Dissection of the shoot tips indicated that when a flower is initiated in sweet pepper, the leaf initiation at the apex ceases, but the last-formed leaf primordia continue to increase in size without younger primordia being formed to take their place. At the same time as the first flower primordium is differentiated, the first lateral shoot primordia begin to develop at the side of the flower primordium. It is believed that leaves subtending the first lateral branches are initiated at this stage and are merely carried up the shoots.

The growth of the primary shoot is terminated with the formation of one to five flowers. Normally only one or at most two of these flowers develop to anthesis. In recording flower development, 6 stages were recognised (see Plate 1). The flowers formed at the tip of the primary shoot are referred to as 1^{o} flowers, those formed at the tips of the first branches are referred to as 2^{o} flowers, those formed on the next set of branches are termed 3^{o} and so on.

The flowers are usually self-pollinated although some cross pollination of up to 16 percent may occur (Cochran, 1938, Odland and Porter, 1941 and Free, 1975).

A typical mature fruit of "Bellboy" is about 8-12 cm long, roughly square in transverse section, thick fleshed and green in colour at first, turning red. Calyx and style persist on the fruit. The fruit is usually 3-4 locular and may contain many seeds (up to 400 have been observed).


Position of 2° flower
"a"
"b"
Position of 2° flower
Position of 1° flower
Larger leaf of the pair subtending branch "a"
Smaller leaf of the pair subtending branch "b"

Chapter 4

Effects of Photoperiod and Radiant Exposure on Flowering and Fruit Set (Exps. 1, 8, 3, 10 and 20)

Few investigations have been carried out concerning effects of photoperiod on flowering in pepper. Cochran (1936) reported that flower initiation and opening of the first flowers were promoted by short days. Salisbury (1963) classified pepper as day-neutral. More recently Rylski (1972) noted that the number of leaves produced below the first flowers was increased in short as compared with long days but observed no effect of photoperiod on time of opening of the first flowers. The object of the experiments described here was to examine effects of photoperiod on the duration of the vegetative phase and to assess separately effects on the time of flower initiation, the number of leaves formed below the first flowers and the time of opening of the first flowers. Effects of daily radiant exposure on flowering were also investigated and the possibility of interactions between photoperiod and total radiation was examined.

4.1 Experimental design

In experiments 1, 3 and 8 treatments were arranged in factorial split-plot randomised blocks design with 3 or 4 replicates.

Results

4.2 (Exps. 1 and 8) Effects of photoperiod, radiant exposure and pot size on flowering and fruit set

In these experiments plants were grown in two photoperiods, short and long days, from the time of cotyledon expansion. Short days comprised 8h day light in the glasshouse followed by 16h darkness; long days comprised 8h of day light followed by 10h artificial lighting of low illuminance and 6h of darkness. In Exp. 1 artificial lighting to lengthen the day was from tungsten filament lamps (170 lux at plant height); in Exp. 8 tungsten filament lamps were again used and a further treatment employing warm white fluorescent lamps (F) (360 lux at plant height) was included.

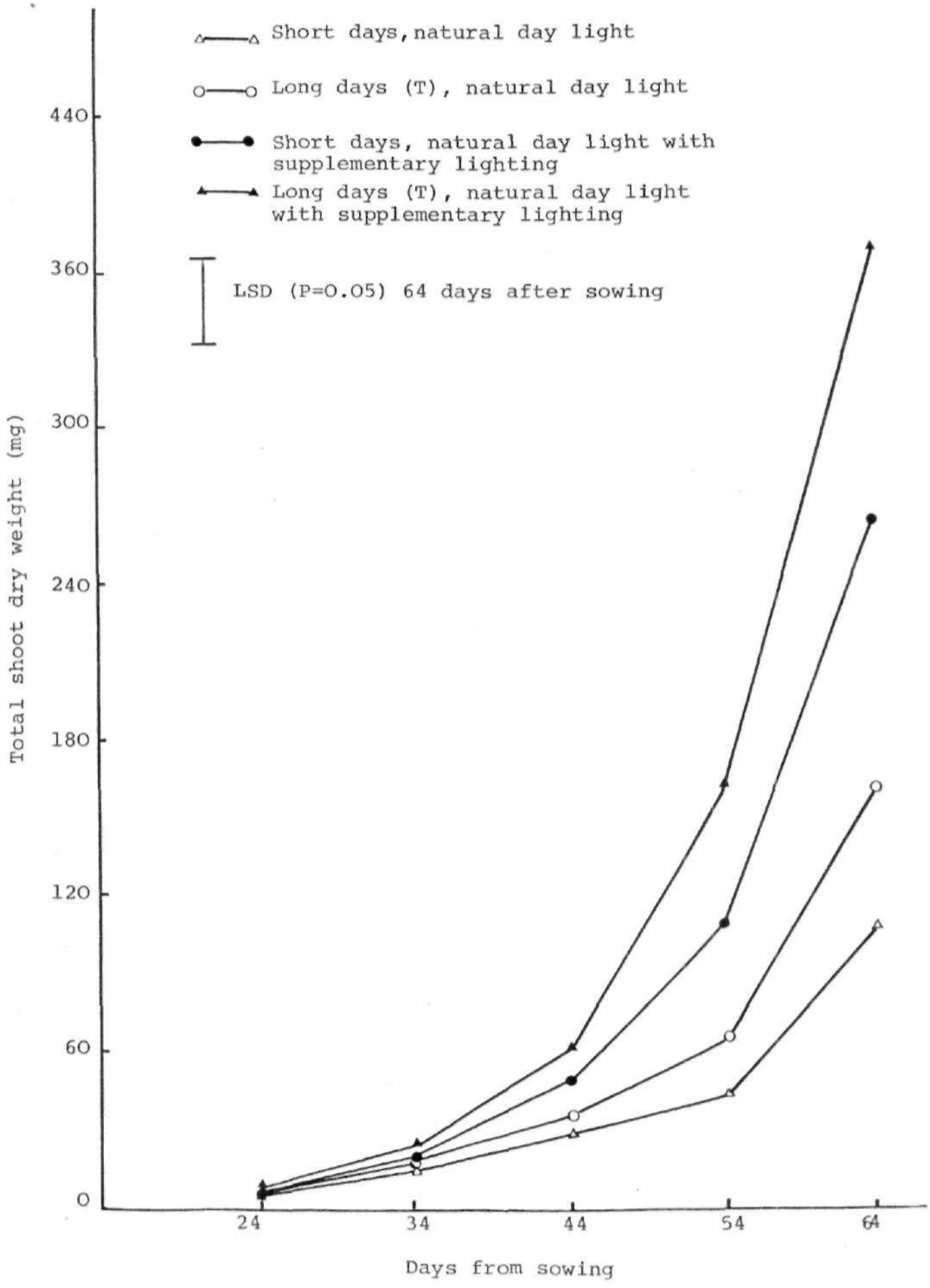
In both experiments plants were grown with and without supplementary lighting from high pressure mercury fluorescent (MBFU) lamps during the 8h of day light (see Materials and Methods, Chapter 2). In the second experiment (Exp. 8) the effect of using a larger pot size was tested and pots of 15.2 cm diameter were included as well as the usual size of 10.8 cm diameter.

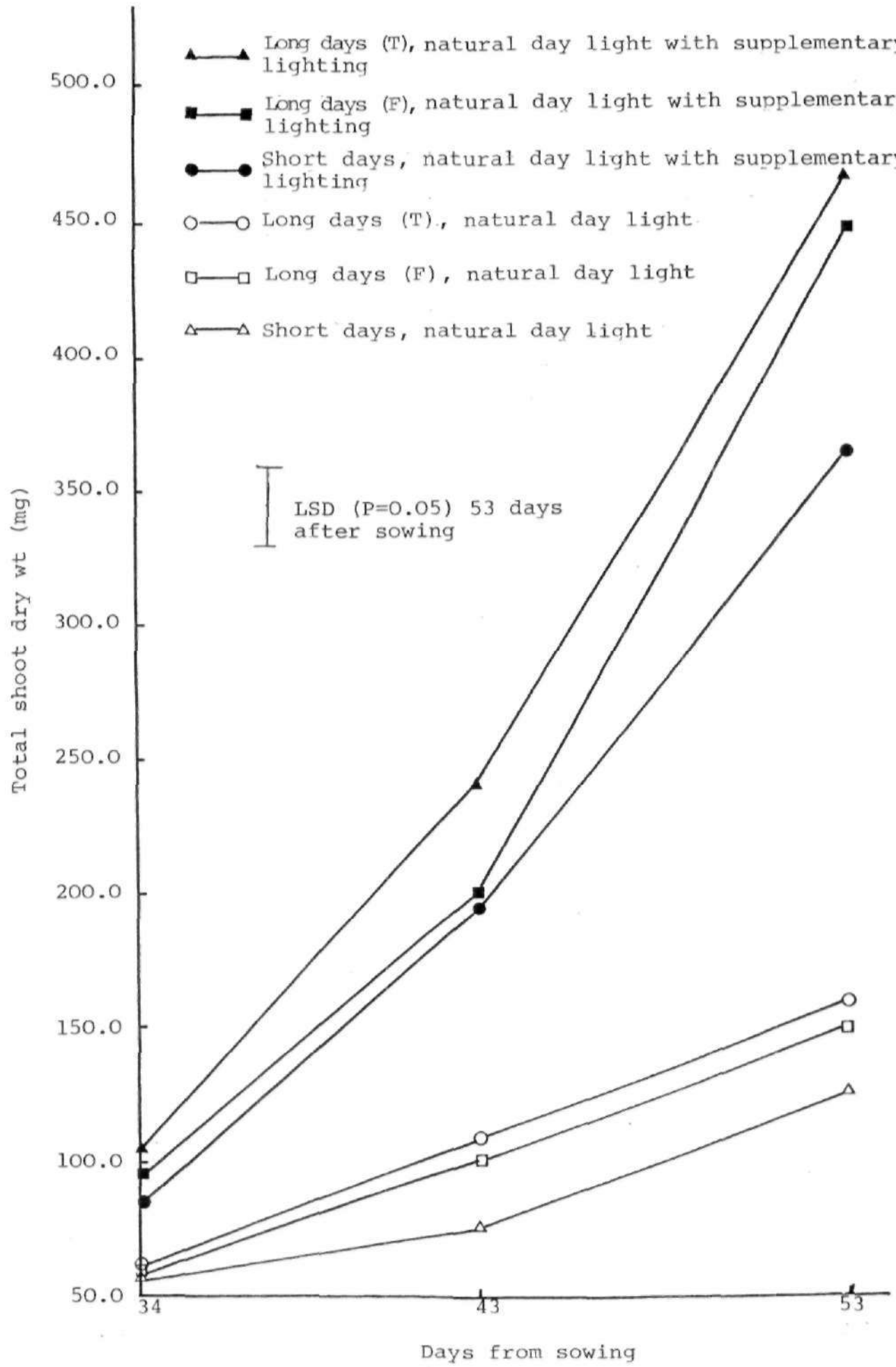
The experiments were started at about the same time of year, Exp. 1 on 17.11.77 and Exp. 8 on 30.11.78 (Table 1).

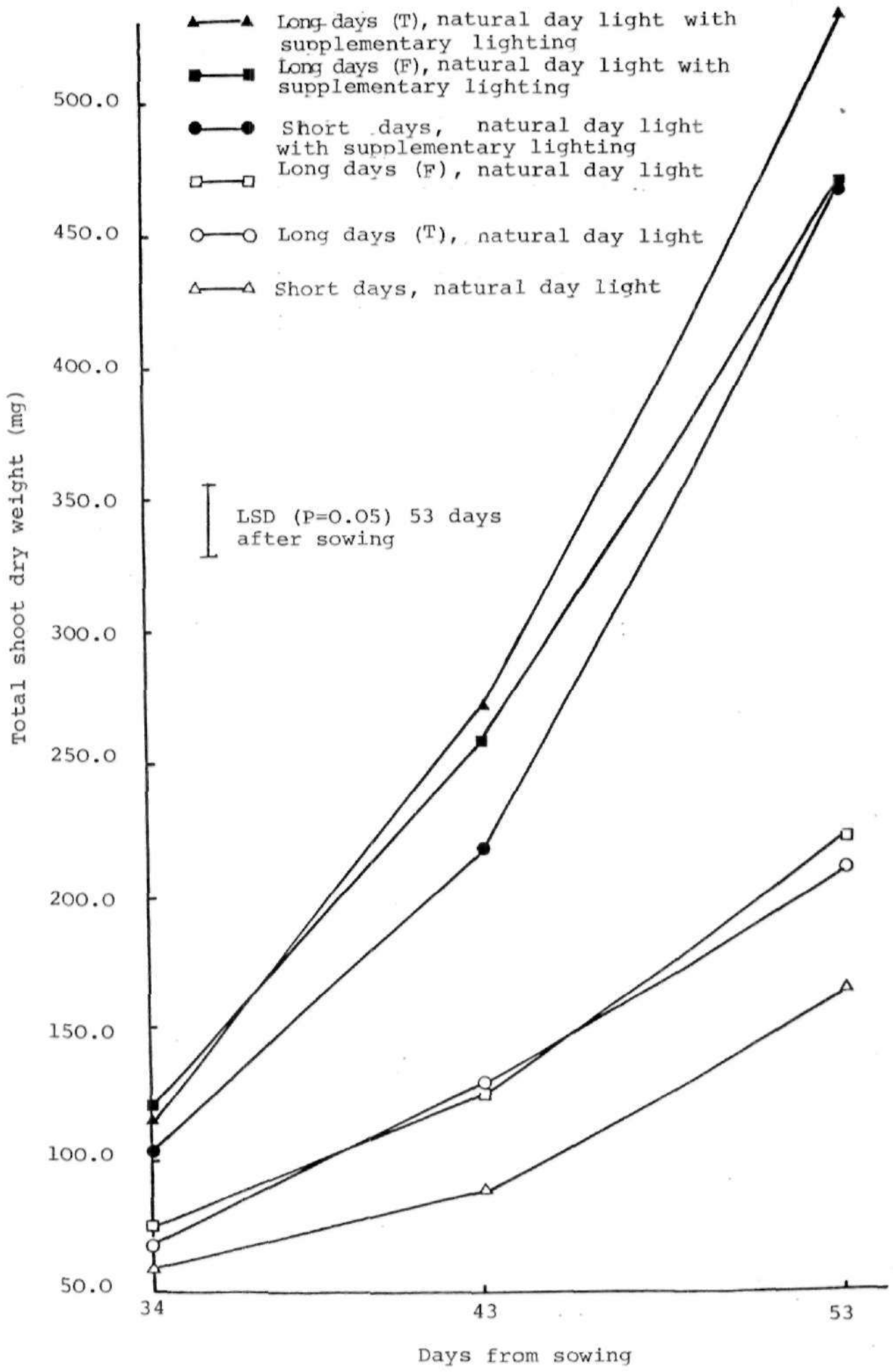
In these experiments, carried out during the late autumn and the winter, supplementary lighting markedly promoted growth in dry weight of the shoot systems (Figs. 3a, 3b and 3c). Associated with the increases in dry weight there were increases in leaf area and plant height (Figs. 4a, 4b, 4c; 5a, 5b, 5c).

Table 1 Detail of Exps. described in Chapter 4

Exp. number	Title of Exp.	Date of sowing the seed	Date that treatments commenced	Stage of plant development at which treatments commenced	Date that Exp. was terminated
1	Effects of photoperiod and radiant exposure on flowering and fruit set (18 plants per treatment)	3.11.77	17.11.77	Cotyledon expansion	23.3.79 (140 days after sowing)
8	Effects of photoperiod, radiant exposure and pot size on flowering and fruit set (12 plants per treatment)	16.11.78	30.11.78	Cotyledon expansion	21.3.79 (125 days after sowing)
3	Effects of photoperiod and shading on flowering and fruit set (18 plants per treatment)	15.3.78	28.3.78	Cotyledon expansion	17.7.78 (124 days after sowing)
10	Effects of varying the photoperiod by the use of tungsten filament lamps at different times during the night period on flowering behaviour (24 plants per treatment)	9.5.79	21.5.79	Cotyledon expansion	17.7.79 (69 days after sowing)
20	Effects of varying the photoperiod by the use of "warm-white" fluorescent lamps at different times during the night period on flowering and fruit set (24 plants per treatment)	10.8.79	24.8.79	Cotyledon expansion	31.10.79 (82 days after sowing)


Short days, natural day light
Long days (T), natural day light
Short days, natural day light with supplementary lighting
Long days (T), natural day light with supplementary lighting
LSD (P=0.05) 64 days after sowing
Total shoot dry weight (mg)
440
360
300
240
180
120
60
0
24
34
44
54
64
Days from sowing


Long days (T), natural day light with supplementary lighting
Long days (F), natural day light with supplementary lighting
Short days, natural day light with supplementary lighting
Long days (T), natural day light
Long days (F), natural day light
Short days, natural day light
LSD (P=0.05) 53 days after sowing
Total shoot dry wt (mg)
500.0
450.0
400.0
350.0
300.0
250.0
200.0
150.0
100.0
50.0
34
43
53
Days from sowing


Long days (T), natural day light with supplementary lighting
Long days (F), natural day light with supplementary lighting
Short days, natural day light with supplementary lighting
Long days (F), natural day light
Long days (T), natural day light
Short days, natural day light
LSD (P=0.05) 53 days after sowing
Total shoot dry weight (mg)
500.0
450.0
400.0
350.0
300.0
250.0
200.0
150.0
100.0
50.0
34
43
53
Days from sowing

It appeared that the increase in plant height due to supplementary lighting was due in part at least to increased extension of the internode (Tables 2a and 2b). How far any increase in internode number due to an increased rate of leaf initiation contributed to the effect was not measured.

The duration of the vegetative phase of growth was reduced in the plants receiving supplementary illumination. Flower initiation in these plants occurred about 20 days earlier than in plants grown with no additional illumination during the 8h of day light (Tables 3a and 3b). In the second experiment where time of first appearance of flower buds was recorded it was found that earlier initiation of flowers due to the supplementary lighting was accompanied by earlier appearance of flower buds (Table 4). In term of days from sowing the seed, the two stages of flowering were promoted to a similar extent. It was concluded that the main effect of supplementary lighting was on time of flower initiation rather than on subsequent growth of the flower initials. Earlier flower initiation due to increased radiant exposure was generally accompanied by a reduction in the number of leaves formed on the primary shoot below the flowers. The reductions were small, usually of the order of one to two leaves (Tables 5a and 5b).

Counts of flower buds made in later stages of growth of the plants (Figs. 6a, 6b and 6c) indicated that the number of flowers formed increased as a result of supplementary lighting. It appeared that the main effect of supplementary lighting was due to earlier formation of flowers at the tip of the primary shoot and after this, rates of flower formation on the branches

Table 2a (Exp. 1) Effects of photoperiod and radiant exposure on length of internodes on the primary shoot. 78 plants per treatment (3.11.77)

Length of internodes (cm) on the primary shoot (100 days after sowing)

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Natural day light	1.4	3.56	2.48
Natural day light with supplementary lighting	2.3	4.77	3.54
Photoperiod mean	1.85	4.17	

LSD to compare photoperiod means (P=0.05) = 0.5
LSD to compare radiant exposure means (P=0.05) = 0.4
Radiant exposure x photoperiod interaction (P=0.05) NS

Table 2b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on length of internodes on the primary shoot. 12 plants per treatment (16.11.78)

Length of internodes (cm) on the primary shoot (95 days after sowing)

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (Tungsten)	Pot size mean	Radiant exposure mean
Natural day light	10.8	1.63	1.76	5.7	3.03	3.05
	15.2	1.73	1.94	5.52	3.06	
Natural day light with supplementary lighting	10.8	1.81	2.11	6.0	3.31	3.46
	15.2	2.04	2.32	6.5	3.62	
Photoperiod mean		1.8	2.03	5.93		

LSD to compare photoperiod means (P=0.05) = 0.1
LSD to compare radiant exposure means (P=0.05) = 0.2
LSD to compare pot size means (P=0.05) = 0.1
Radiant exposure x photoperiod x pot size interaction (P=0.05) NS

Table 3a (Exp. 1) Effects of photoperiod and radiant exposure on initiation of first flowers. 18 plants per treatment (3.11.77)

Number of days from sowing to the time 50% of plants initiated first flowers

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Natural day light	52.6	62.0	57.3
Natural day light with supplementary lighting	34.0	40.0	37.0
Photoperiod mean	43.3	51.0	

LSD (P=0.05) = 7.2
Photoperiod x radiant exposure interaction (P=0.05) NS

Table 3b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on initiation of first flowers. 12 plants per treatment (16.11.78)

Number of days from sowing to the time 50% of plants initiated first flowers

Radiant exposure	Short days	Long days (F)	Long days (tungsten)	Radiant exposure mean
Natural day light	50.1	48.0	54.3	50.8
Natural day light with supplementary lighting	32.0	32.2	36.7	33.6
Photoperiod mean	41.1	40.1	45.5	

No effect of pot size on time of flower initiation was observed

Table 4 (Exp. 8) Effects of photoperiod, radiant exposure and pot size on time that first flower buds became visible. 12 plants per treatment (16.11.78)

Number of days from sowing to the first appearance of flower buds

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size mean	Radiant exposure mean
Natural day light	10.8	70.6	64.9	75.4	70.3	70.1
	15.2	69.7	65.5	74.4	69.9	
Natural day light with supplementary lighting	10.8	50.3	51.7	57.9	53.3	53.3
	15.2	50.6	51.6	57.8	53.3	
Photoperiod mean		60.3	58.4	66.4		

LSD to compare photoperiod means (P=0.05) = 1.4
LSD to compare radiant exposure means (P=0.05) = 3.0
LSD to compare pot size means (P=0.05) NS
Radiant exposure x photoperiod x pot size interaction (P=0.05) NS

Table 5a (Exp. 1) Effects of photoperiod and radiant exposure on number of leaves formed on the primary shoot before initiation of first flowers. 18 plants per treatment (3.11.77)

Number of leaves formed per plant on the primary shoot

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Natural day light	12.2	12.7	12.5
Natural day light with supplementary lighting	11.4	11.8	11.6
Photoperiod mean	11.8	12.3	

LSD to compare photoperiod means (P=0.05) = 0.3
LSD to compare radiant exposure means (P=0.05) = 0.6
Radiant exposure x photoperiod interaction (P=0.05) NS

Table 5b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on number of leaves formed on the primary shoot before initiation of first flowers. 12 plants per treatment (16.11.78)

Number of leaves formed per plant, on the primary shoot

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size (cm)	Radiant exposure mean
Natural day light	10.8	13.3	12.9	13.3	13.2	13.1
	15.2	13.6	12.3	13.1	13.0	
Natural day light with supplementary lighting	10.8	11.1	11.8	12.1	11.7	11.5
	15.2	10.8	11.1	12.2	11.4	
Photoperiod mean		12.2	12.0	12.7		

LSD to compare photoperiod means (P=0.05) = 0.4
LSD to compare radiant exposure means (P=0.05) = 0.7
LSD to compare pot size means (P=0.05) NS
Radiant exposure x photoperiod x pot size interaction (P=0.05) NS

were not markedly affected by the treatment.

There was no consistent effect of photoperiod on time to flower initiation; effects appeared to vary with the light source used to extend the photoperiod. In Exp. 1 where tungsten filament lamps were used, plants in short days initiated flowers 6 to 11 days earlier than plants in long days (Table 3a). In Exp. 8 there was again a small delay in flower initiation due to the long day treatments using tungsten filament lamps; in this experiment the delay amounted to 4 to 5 days (Table 3b). Where the photoperiod was extended using warm white fluorescent lamps, however, flower initiation occurred at about the same time as in short days (Tables 3b and 3c).

Records of the time flower buds first became visible kept in Exp. 8 (Table 4) showed that delays in flower initiation due to the use of tungsten filament lamps to lengthen the day were reflected in delays in the appearance of the flower buds. Where plants received supplementary lighting during the 8h of day light there appeared to be no effect of extension of the day with warm white fluorescent lamps. In the absence of supplementary lighting, the long day treatments with fluorescent lamps hastened the appearance of flower buds by about five days.

Associated with the delay in flower initiation due to the long day treatment with tungsten lamps used in Exp. 1 there was a very small increase in the number of leaves formed on the primary shoot below the flowers (Table 5a). In Exp. 8 the corresponding treatment had no apparent effect on the leaf

number to flower when plants were grown without supplementary lighting but caused an increase of between one and two leaves when supplementary lighting was used (Table 5b).

Figs. 6a, 6b and 6c indicate that effects of photoperiod treatments on flowering were apparent at later stages of development of the plants. In plants given supplementary lighting, the number of flowers that had been formed in short days was greater than in long days (using light from either tungsten filaments or warm white fluorescent lamps) at the time of the last counts (114 days in Exp. 1, 117 days in Exp. 8). There was no evidence that the difference in the number of flowers formed produced by the photoperiodic treatments was increasing as the experiment progressed; it appeared that the effect of short days was due to earlier formation of the first flowers at the tips of primary shoot rather than any promotion of flower formation in the branches that developed subsequently. Where no supplementary lighting was used no effect of photoperiod on the number of flowers formed was apparent.

Growth in dry weight of the primary shoots before flower initiation occurred was affected by the photoperiodic treatments given. Extension of the day length using either tungsten filament lamps (Exp. 1 and Exp. 8) or warm white fluorescent lamps (Exp. 8) produced increase in the growth in dry weight (Figs. 3a, 3b and 3c) and increases in leaf area (Figs. 4a, 4b and 4c). There was little difference between the two types of lamp in producing these increases in growth at the early stages of development of the plants. However, at the time the experiments were terminated (114 days in Exp. 1 and 117 days in

Fig. 4a (Exp. 1) Effects of photoperiod and radiant exposure on leaf area (cm^2) (18 plants per treatment. 3.11.77)

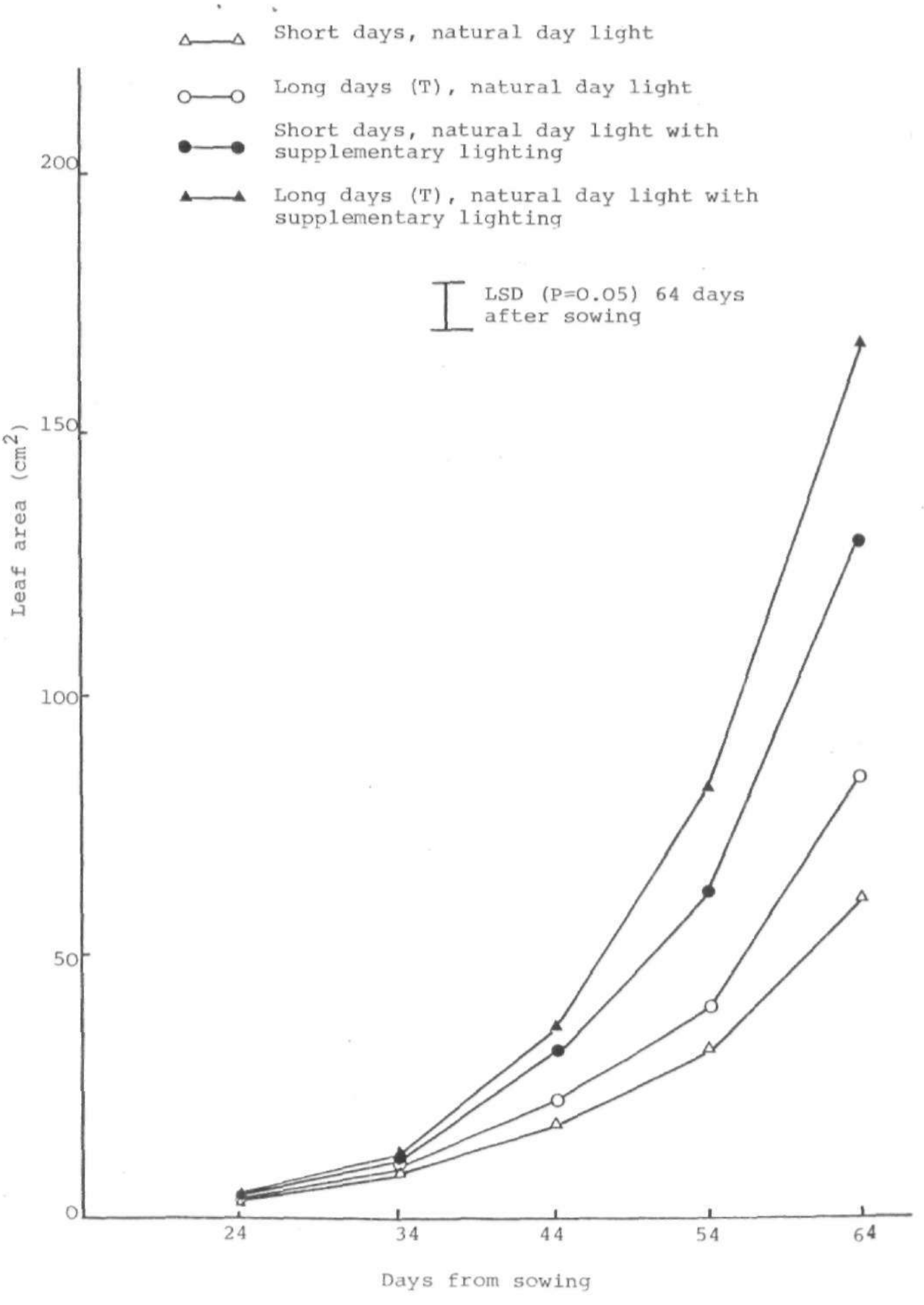

Short days, natural day light
Long days (T), natural day light
Short days, natural day light with supplementary lighting
Long days (T), natural day light with supplementary lighting
LSD (P=0.05) 64 days after sowing
Leaf area (cm2)
200
150
100
50
0
24
34
44
54
64
Days from sowing

Fig. 4b (Exp. 8) Effects of photoperiod, radiant exposure and 10.2 cm diameter pot on leaf area (cm^2) (12 plants per treatment. 16.11.78)

■——■ Long days (F), natural day light with supplementary lighting

▲——▲ Long days (T), natural day light with supplementary lighting

●——● Short days, natural day light with supplementary lighting

□——□ Long days (F), natural day light

○——○ Long days (T), natural day light

△——△ Short days, natural day light

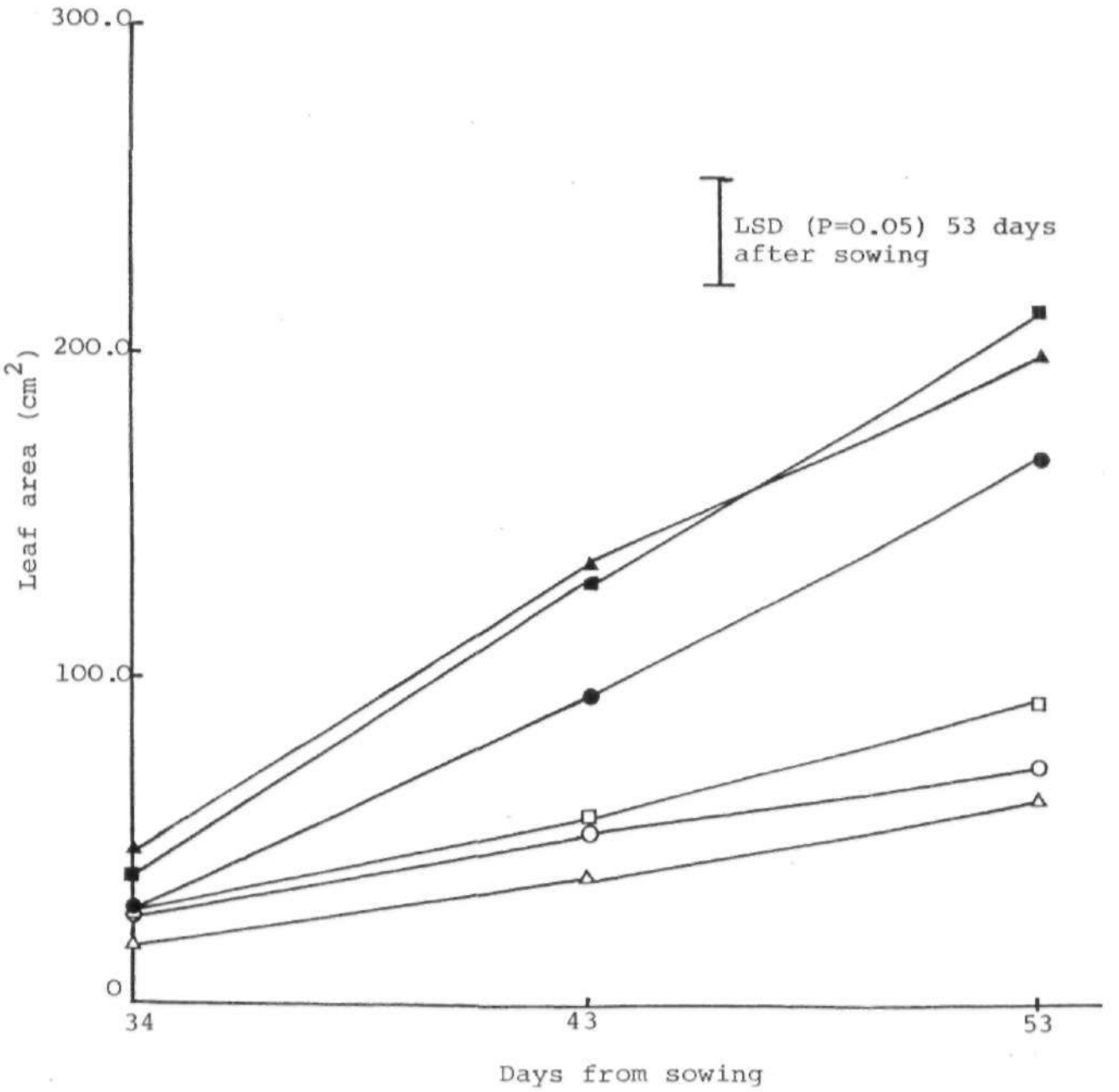
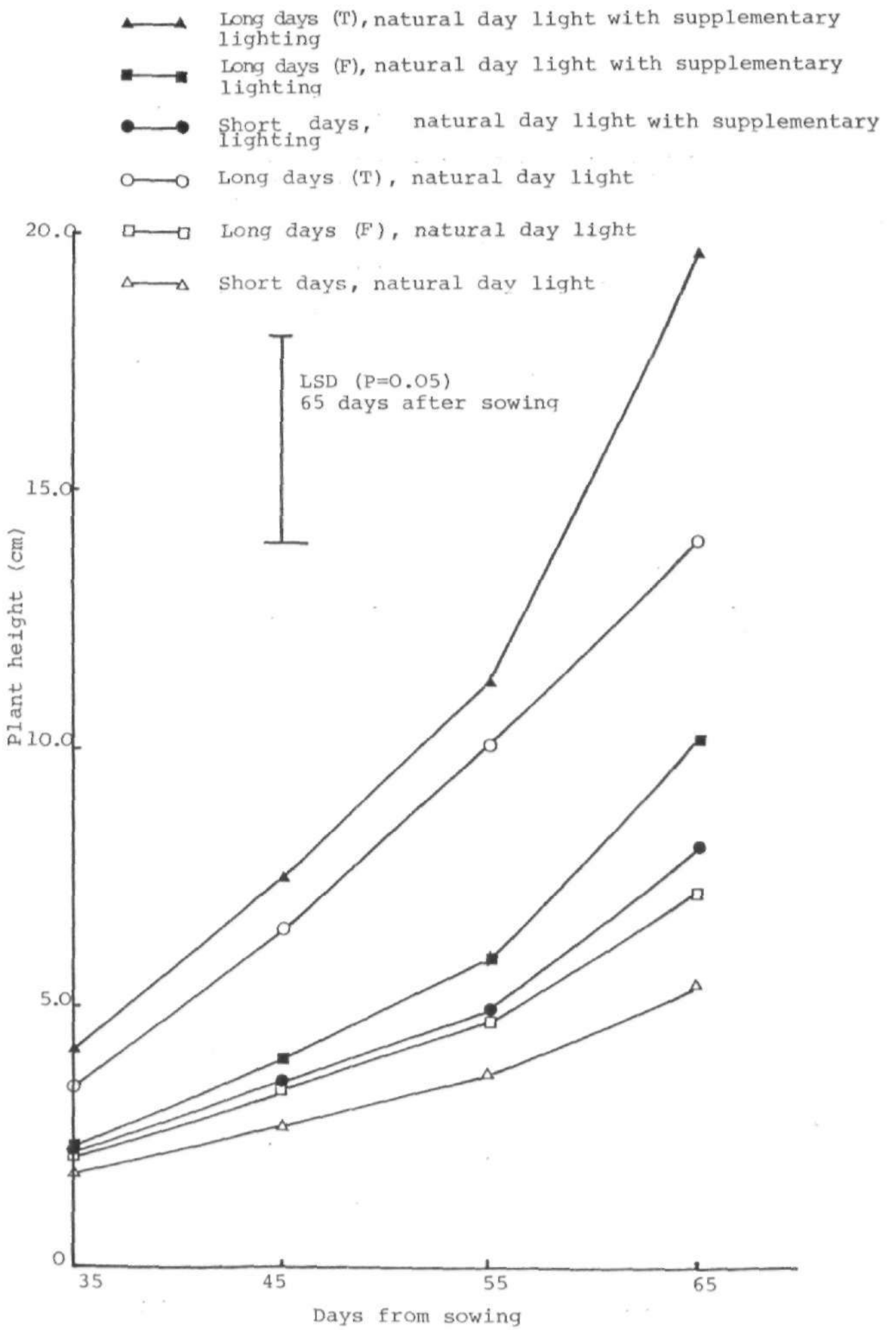
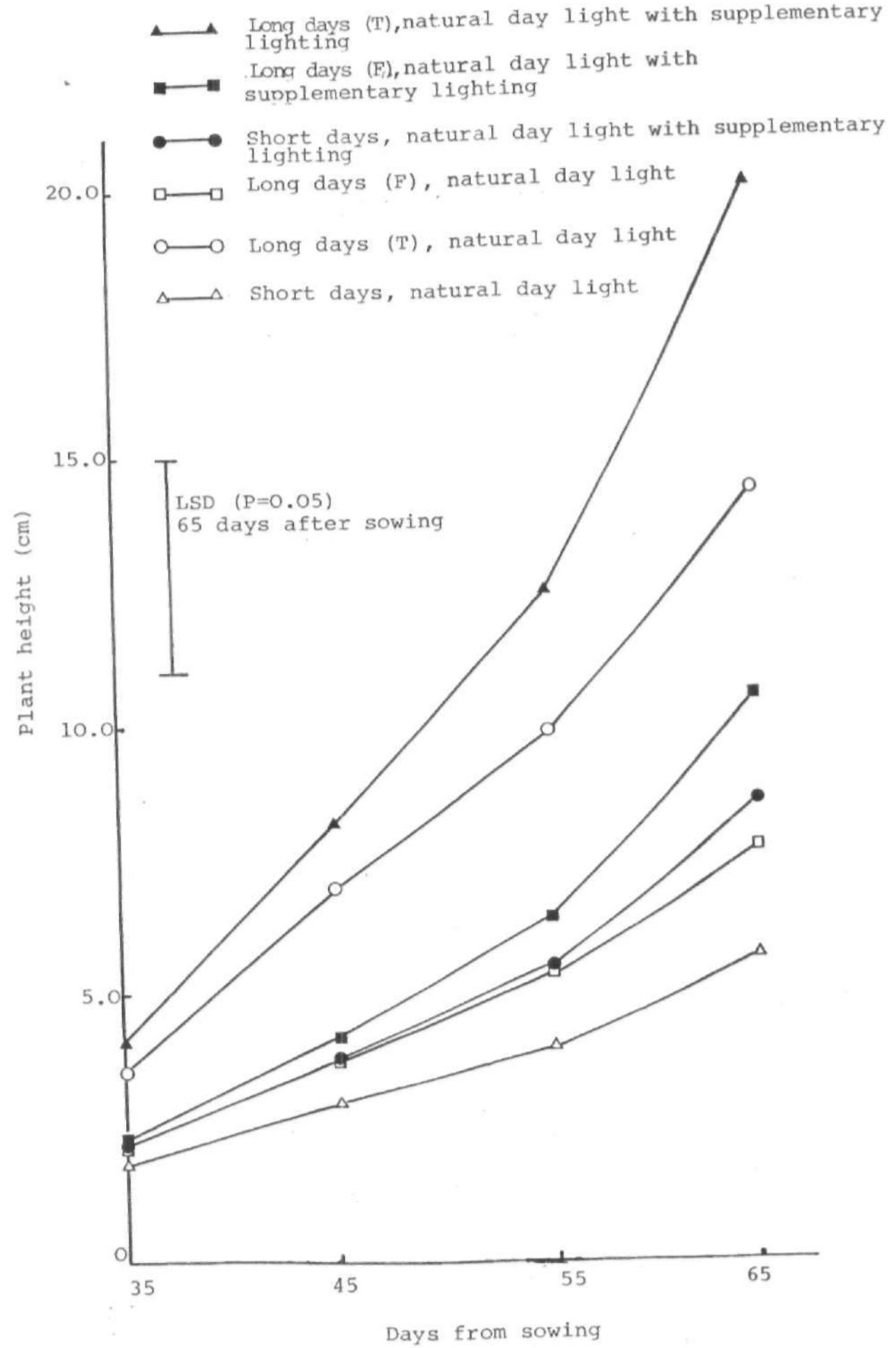


Fig. 5c (Exp. 8) Effects of photoperiod, radiant exposure and 15.2 cm diameter pot on plant height (cm) (12 plants per treatment. 16.11.78)


Long days (T), natural day light with supplementary lighting
Long days (F), natural day light with supplementary lighting
Short days, natural day light with supplementary lighting
Long days (T), natural day light
Long days (F), natural day light
Short days, natural day light
LSD (P=0.05)
65 days after sowing
Plant height (cm)
20.0
15.0
10.0
5.0
0
35
45
55
65
Days from sowing

(b) (Exp. 10) Photograph showing effects of a 2h period lighting with tungsten filament lamps at different times in the 16h night (17.00h to 9.00h) on elongation of the primary shoot up to 60 days after sowing (8.7.79)

From left to right lighting was as follows:- 7.00h to 9.00h; 17.00h to 19.00h; 24.00h to 2.00h; short days (9.00h to 17.00h of natural day light).


Long days (T),natural day light with supplementary lighting
Long days (F),natural day light with supplementary lighting
Short days, natural day light with supplementary lighting
Long days (F), natural day light
Long days (T), natural day light
Short days, natural day light
LSD (P=0.05)
65 days after sowing
Plant height (cm)
20.0
15.0
10.0
5.0
0
35
45
55
65
Days from sowing



(a)



(b)

Exp. 8), increase in growth of dry weight was greater in long days with tungsten filament than with warm white fluorescent lamps. Tables 6a and 6b indicate that there was a greater contribution to the growth in dry weight of the stems than of the leaves of the plants.

Long days also promoted the growth in height of the plants (Figs. 5a, 5b, 5c and Plate 3), and here the promotion was markedly greater using tungsten filament as compared with warm white fluorescent lamps (Plate 3a). Associated with the increases in height were increments in the extension of the internodes (Tables 2a and 2b).

Results of Exp. 8 indicated that there was no effect of pot size on the time of change from vegetative to reproductive development. Time of flower initiation (Table 3b), time of first appearance of flower buds (Table 4) and number of leaves formed below the first flowers (Table 5b) were all apparently unaffected. With further development of the plants, those growing in large pots generally formed more flowers than those growing in small pots (Figs. 6b and 6c). This effect of pot size was greater in the long day treatments that employed warm white fluorescent lamps than tungsten filament lamps. The increases in flower number were associated with more advanced stages of growth in the plants; by the end of treatments, plants in large pots had produced a markedly greater number of generations of branches than those plants in the small pots. Growth in dry weight of the shoot systems was greater in the large pots than in the small pots (Figs. 3b and 3c).

The results described so far have been concerned primarily

Table 6a (Exp. 8) Effects of photoperiod, radiant exposure and pot size on dry weight of stems. 12 plants per treatment (16.11.78)

Dry weight (g) of stems per plant (117 days after sowing)

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size mean	Radiant exposure mean
Natural day light	10.8	10.54	11.21	14.13	11.96	14.13
	15.2	12.92	18.63	17.34	16.3	
Natural day light with supplementary lighting	10.8	8.78	10.64	16.60	12.01	18.3
	15.2	19.69	24.19	29.91	24.6	
Photoperiod mean		12.98	16.17	19.5		

Table 6b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on dry weight of leaves. 12 plants per treatment (16.11.78)

Dry weight (g) of leaves per plant (117 days after sowing)

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size (cm)	Radiant exposure mean
Natural day light	10.8	3.87	4.1	4.0	3.99	5.16
	15.2	5.96	7.27	5.74	6.32	
Natural day light with supplementary lighting	10.8	3.75	4.07	8.89	5.57	6.6
	15.2	8.2	8.98	5.73	7.64	
Photoperiod mean		5.45	6.11	6.09		

Fig. 6a (Exp. 1) Effects of photoperiod and radiant exposure on flower formation (18 plants per treatment. 3.11.77)

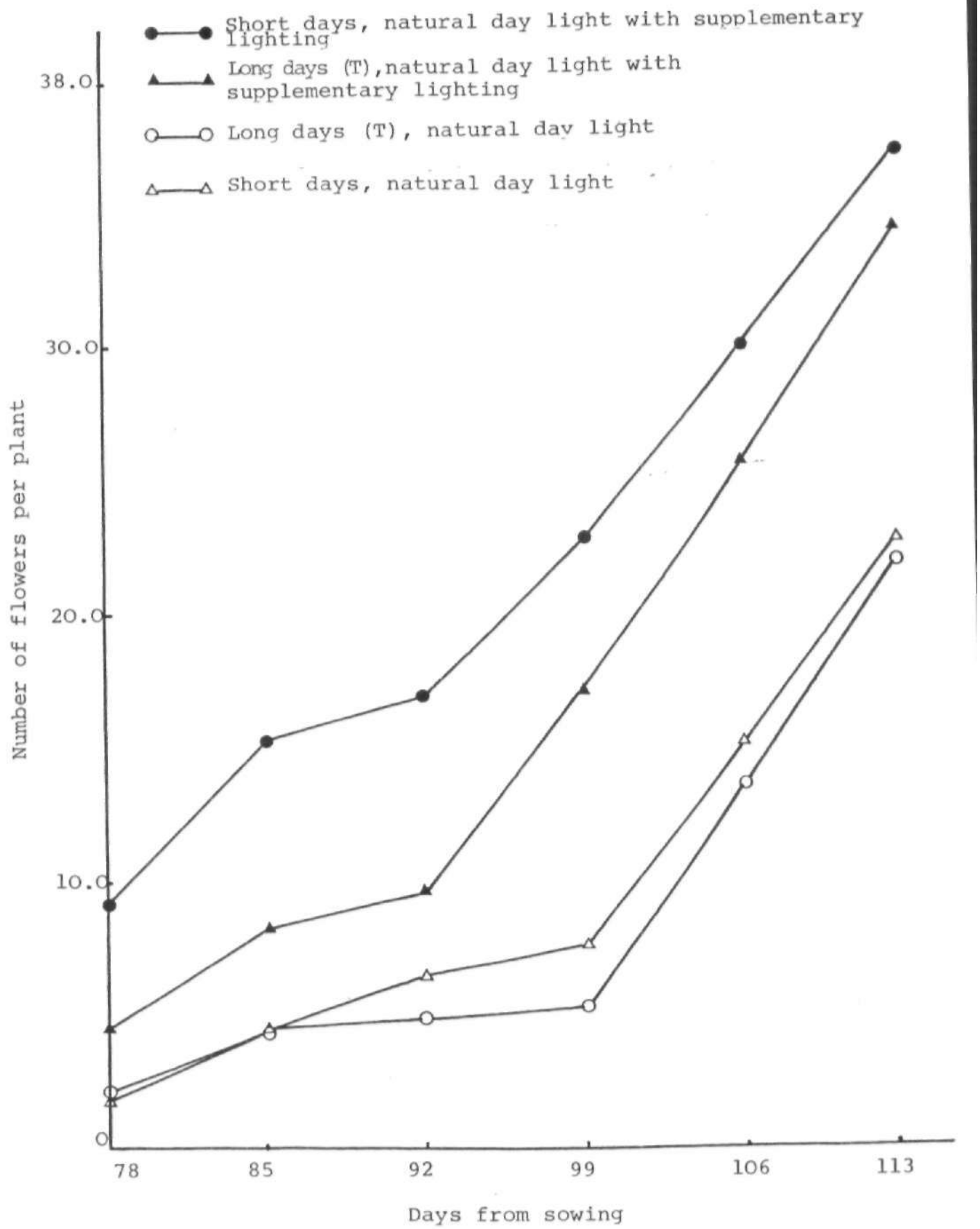

Short days, natural day light with supplementary lighting
Long days (T),natural day light with supplementary lighting
Long days (T), natural day light
Short days, natural day light
38.0
30.0
20.0
10.0
0
Number of flowers per plant
78
85
92
99
106
113
Days from sowing

Fig. 6b (Exp. 8) Effects of photoperiod, radiant exposure and 10.2 cm diameter pot on flower formation (12 plants per treatment. 16.11.78)

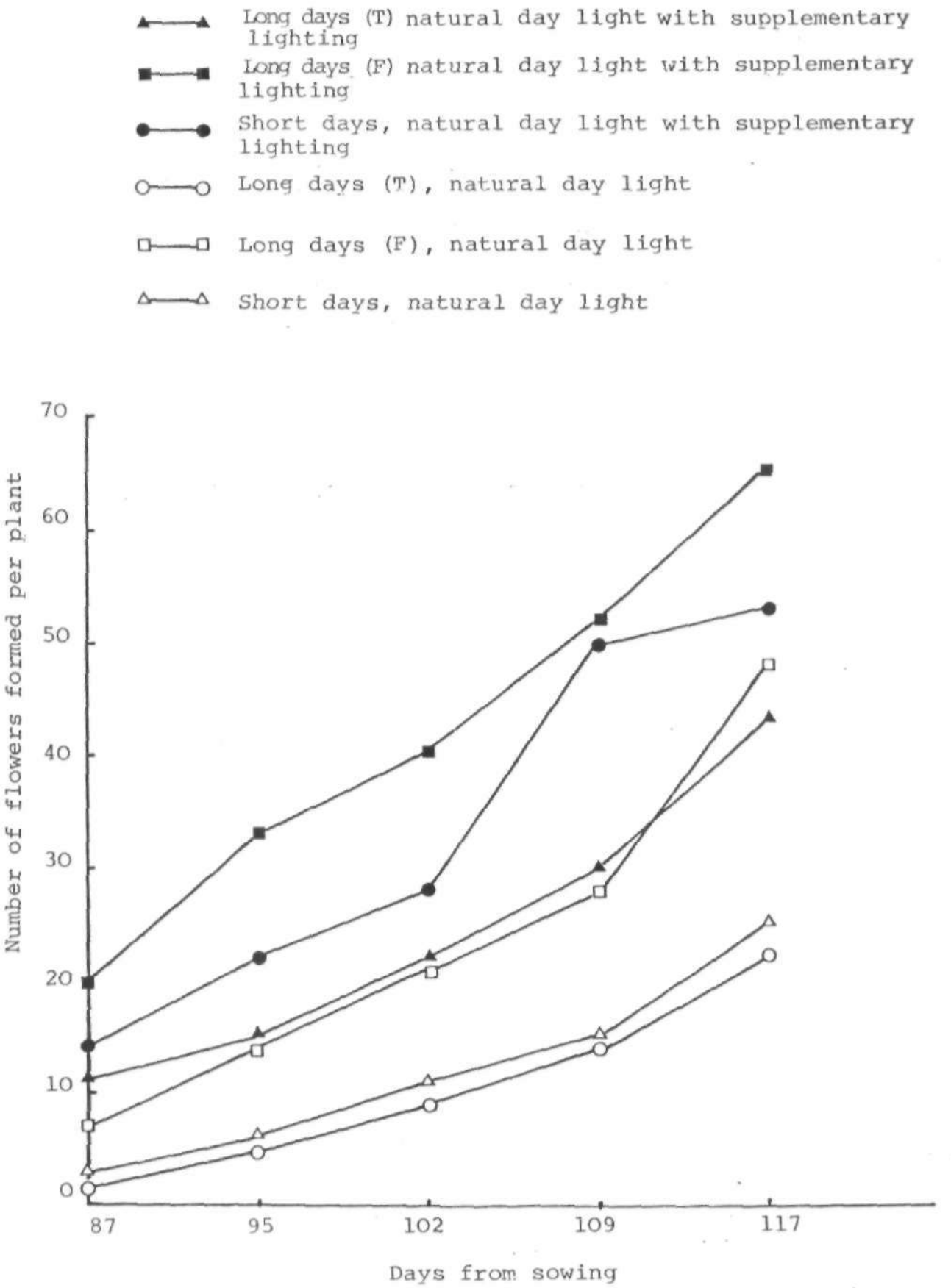
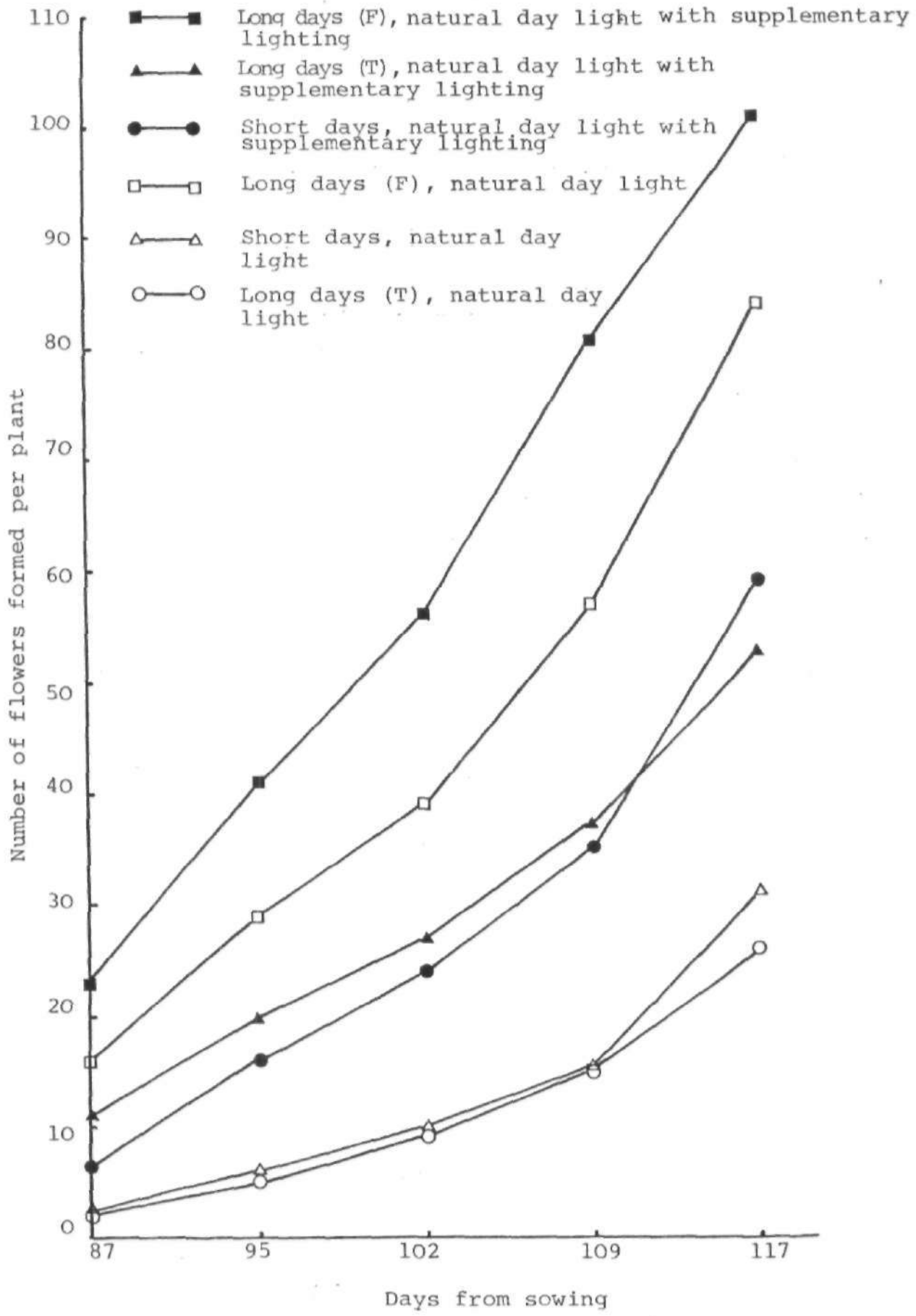

Long days (T) natural day light with supplementary lighting
Long days (F) natural day light with supplementary lighting
Short days, natural day light with supplementary lighting
Long days (T), natural day light
Long days (F), natural day light
Short days, natural day light
Number of flowers formed per plant
70
60
50
40
30
20
10
0
87
95
102
109
117
Days from sowing

Fig. 6c (Exp. 8) Effects of photoperiod, radiant exposure and 15.2 cm pot on flower formation (12 plants per treatment. 16.11.78)


Long days (F), natural day light with supplementary lighting
Long days (T), natural day light with supplementary lighting
Short days, natural day light with supplementary lighting
Long days (F), natural day light
Short days, natural day light
Long days (T), natural day light
Number of flowers formed per plant
0
10
20
30
40
50
60
70
80
90
100
110
87
95
102
109
117
Days from sowing

with effects of the treatments on vegetative growth and on flower formation. Some of the data collected in Exps. 1 and 8 were relevant to the development of the flowers after their initiation and these will now be described.

Tables 7a and 7b show that increased radiant exposure due to supplementary lighting hastened first opening of flowers. The magnitude of the effect varied from about 9 to 25 days depending on other conditions. Increasing the day length by the use of tungsten filament lamps delayed flower opening by 9 to 19 days. Where warm white fluorescent lamps were used to extend the day length however (Exp. 8, Table 7b), the first opening of flower occurred at about the same time as in short days.

The promotion of flower opening by supplementary lighting and the delay due to long days (tungsten filament lamps) were greater than the promotion and delay of flower initiation produced by the same treatments (Table 7a). An explanation of this difference might be that the treatments affected not only the time of flower initiation but also the subsequent development of the flowers initiated. Another possible explanation was that certain treatments increased the incidence of flower abortion among the first formed flowers so that when flower opening was first observed it was opening of later formed flowers carried on the first branches rather than those formed at the tip of the primary shoot. Evidence that this second explanation applied to the effects of the long day (tungsten filament lamps) treatments came from data on the number of plants that produced open flowers at the tips of the primary shoots. Tables 8a and 8b show that a high proportion of plants grown in

Table 7a (Exp. 1) Effects of photoperiod and radiant exposure on first opening of flowers. 18 plants per treatment (3.11.77)

Number of days from sowing to first flower opening

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Natural day light	114.7	119.3	117.0
Natural day light with supplementary lighting	93.7	110.6	102.2
Photoperiod mean	104.2	115.0	

LSD to compare photoperiod means (P=0.05) = 3.1
LSD to compare radiant exposure means (P=0.05) = 1.5
Radiant exposure photoperiod interaction (P=0.05) Significant

Table 7b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on first opening of flowers. 12 plants per treatment (16.11.78)

Number of days from sowing to first flower opening

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size (cm)	Radiant exposure mean
Natural day light	10.8	109.0	102.5	119.6	110.4	111.6
	15.2	111.1	105.9	121.7	112.9	
Natural day light with supplementary lighting	10.8	84.8	84.2	98.3	89.1	89.9
	15.2	85.4	82.7	104.2	90.8	
Photoperiod mean		97.6	93.8	111.0		

LSD to compare photoperiod means (P=0.05) = 2.8
LSD to compare radiant exposure means (P=0.05) = 4.5
LSD to compare pot size means (P=0.05) NS
Radiant exposure photoperiod x pot size interaction (P=0.05) NS

Table 8a (Exp. 1) Effects of photoperiod and radiant exposure on number of plants that had flowers formed at the tip of the primary shoot opened. 18 plants per treatment (3.11.77)

Number of plants (out of 18) on which first flowers opened

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Natural day light	13.0	4.0	8.5
Natural day light with supplementary lighting	18.0	3.0	10.2
Photoperiod mean	15.2	3.5	

Table 8b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on number of plants that had flowers formed at the tip of the primary shoot opened. 12 plants per treatment (16.11.78)

Number of plants (out of 12) on which first flowers opened

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size (cm)	Radiant exposure mean
Natural day light	10.8	11.0	2.0	0	4.3	3.3
	15.2	7.0	0	0	2.3	
Natural day light with supplementary lighting	10.8	12.0	10.0	4.0	8.7	7.8
	15.2	10.0	9.0	2.0	7.0	
Photoperiod mean		10.0	5.3	1.5		

days extended by the use of tungsten filament lamps failed to produce open flowers in this position. In this treatment most of the flowers formed at the tip of the primary shoot aborted before they reached anthesis.

When the experiments were terminated a few fruits had developed at the tips of some of the primary shoots and the lower branches. Tables 9a and 9b show the fresh weight of fruits per plant. The weight of fruits produced was increased by supplementary lighting and decreased by extension of the photoperiod using tungsten filament lamps. There was no consistent effect of supplementary lighting on the number of fruits set and it appeared that this treatment might have exerted its effect by increasing the growth of the individual fruits. Where tungsten filament lamps were used to extend the day length, the number of fruits set was generally reduced; there was no evidence that photoperiod affected the growth rate of individual fruits.

4.3 (Exp. 3) Effects of photoperiod and shading

In Exps. 1 and 8 radiant exposure was varied by the use of supplementary lighting. In the present experiment shading was used for this purpose. The experiment was carried out in the summer when natural radiation levels were high and the shaded plants would have received more light than the plants grown in natural day light in Exps. 1 and 8.

Natural radiation levels outside the glasshouse were measured daily throughout the duration of the experiment with Kipp's Solarimeter. Total natural radiation from November 17, 1977 to March 23, 1978 (Exp. 1) was 462.7 MJ m^{-2}; November 30,

Fig. 9 (Exp. 3) Effects of photoperiod and shading on plant height (cm) (18 plants per treatment. 15.3.78)

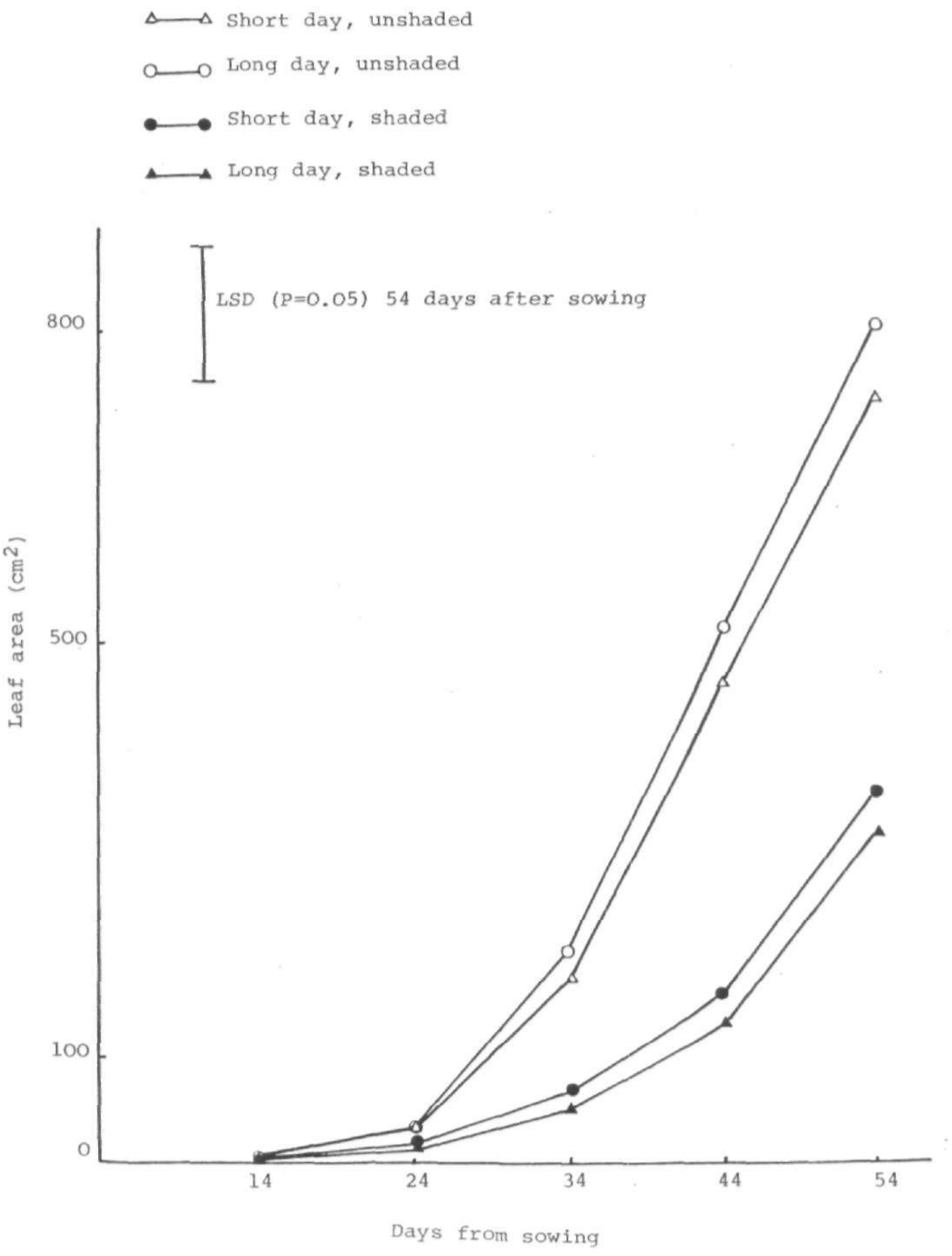

Short day, unshaded
Long day, unshaded
Short day, shaded
Long day, shaded
LSD (P=0.05) 54 days after sowing
800
500
100
0
Leaf area (cm2)
14
24
34
44
54
Days from sowing

Fig. 8 (Exp. 3) Effects of photoperiod and shading on leaf area (cm^2) (18 plants per treatment. 15.3.78)

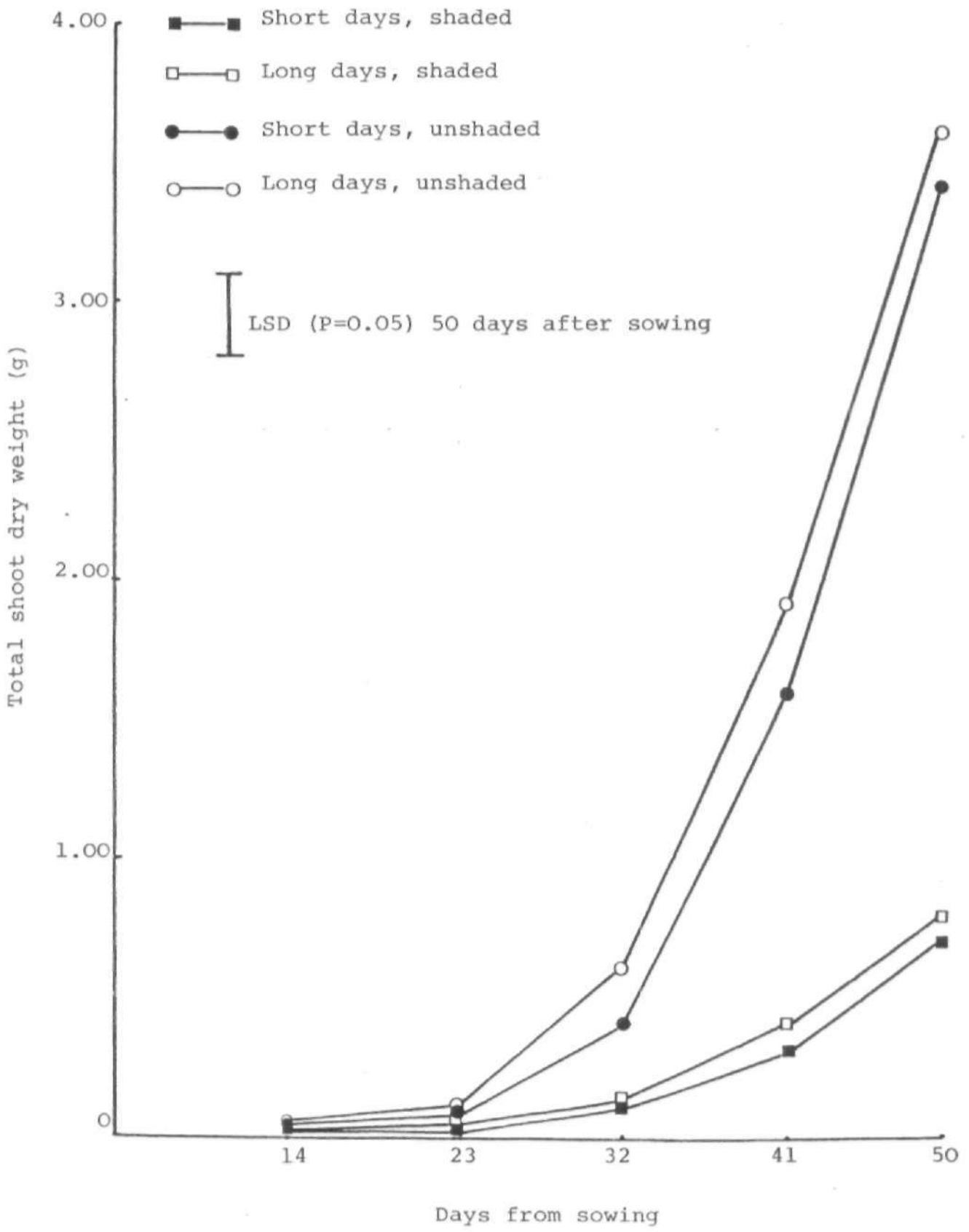

4.00
3.00
2.00
1.00
0
Short days, shaded
Long days, shaded
Short days, unshaded
Long days, unshaded
LSD (P=0.05) 50 days after sowing
Total shoot dry weight (g)
14
23
32
41
50
Days from sowing

Fig. 7 (Exp. 3) Effects of photoperiod and shading on total shoot dry weight (mg) (18 plants per treatment. 15.3.78)

Table 9a (Exp. 1) Effects of photoperiod and radiant exposure on fruit weight. 18 plants per treatment (3.11.77)

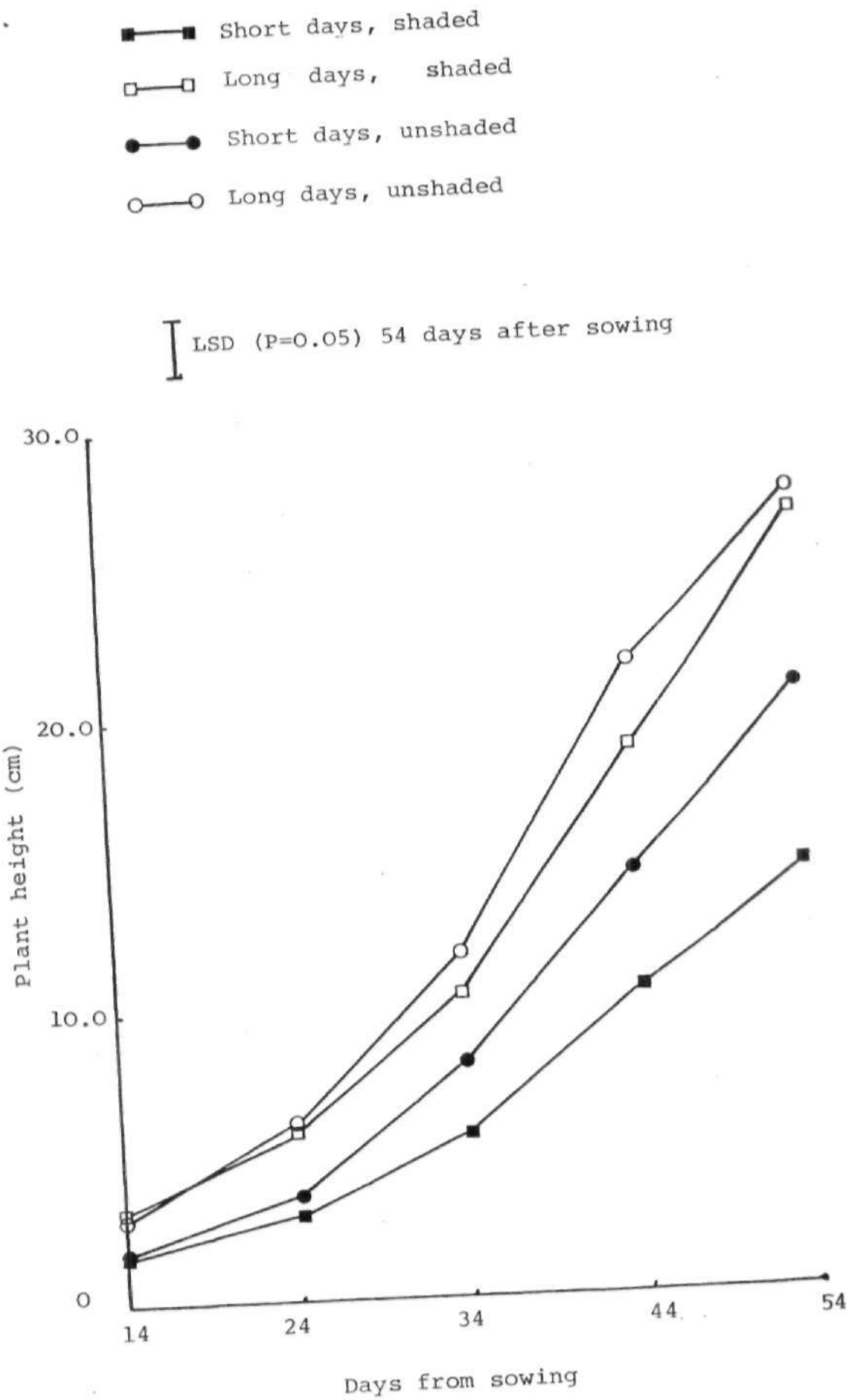
Fruit fresh weight (g) per plant. (Number of fruits set per plant is indicated in brackets)(149 days after sowing)

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Natural day light	26.0 (2.5)	21.5 (1.8)	23.8 (2.2)
Natural day light with supplementary lighting	84.7 (1.8)	39.5 (1.7)	62.1 (1.8)
Photoperiod mean	55.4 (2.3)	30.6 (1.8)	

Table 9b (Exp. 8) Effects of photoperiod, radiant exposure and pot size on fruit weight. 12 plants per treatment (16.11.78)

Fruit fresh weight (g) per plant. (Number of fruits set per plant is indicated in brackets)(127 days from sowing)

Radiant exposure	Pot size (cm)	Short days	Long days (F)	Long days (tungsten)	Pot size (cm)	Radiant exposure mean
Natural day light	10.8	32.8 (1.4)	91.4 (2.1)	0 (0)	41.4 (1.2)	23.5 (0.7)
	15.2	1.9 (0.1)	14.8 (0.3)	0 (0)	5.6 (0.1)	
Natural day light with supplementary lighting	10.8	248.2 (2.9)	219.6 (2.0)	43.7 (0.8)	170.5 (1.9)	137.2 (1.7)
	15.2	132.8 (2.8)	176.0 (1.6)	2.7 (0.3)	103.8 (1.6)	
Photoperiod mean		103.9 (1.8)	125.5 (1.5)	11.6 (0.3)		


Short days, shaded
Long days, shaded
Short days, unshaded
Long days, unshaded
LSD (P=0.05) 54 days after sowing
30.0
20.0
10.0
0
Plant height (cm)
14
24
34
44
54
Days from sowing

1978 to March 21, 1979 (Exp. 8) 410.1 MJ m^{-2} and March 28, 1978 to July 17, 1978 (Exp. 3) 1303.9 MJ m^{-2}.

Treatments consisted of either (a) shading to reduce total radiation during the 8h of day light by about 60 percent (see Chapter 2 for details) and (b) no shading. These were combined factorially with two photoperiodic treatments, short days and long days. In the long day treatment, tungsten filament lamps were used to extend the day length to 18h as in Exp. 1.

Figs. 7 and 8 show that shading markedly reduced the growth in dry weight of the shoots and also reduced the leaf area. Growth in height was also reduced by shading but more in plants grown in short days than those grown in long days (Fig. 9). Associated with the decrease in growth in plant height was a decrease in length of the internodes on the primary shoot (Table 10).

Accompanying the reductions in growth due to shading there were delays in flower initiation of about 10 days (Table 11). Shaded plants produced more leaves on the primary shoot below the first flowers but the increase in leaf number due to shading was small and amounted to less than one leaf on average (Table 12a). Shading delayed the first appearance of flower buds by about 20 days (Table 12b). Unshaded plants were ahead of shaded plants in development and by the end of the experiment the unshaded plants had formed considerably more flowers (Table 13a).

Any effects of photoperiod on growth in shoot dry weight or leaf area were small relative to those observed in Exp. 1 and 8. Differences in shoot dry weight and leaf area observed between the photoperiodic treatments and shown in Figs. 7 and 8

Table 10 (Exp. 3) Effects of photoperiod and shading on length of internodes on the primary shoot. 18 plants per treatment (15.3.78)

Length of internodes (cm) on the primary shoot

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Shaded	1.9	3.0	2.5
Unshaded	2.3	4.9	3.6
Photoperiod mean	2.1	4.0	

LSD to compare photoperiod means (P=0.05) = 0.2
LSD to compare radiant exposure means (P=0.05) = 0.3
Radiant exposure x photoperiod interaction (P=0.05) Significant

Table 11 (Exp. 3) Effects of photoperiod and shading on time of initiation of first flowers. 18 plants per treatment (15.3.78)

Days from sowing that 50% of plants initiated first flowers

Radiant exposure	Short days	Long days (tungsten)	Mean
Shaded	26.0	29.0	27.5
Unshaded	14.2	19.4	16.8
Photoperiod mean	20.1	24.2	

Table 12a (Exp. 3) Effects of photoperiod and shading on number of leaves formed below the first flowers. 18 plants per treatment (15.3.78)

Number of leaves formed on the primary shoot, below first flowers

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Shaded	11.50	12.05	11.78
Unshaded	11.17	11.30	11.24
Photoperiod mean	11.34	11.68	

LSD to compare photoperiod means (P=0.05) = 0.3
LSD to compare radiant exposure means (P=0.05) = 0.4
Radiant exposure x photoperiod interaction (P=0.05) Significant

Table 12b (Exp. 3) Effects of photoperiod and shading on time that the first flower buds became visible. 18 plants per treatment (15.3.78)

Number of days from sowing to the first appearance of flower buds

Radiant exposure	Short day	Long days (tungsten)	Radiant exposure mean
Shaded	62.0	65.0	63.5
Unshaded	39.7	42.8	41.2
Photoperiod mean	50.8	53.9	

LSD to compare photoperiod means (P=0.05) = 1.3
LSD to compare radiant exposure means (P=0.05) = 2.0
Radiant exposure x photoperiod interaction (P=0.05) NS

Table 13a (Exp. 3) Effects of photoperiod and shading on flower formation. 18 plants per treatment (15.3.78)

Number of flower buds that had become visible (124 days after sowing)

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Shaded	18.5	11.0	14.8
Unshaded	46.4	33.6	40.0
Photoperiod mean	32.5	22.3	

LSD to compare photoperiod means (P=0.05) = 2.6
LSD to compare radiant exposure means (P=0.05) = 4.1
Radiant exposure x photoperiod interaction (P=0.05) Significant

Table 13b (Exp. 3) Effects of photoperiod and shading on number of plants that had first flowers opened. 18 plants per treatment (15.3.78)

Number of plants (out of 18) on which first flowers opened

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Shaded	0	0	0
Unshaded	18	7	12.5
Photoperiod mean	9	3.5	

were not significant. Long days promoted the growth in height of the plants (Fig. 9) and this effect was associated with greater internode extension in the primary shoot (Table 11a).

Table 11b shows that flower initiation in the long day treatment was 3 to 5 days later than in the short day treatment. Photoperiod had little or no effect on the number of leaves initiated before the first flowers in unshaded plants but there was evidence of a very small reduction in leaf number due to short days in shaded plants (Table 12a). Short days hastened the appearance of the first flower buds by about 3 days (Table 12b). By the end of the experiment (124 days after sowing) plants grown in short days had produced more flower buds than those grown in long days (Table 13a).

There was evidence that the development of the flowers after their initiation was affected by both shading and photoperiodic treatments. The first opening of flowers on the plants occurred about 20 days earlier in unshaded than shaded plants and about 10 days earlier in short days than in long days (Table 14a). These differences were attributable, in part at least, to diferences in the incidence of abortion among the first formed flowers. Table 13b shows that in many of the plants flowers formed at the tip of the primary shoot never reached the opening stage. In shaded plants none of these flowers reached anthesis while in unshaded plants the incidence of abortion was higher in plants grown in long days than in those grown in short days. Abortion of the first formed flowers must have been a major factor in producing delays in flower opening.

Determinations of fresh weight of the few fruits that had

Table 14a (Exp. 3) Effects of photoperiod and radiant exposure on first anthesis. 18 plants per treatment (15.3.78)

Number of days from sowing to first flower opening

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Shaded	86.5	94.7	90.6
Unshaded	63.5	73.7	68.6
Photoperiod mean	75.0	84.2	

LSD to compare photoperiod means (P=0.05) = 3.9
LSD to compare radiant exposure means (P=0.05) = 2.2
Radiant exposure x photoperiod interaction (P=0.05) NS

Table 14b (Exp. 3) Effects of photoperiod and shading on fruit fresh weight. 18 plants per treatment (15.3.78)

Fruit fresh weight (g) per plant (number of fruits set per plant is indicated in brackets)(124 days after sowing)

Radiant exposure	Short days	Long days (tungsten)	Radiant exposure mean
Shaded	3.26 (0.7)	0 (0)	1.63 (0.4)
Unshaded	65.09 (7.0)	30.35 (4.3)	47.72 (5.7)
Photoperiod mean	34.17 (3.8)	15.17 (2.2)	

set by the end of the experiment (124 days after sowing) showed that the fresh weight of fruits per plant was decreased by shading or by long days (Table 14b). These differences were associated with marked difference in the number of fruits set per plant.

4.4 (Exps. 10 and 20) Effects of varying the photoperiod by the use of artificial lighting at different times during the night period

Artificial lighting used in the middle of the dark period may be more effective in producing photoperiodic effects than equivalent lighting used at the end of the day (Vince-Prue and Guttridge, 1973; Vince-Prue, 1975; Guttridge, 1976). The present experiments were designed to determine whether delays in flower initiation due to extension of the day length to 18h by illumination from tungsten filament lamps might also be produced by interrupting the dark period. A period of 2h lighting was given either in the middle of the dark period (from 24.00h to 2.00h), to extend the day in the evening (from 17.00h to 19.00h, "evening lighting") or to extend the day in the morning (from 7.00h to 9.00h, "morning lighting"). Either tungsten filament lamps (Exp. 10) or warm white fluorescent lamps (Exp. 20) were used for this purpose and levels of illuminance at plant height was as used in Exps. 1, 8 and 3 previously described.

Seedlings were transferred to plastic pots (10.8 cm diameter) as soon as the cotyledons had expanded fully and treatments commenced on the same day. A randomised block design

with 4 replications (6 plants per replicate) were used in each experiment.

Tables 15a, 15b, 16a, 16b, 17a and 17b show that the lighting treatments used in Exps. 10 and 20 had no apparent effect on the duration of the vegetative stage of growth whether thiswas assessed in terms of time to first appearance of flower buds (Tables 16a and 16b) or number of leaves formed on the primary shoot below the first-formed flowers (Tables 15a and 15b). Any effects on time to flower opening were small; delays of 3 to 5 days in flower opening were observed in the night break treatments. In Exp. 10 where tungsten filament lamps were used as the light source plants in the night break treatments failed to produce any open flowers at the tip of the primary shoot. Flower buds at this position aborted and the first flowers to open were on the branches. This could explain the delay in flower opening in this treatment but a similar explanation cannot account for the delay in flower opening in the night break treatment using warm white fluorescent lamps (Exp. 20); in this treatment there was little flower abortion and all the plants produced open flowers at the tip of the primary shoot (Table 17b).

The growth in dry weight of the shoots and leaf areas were measured about 10 days (Exp. 10) or 20 (Exp. 20) after the time flower buds first appeared. In Exp. 10 where the light sources used were tungsten filament lamps, the 2h periods of lighting had no significant effect on shoot dry weight (Table 18a). There was small, but significant decrease in leaf area due to the night break treatment from 24.00h to 2.00h (Table 19a).

Table 15a (Exp. 10) Effects of night-break (by tungsten lamps) on number of leaves formed below the first flower. 24 plants per treatment (9.5.79)

Number of leaves formed on the primary shoot

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
10.1	10.1	10.5	10.0

LSD (P=0.05) NS

Table 15b (Exp. 20) Effects of night-break by fluorescent lamps on number of leaves formed below the first flower. 24 plants per treatment (10.8.79)

Number of leaves formed on the primary shoot

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
9.7	9.4	9.8	9.5

LSD (P=0.05) NS

Table 16a (Exp. 10) Effects of night-break by tungsten lamps on flower bud visibility. 24 plants per treatment (9.5.79)

Number of days from sowing to time first flower buds became visible

Short day	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
37.6	38.1	38.6	38.1

LSD (P=0.05) NS

Table 16b (Exp. 20) Effects of night-break by fluorescent lamps on flower bud visibility. 24 plants per treatment (10.8.79)

Number of days from sowing to time first flower buds became visible

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
42.2	41.0	43.1	41.3

LSD (P=0.05) NS

Table 17a (Exp. 10) Effects of night-break by tungsten lamps on first anthesis. 24 plants per treatment (9.5.79)

Number of days from sowing to first anthesis in the plant; and number of plants that produced open flowers at the tip of the primary shoot in brackets

Short day	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
60.7	61.4	65.6	63.6
(24.0)	(24.0)	(6.0)	(22.0)

Table 17b (Exp. 20) Effects of night-break by fluorescent lamps on first anthesis. 24 plants per treatment (10.8.79)

Number of days from sowing to first anthesis in the plant; and number of plants that produced open flowers at the tip of the primary shoot in brackets

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
66.5	64.7	69.9	65.5
(24.0)	(24.0)	(24.0)	(24.0)

Table 18a (Exp. 10) Effects of night-break by tungsten lamps on shoot dry weight. 12 plants per treatment (9.5.79)

Dry weight (g) of shoot system per plot (4 plants per plot) (49 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
0.4986	0.509	0.4564	0.4512

LSD (P=0.05) NS

Table 18b (Exp. 20) Effects of night-break by fluorescent lamps on shoot dry weight. 12 plants per treatment (10.8.79)

Dry weight (g) of shoot system per plot (4 plants per plot) (52 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
3.522	4.695	2.646	3.401

LSD (P=0.05) = 0.69

Table 19a (Exp. 10) Effects of night-break on tungsten filament lamps on leaf area. 12 plants per treatment (9.5.79)

Leaf area (cm^2) per plot (4 plants per plot) (49 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
175.07	179.24	153.61	159.56

LSD (P=0.05) = 18.69

Table 19b (Exp. 20) Effects of night-break by fluorescent lamps on leaf area. 12 plants per treatment (10.8.79)

Leaf area (cm^2) per plot (4 plants per plot) (52 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
244.1	308.83	288.49	245.46

LSD (P=0.05) = 49.35

In Exp. 20 in which warm white fluorescent lamps were used, evening lighting from 17.00h to 19.00h caused an increase in shoot dry weight and also in leaf area (Tables 18b and 19b). The night—break treatment caused a significant decrease in the dry weight of the shoot as compared with short days. Leaf area was apparently unaffected. When Exp. 20 was ended 82 days after sowing the seeds, fruits had started to develop at the tip of the primary shoot and on the lower branches. Table 20 shows that in the evening lighting treatment where a promotion of growth in dry weight of the shoot had been observed, the dry weight of the fruits was greater than in the short day treatment.

The use of tungsten filament lamps to illuminate plants for 2-h periods in Exp. 10 produced increases in plant height (Table 21a). Of the three periods of illumination used, morning lighting (7.00h to 9.00h) was the most efficient in promoting growth in height (Plate 3b). In this treatment the mean length of internodes of the primary shoot was markedly greater than in the other treatments (Table 22a). The use of warm white fluorescent lamps (Exp. 20) for the circles providing 2-h periods had no significant effect on plant height or internode length (Tables 21b and 22b).

4.5 Discussion

The experiments reported here showed that radiant exposure can be an important factor affecting flowering in sweet pepper plants. Increases in radiant exposure produced by the use of artificial lighting to supplement natural day light

Table 20 (Exp. 20) Effects of night-break by fluorescent lamps on fruit dry weight. 24 plants per treatment (10.8.79)

Dry weight (g) of fruits, per plot with number of fruits set, per plot in brackets (80 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
1.3	3.19	0.56	2.41
(7.7)	(13.3)	(3.7)	(8.7)

LSD (P=0.05) = 1.27; (5.8)

Table 21a (Exp. 10) Effects of night-break by tungsten filament lamps on plant height. 24 plants per treatment (9.5.79)

Plant height (cm) (49 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
15.2	19.1	18.5	30.3

LSD (P=0.05) = 1.7

Table 21b (Exp. 20) Effects of night-break by fluorescent lamps on plant height. 24 plants per treatment (10.8.79)

Plant height (cm) (52 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
8.9	9.9	8.8	8.6

LSD (P=0.05) NS

Table 22a (Exp. 10) Effects of night-break by tungsten filament lamps on internode elongation. 24 plants per treatment (9.5.79)

Length of internodes (cm) on primary shoot (55 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
2.1	2.3	2.4	4.4

LSD (P=0.05) = 0.05

Table 22b (Exp. 20) Effects of night-break on fluorescent lamps on internode elongation. 24 plants per treatment (10.8.79)

Length of internode (cm) on primary shoot (52 days after sowing)

Short days	Evening lighting (17h-19h)	Night-break (24h-02h)	Morning lighting (07h-09h)
2.8	3.1	2.8	3.0

LSD (P=0.05) NS

in the winter hastened flower initiation at the tip of the primary shoot by 20 to 30 days. A shading treatment that cut out about 60 per cent of radiation incident on the plants was shown to delay flower initiation by about 10 days during the summer.

It appeared that effects of radiant exposure on the time of change from vegetative to reproductive development were related to effects on rates of growth. Lang (1952) noted that environmental factors could influence flowering in a non-specific manner by affecting the rate of growth and development of the whole plant and there is evidence that radiant exposure acted in this way on flowering in sweet pepper. Earlier flower initiation due to increased radiant exposure was always accompanied by increased growth rates measured in terms of shoot dry weight, leaf area or shoot height.

An extension of the hypothesis that radiant exposure affected flowering by affecting the growth rate of the whole plant is that flower initiation could occur only when a particular size or "physiological age" was attained. Klapwijk and de Lint (1975) found that in tomatoes grown under conditions where supplies of water and nutrients were unlikely to be limiting, stages of reproductive development were closely correlated with growth in fresh weight of the plants. Experiments here were not designed to test the hypothesis that flower initiation occurred after a particular dry weight had been attained. However, examination of the data presented here for growth in dry weight of the shoot of sweet pepper (Figs. 3a, 3b and 3c) and times of flower initiation (Tables 3a

and 3b) suggests that initiation must have occurred when plants subjected to different radiant exposures had attained similar dry weights.

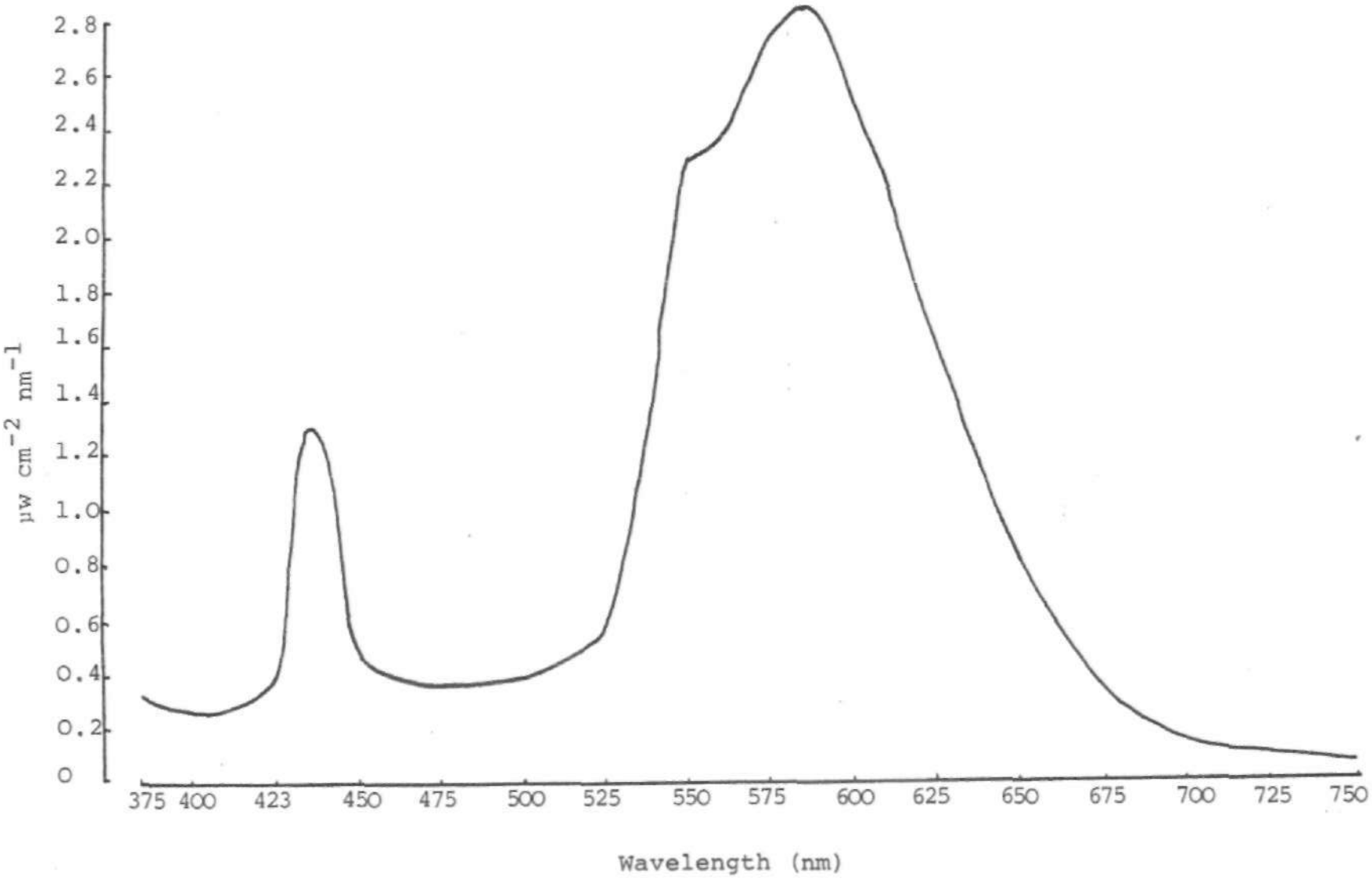
The number of leaves formed before flowers were initiated was determined by counting the leaves on the primary shoots below the terminal flowers. Plants subjected to high radiant exposures were observed to have formed one or two leaves fewer before initiating flowers than plants grown at lower light levels.

In many studies of flowering behaviour "leaf number to flower" has been used as a measure of physiological age at the time of flower initiation (Lang, 1952 and 1965) and differences in the number of leaves formed before the initiation of flowers have been taken as evidence of "specific" effects on flower initiation. While leaf counts can be accepted as a useful measure of the amount of vegetative growth that has preceded flower initiation there is no reason to suppose that there is any close dependence of flower initiation on leaf number in a physiological sense. Evidence contrary to the view that a minimum leaf number is required for flower initiation to occur has been presented by Holdsworth (1956). The small differences in leaf number to flower in sweet pepper plants produced by differences in radiant exposure are not inconsistent with the hypothesis that growth rate of the whole plants was an important factor in determining the time of flower initiation.

The change from vegetative to reproductive development in sweet pepper was affected less by photoperiodic treatments than by treatments involving substantial differences in radiant exposure. Although extension of an 8h day to 18h by the use of

tungsten filament lamps consistently delayed flower initiation by a few days, the classification of sweet pepper as a quantitative short day plant was not supported by other experimental results obtained here. Delays of flower initiation in pepper due to extension of the day with low intensity lighting from tungsten filament lamps had previously been reported by Cochran (1942). While the present experiments confirmed this observation, they did not demonstrate any consistent and significant increase in leaf number to flower due to extension of the day using tungsten filament lamps. Furthermore extension of an 8h day to 18h with low intensity lighting from warm-white fluorescent lamps had no apparent effect on time of flower initiation. Interruption of a 16h night using a 2h period of lighting from either tungsten filament lamps or warm-white fluorescent lamps appeared to have no effect on the time of flower formation or on the number of leaves formed before flowers were initiated. The absence of flowering responses to these lighting treatments could not be regarded as typical of quantitative short-day plants.

There is evidence that night-break will normally prevent or delay flowering in short-day plants. In some plants only a few minutes of light is usually adequate; 30 minutes of lighting with tungsten filament lamps will prevent *Perilla* (Carr, 1952), *Glycine* cv Biloxi (Parker *et al.*, 1946) and *Xanthium* (Salisbury, 1963) from flowering. *Chrysanthemum* requires several hours of lighting from tungsten filament lamps to prevent flowering; however, exposure to high intensity fluorescent lamps for only a few minutes will completely inhibit flowering in this plant

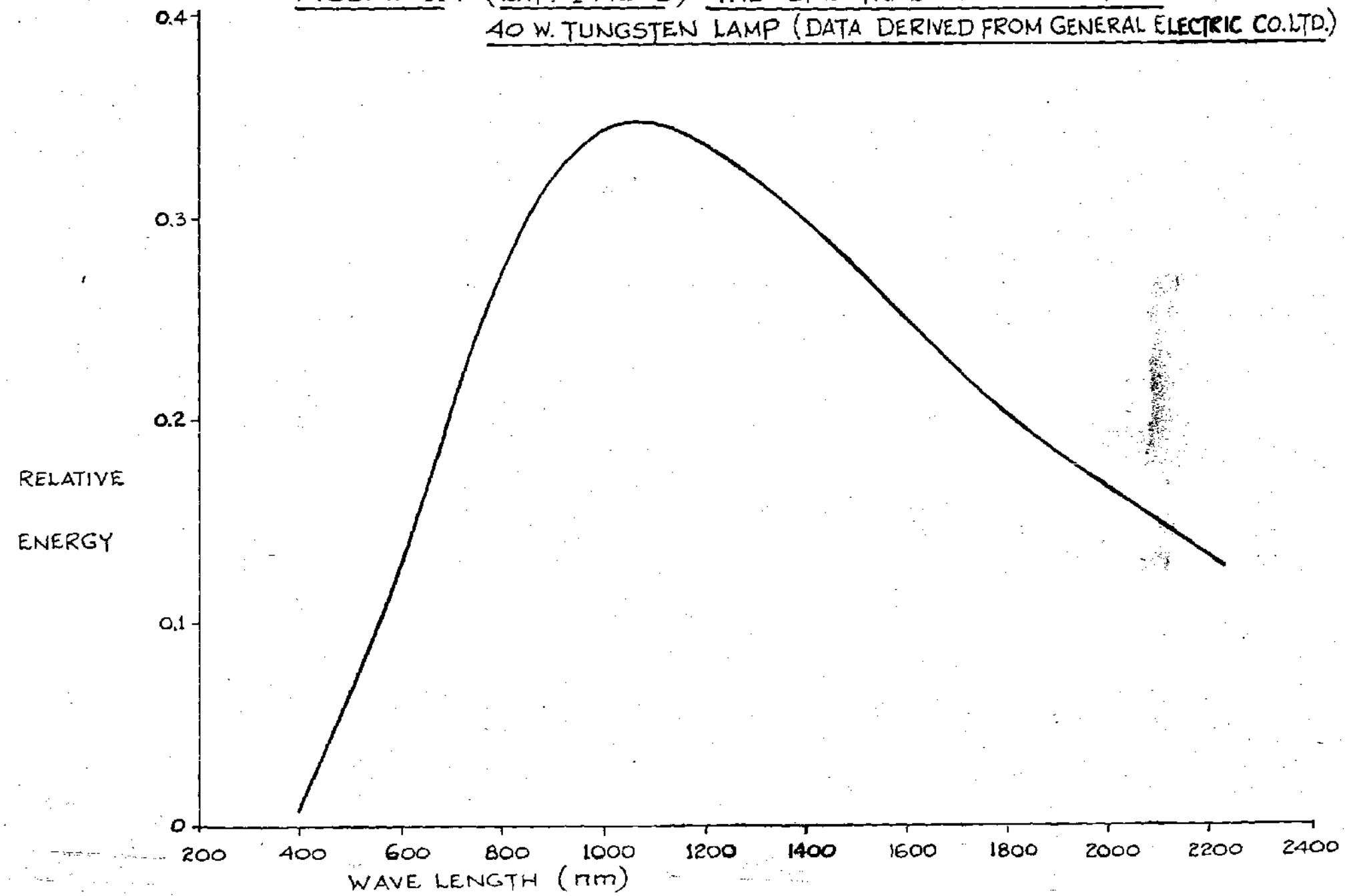

2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
µw cm⁻² nm⁻¹
375 400 423 450 475 500 525 550 575 600 625 650 675 700 725 750
Wavelength (nm)

(Vince-Prue, 1975). Lighting from midnight to dawn with fluorescent or tungsten filament lamps inhibited flowering in strawberry (Guttridge, 1976).

The doubt surrounding the classification of sweet pepper as a quantitative short-day plant raised the question of whether delays in flower initiation due to long day lighting treatments could be regarded as a direct response to photoperiod or whether growth correlation might be involved. Delays in flower initiation due to the use of tungsten filament lamps to extend the day to 18h cannot be attributed to any adverse effects on growth of the whole plant. In fact the lighting treatments when used in the winter promoted growth in dry weight, in leaf area and in shoot height. A delay in flower initiation accompanying a promotion of growth in dry weight suggests that the treatments exerted a specific effect on flowering.

A noticeable effect of the tungsten filament lighting treatment was the markedly increased elongation of the primary shoot accompanied by increased elongation of the individual internodes and a relatively high dry weight of stem. This suggested the possibility that increased stem growth might in some way be antagonistic to flower initiation. Lighting from warm-white fluorescent lamps, which have a very low emission in the far-red (Fig. 10) had no apparent effect on the time of flower formation and was less effective in promoting stem elongation than lighting from tungsten filament lamps. However, the experiments in which 2h periods of illumination were given at different times during the 16-h night failed to show any relation between the time of flower initiation and elongation

FIGURE 11. (EXP. 1 AND 8) THE SPECTRAL EMISSION OF A 40 W. TUNGSTEN LAMP (DATA DERIVED FROM GENERAL ELECTRIC CO. LTD.)



of stem and internodes. A 2h period of illumination from tungsten filament lamps given immediately before the 8h of natural day length was very effective in promoting stem elongation but had no significant effect on the time of appearance of flower buds or on the number of leaves formed below the flowers.

The greater elongation of stem obtained by extending the 8h day with tungsten filament lamps as compared with warm-white fluorescent lamps may be due to differences in their spectral emissions (Figs. 10 and 11). This suggestion seems to be supported by Deutch and Rasmussen (1974) who reported that fluorescent lamps supply enough radiation in the red wave lengths to reduce stem elongation while tungsten filament lamps contain enough far-red to promote stem elongation in many species including *Phaseolus vulgaris* L., *Triticum aestivum* L. and *Lycopersicum esculentum* Mill.

The reason for greater effectiveness of illumination from tungsten filament lamps in promoting stem elongation when given as a 2h period immediately before 8h of natural day light as compared to a 2h period immediately after the natural day light is not clear. It is possible that lighting increased the temperature of the plant tissues which might have influenced elongation. However, no reason can be offered as to why such an increase in temperature should be more effective in the morning than the evening. Guttridge (1976), Vince-Prue and Guttridge (1973) and Vince-Prue *et al*. (1976) did not obtain a similar effect to that obtained here in petiole length of strawberry when a period of lighting with tungsten filament

lamps was given immediately before the 8h of natural day light. The increase in petiole length they obtained was similar whether lighting immediately preceded or followed natural day light.

The experiments reported here indicated that flower abortion was of common occurrence in sweet pepper and showed that the incidence of abortion was influenced more by radiant exposure than by photoperiod. The use of high intensity artificial illumination to supplement day light during the winter reduced the incidence of flower abortion among flowers formed at the tip of the primary shoot while in the summer shading to reduce natural radiation by 60 percent significantly increased the incidence of flower abortion of the first-formed flowers. Similar effects of radiant exposure on incidence of flower abortion in peppers were reported by Rylski and Harlevy (1974), Park and Jeong (1976) and Song *et al.* (1976). A complete abortion of the truss in tomato was observed by Kinet (1977) when plants were grown in low light intensity.

Abortion of flowers due to a reduction in total radiation suggested that little assimilates were reaching the developing buds because of limited photosynthetic activities in plant. This explanation is supported by the observation that in plants subjected to low radiant exposures that decreases in growth in dry weight and in leaf area accompanied increases in the incidence of flower abortion.

A general observation was made that a substantial number of flowers failed to develop beyond anthesis. This was reflected in the small number of fruits set. The incidence of post-anthesis shedding of flowers could be attributed to failure of pollination

and lack of fertilization. There is evidence that pollination and fertilization may fail to occur when light conditions are poor; an increase in fruit set was obtained at higher radiant exposure as compared with lower radiant exposure. Evidence here shows that shading inhibited fruit set.

Reports of previous workers on effects of radiant exposure on fruit set in pepper are conflicting. Whereas Park and Jeong (1976) and Quagliotti (1976) obtained a decrease in fruit set with shading, Cochran (1936) and Schoch (1976) reported that shading increased fruit set. In tomato, Went (1957), Nitsch (1965) and Howlet (1966) had reported that a reduced light intensity was generally unfavourable for maximum fruit set and development.

No consistent effects of photoperiod on fruit set were observed in the experiments reported here. The apparent increase in fruit weight recorded for plants grown in 8h day was probably due to less flower abortion that occurred than 8h day extended to 18h with tungsten lamps which led to earlier fruit set in short days than long days. This explanation probably accounted for an increase of 5.6 percent in fruit set obtained by Cochran (1936) in pepper plants grown in 10h day as compared with 10h day extended to 18h with incandescent lamps.

4.6 Summary

(1) The initiation of flowers at the tip of the primary shoot of sweet pepper plants were hastened by the use of high intensity artificial lighting to supplement day light in the winter and was delayed by the use of shading that reduced

radiation by about 60 percent in the summer.

(2) Reductions in the duration of the vegetative phase of growth produced by high radiant exposures were associated with increases in the rate of growth in dry weight of the shoot system.

(3) Once the first flowers had been formed, further flower buds were generally formed more rapidly in plants subjected to high radiant exposure than in plants subjected to low radiant expsoure.

(4) Shading plants during the summer resulted in an increase in the incidence of flower abortion and a reduction in the fresh weight of the first fruits produced. The use of supplementary lighting during the winter resulted in an increase in early fruit growth.

(5) In experiments designed to compare effects of long and short photoperiods on flowering, results varied with the source and timing of illumination used to provide the long day treatment.

(6) Extension of an 8h day to 18h using low intensity illumination from tungsten filament lamps delayed the onset of flower initiation by a few days. When warm white fluorescent lamps were used to extend the day to 18h no effect on the time of flower initiation was observed. In both of these long day treatments, rates of growth in dry weight of the shoot were higher than in short days. Nightbreak treatments of 2h duration using either tungsten filament lamps or warm white fluorescent lamps had no apparent effect on flower initiation.

(7) Once flowers had been initiated at the tip of the primary

shoot, the rate of formation of further flowers appeared to be unaffected by the photoperiodic treatments used.

(8) Where tungsten filament lamps were used to extend the day or to provide a night break treatment the incidence of abortion among the first formed flowers was increased.

Chapter 5

Effects of Night Temperatures and Radiant Exposures on Flowering, Fruit Set and Fruit Development (Exps. 2, 21, 25 and 4)

The main object of the experiments described in this chapter was to investigate the influence of night temperatures on the onset of the reproductive phase, flowering, fruit set and fruit development in sweet pepper.

5.1 (Exp. 2) Effects of night temperatures and radiant exposure on flowering

This experiment was carried out in the winter of 1978 to examine effects of night temperature treatments and of different radiant exposures applied as soon as seedlings had emerged and the cotyledons had expanded. The timing of the experiment is shown in Table 23.

Plants were grown in natural day light (9.00h-17.00h) or in natural day light supplemented by artificial illumination from 400 W high pressure mercury fluorescent (MBFU) lamps which were suspended at 100 cm above the plants. At night (17.00h-9.00h) plants were grown in dark rooms adjoining the glasshouse and maintained at 20^{o}C ± 1.5 ("high" night temperature) or 13^{o}C ± 1.5 ("low" night temperature).

Treatments were arranged in a 2 x 2 factorial split-plot randomised blocks, replicated three times with radiant exposure as the main plots.

Table 23 Detail of Exps. described in Chapter 5

Exp. number	Title of Exp.	Date of sowing seed	Date treat-ments commenced	Stage of plant development at which treatments commenced	Date Exp. was terminated
2	Effects of night temperatures and radiant exposure on flowering (18 plants per treatment)	10.1.78	24.1.78	Full cotyledon expansion (Pricking out stage)	21.4.78 (101 days after sowing)
21	Effects of night temperatures and shading on flowering (16 plants per treatment)	4.9.79	24.10.79	First flower bud visible stage	15.12.79 (102 days after sowing)
25	Effects of night temperatures, shading and pruning on flowering and fruit set (9 plants per treatment)	15.11.79	29.2.80	Visible stage of 3^{o} flowers	4.4.80 (141 days after sowing)
4	Effects of night temperatures on fruit set and development (12 plants per treatment)	24.3.78	29.5.78	2-3 days before anthesis a) Flowers on first branches b) Flowers on second branches	19.7.78 (117 days after sowing)

Results

Vegetative growth was affected by night temperature. Growth in dry weight was significantly increased in plants growing at a high night temperature (Fig. 12). Growth in leaf area and plant height was similarly increased by the higher temperature (Figs. 13 and 14). No significant effect of temperature on internode length was observed (Table 24a) and the effect on height must have been associated with differences in the number of internodes that extended.

Time from sowing the seed to the initiation of flowers was reduced by about 10 (Table 24b) days by the high night temperature while the number of leaves formed on the primary shoot below the flowers was reduced by one or two (Table 25a). The time to the first appearance of flower buds was also reduced by the high night temperature (Table 25b), but this appeared to reflect the earlier initiation of the flowers rather than a reduction in the time from initiation to appearance of the buds.

The rate of flower development from the time flower buds became visible to the time the flowers opened was assessed by allotting "scores" (Plate 1) to recognizable stages of flower development (Fig. 15). Fig. 15 shows that flower development to anthesis was more rapid when the night temperature was high. Table 26a shows that first opening of flowers occurred earlier in plants grown at a high night temperature than in plants grown at a low night temperature. This difference was attributable to the difference in time of flower initiation and also the difference in rates of flower development.

Fig. 12 (Exp. 2) Effects of night temperature and radiant exposure on total shoot dry weight (18 plants per treatment. 10.1.78)

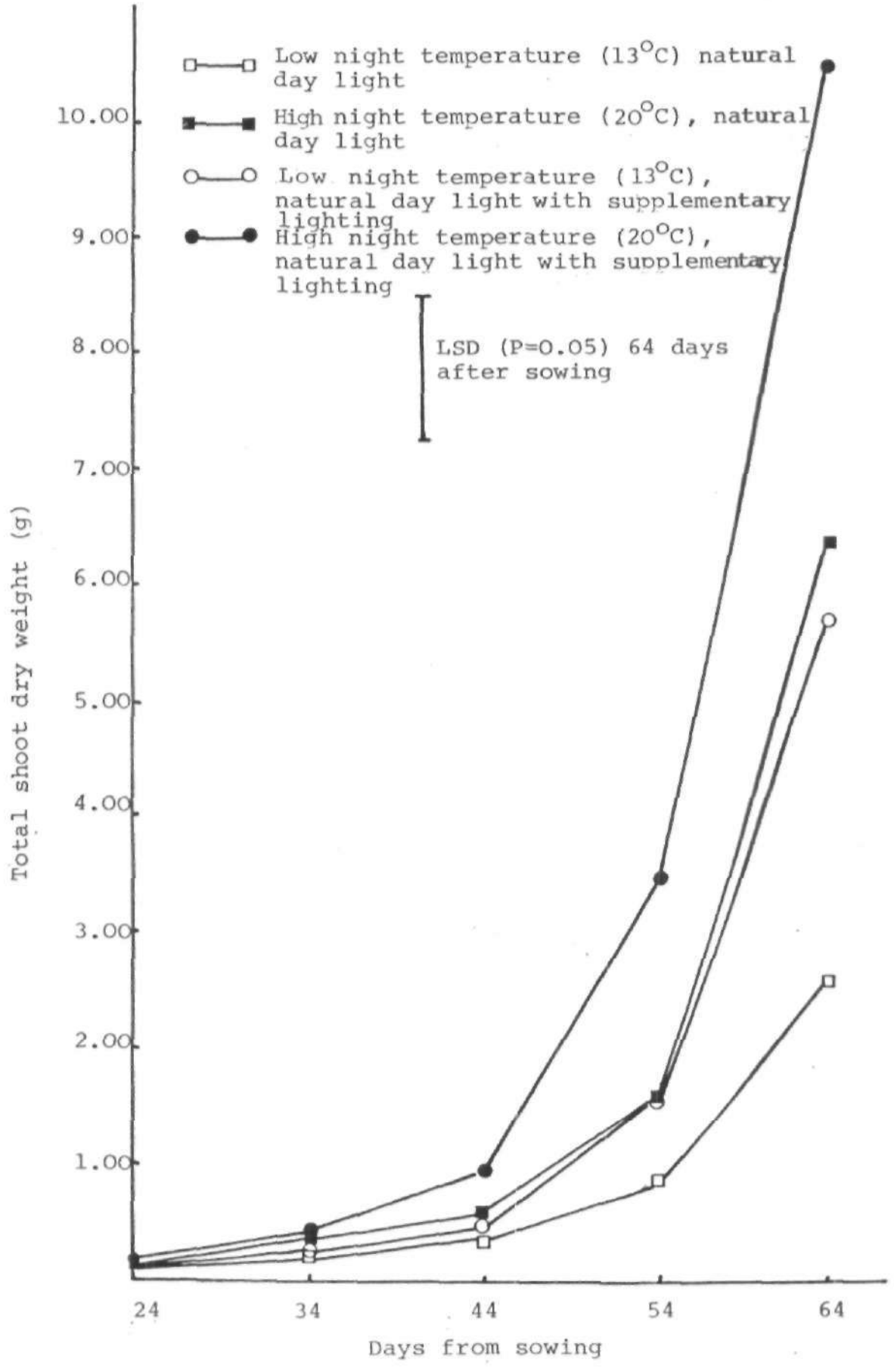

Low night temperature (13°C) natural day light
High night temperature (20°C), natural day light
Low night temperature (13°C), natural day light with supplementary lighting
High night temperature (20°C), natural day light with supplementary lighting
LSD (P=0.05) 64 days after sowing
Total shoot dry weight (g)
10.00
9.00
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
24
34
44
54
64
Days from sowing

Table 24a (Exp. 2) Effects of night temperature and radiant exposure on length of internodes. 18 plants per treatment (10.1.78)

Length of internodes (cm) on the primary shoot (100 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Natural day light	1.4	1.3	1.4
Natural day light with supplementary lighting	1.5	1.2	1.4
Mean	1.5	1.3	

LSD (P=0.05) NS

Table 24b (Exp. 2) Effects of night temperature and radiant exposure on initiation of first flowers. 18 plants per treatment (10.1.78)

Number of days from sowing to time 50% of plants initiated first flowers

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Natural day light	49.0	38.6	43.8
Natural day light with supplementary lighting	40.5	29.2	34.9
Mean	44.8	33.9	

Table 25a (Exp. 2) Effects of night temperature and radiant exposure on number of leaves formed before initiation of first flowers. 18 plants per treatment (10.1.78)

Number of leaves per plant formed on the primary shoot (95 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Natural day light	13.3	12.2	12.8
Natural day light with supplementary lighting	12.7	11.1	11.9
Mean	13.0	11.7	

LSD (P=0.05) to compare temperature means = 0.9
LSD (P=0.05) to compare radiant exposure means = 0.7
Night temperature x radiant exposure interaction (P=0.05) NS

Table 25b (Exp. 2) Effects of night temperature and radiant exposure on first flower bud visibility. 18 plants per treatment (10.1.78)

Number of days from sowing to appearance of first flower buds

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Natural day light	68.3	55.7	62.0
Natural day light with supplementary lighting	54.0	49.3	51.65
Mean	61.15	52.50	

LSD (P=0.05) to compare temperature means = 4.3
LSD (P=0.05) to compare radiant exposure means = 2.4
Night temperature x radiant exposure interaction (P=0.05) NS

Fig. 13 (Exp. 2) Effects of night temperature and radiant exposure on leaf area (18 plants per treatment. 10.1.78)

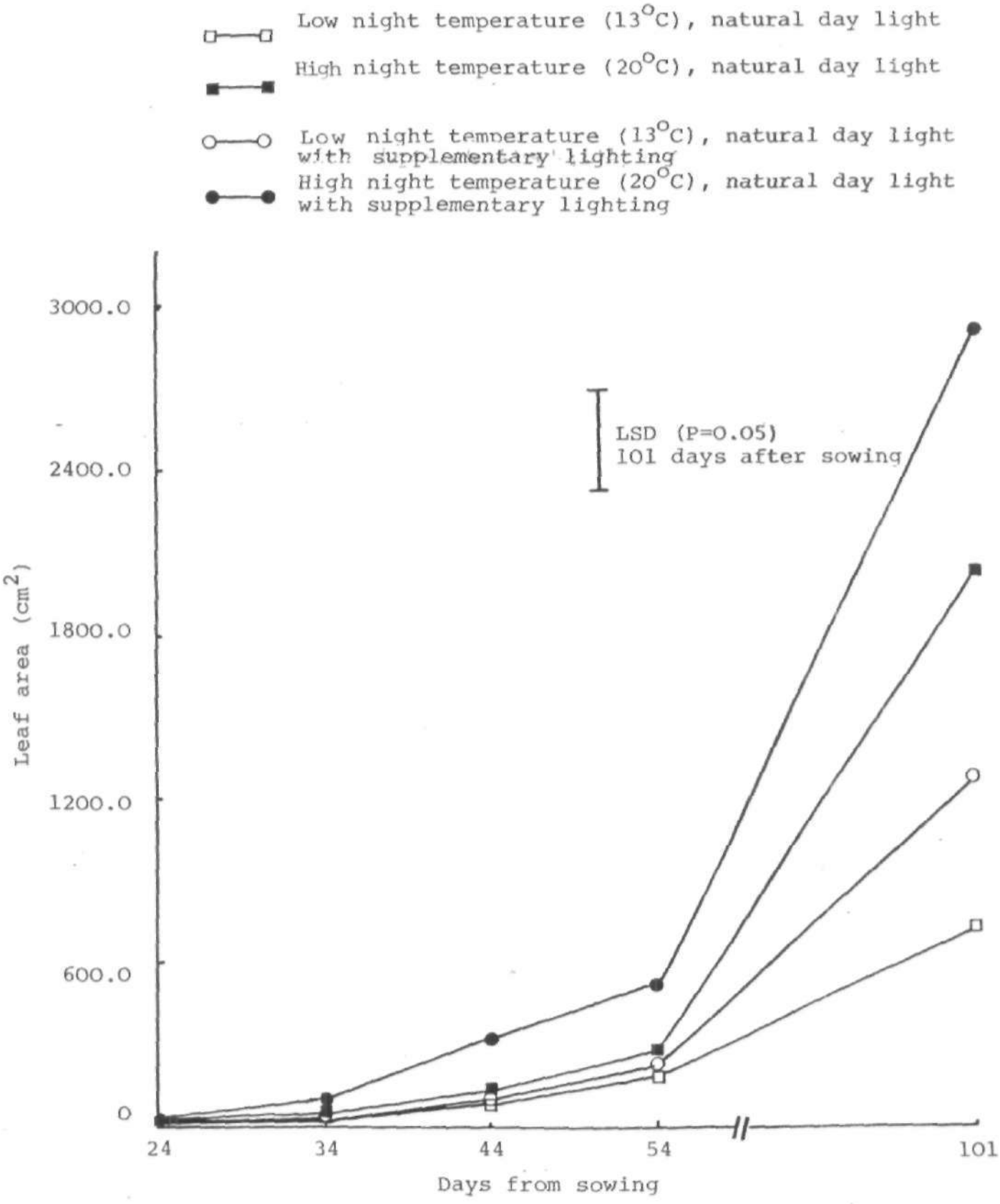

Low night temperature (13°C), natural day light
High night temperature (20°C), natural day light
Low night temperature (13°C), natural day light with supplementary lighting
High night temperature (20°C), natural day light with supplementary lighting
LSD (P=0.05) 101 days after sowing
Leaf area (cm²)
3000.0
2400.0
1800.0
1200.0
600.0
0
24
34
44
54
101
Days from sowing

Fig. 14 (Exp. 2) Effects of night temperature and radiant exposure on shoot height (18 plants per treatment. 10.1.78)

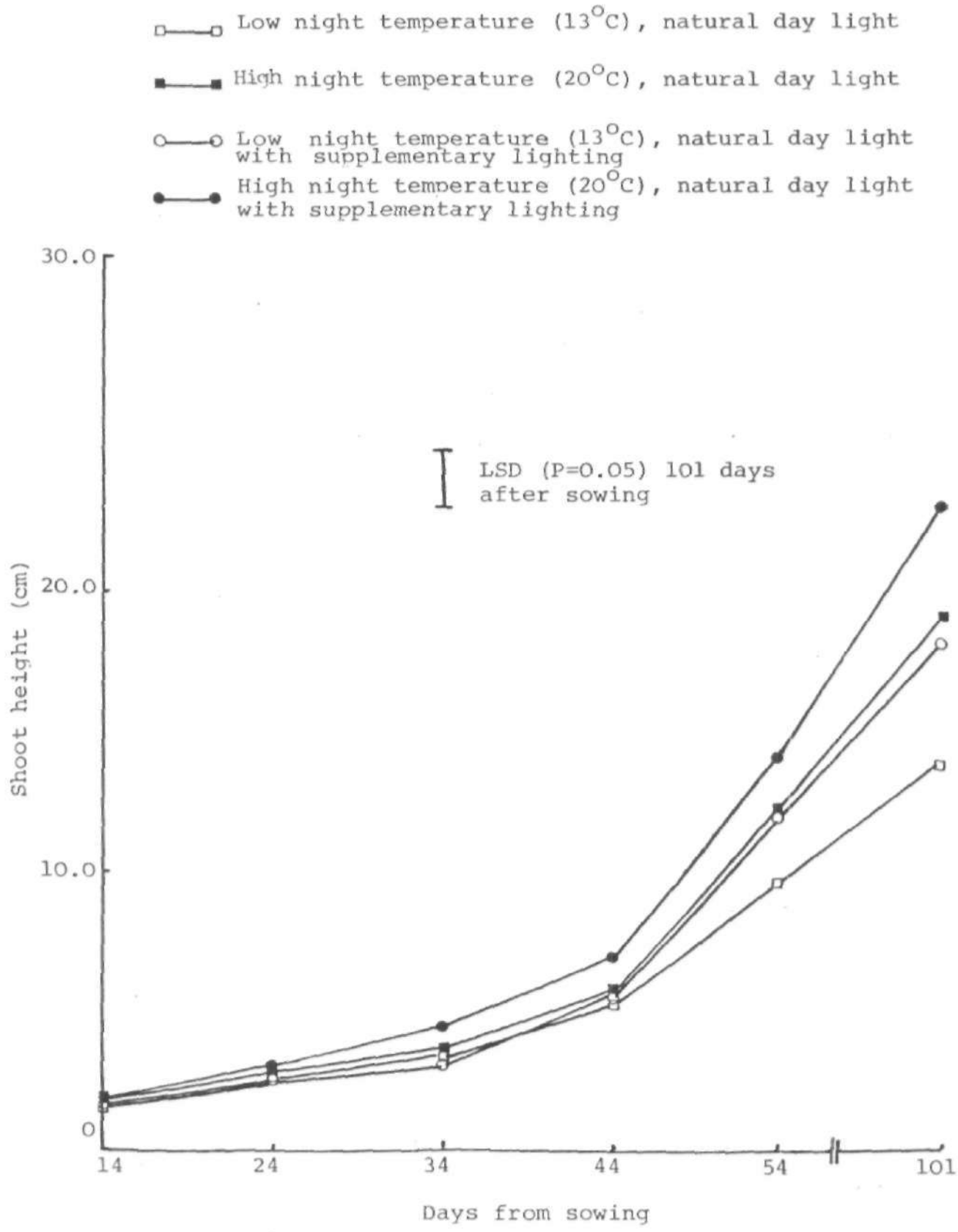
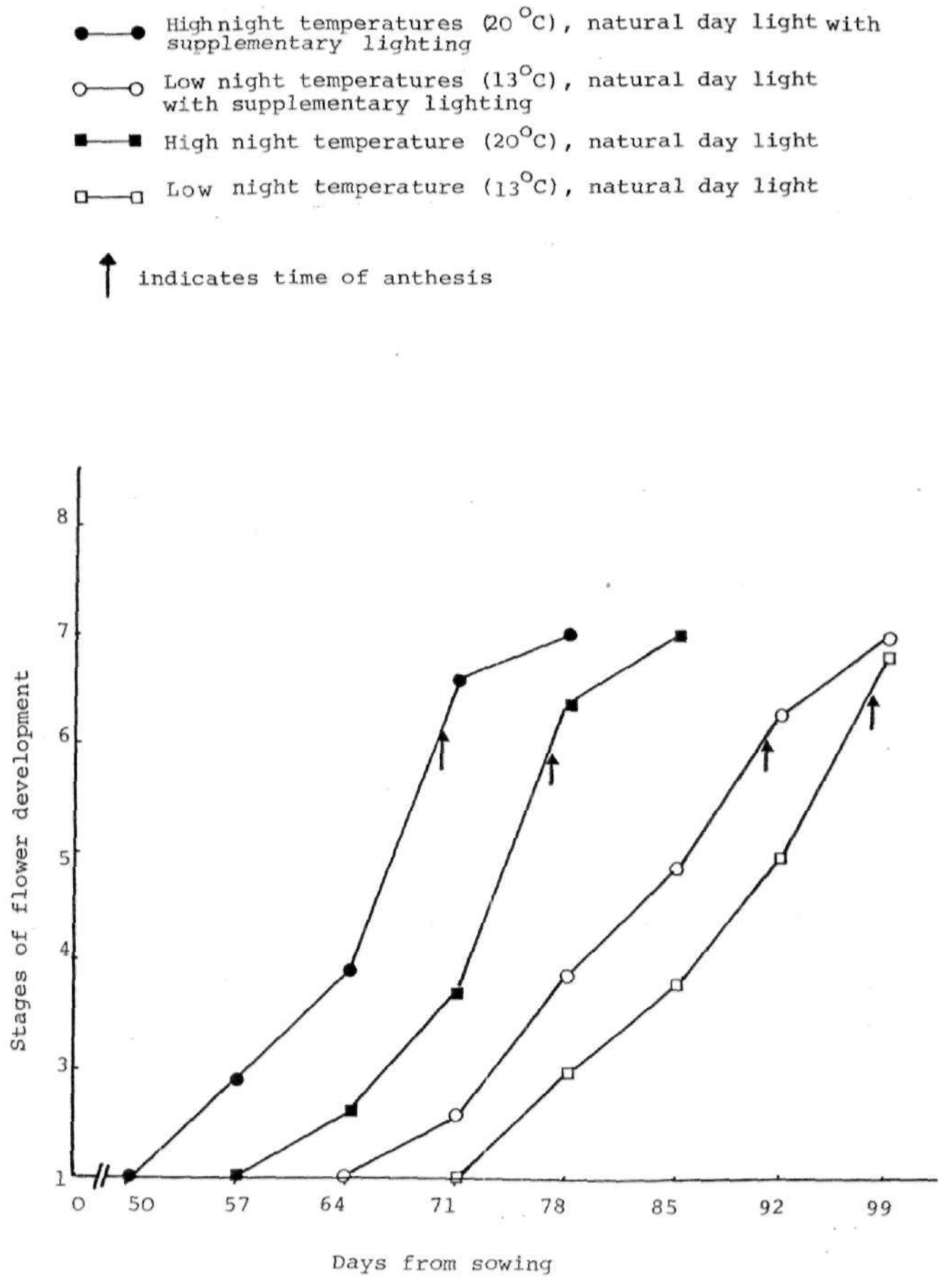

Low night temperature (13°C), natural day light
High night temperature (20°C), natural day light
Low night temperature (13°C), natural day light with supplementary lighting
High night temperature (20°C), natural day light with supplementary lighting
LSD (P=0.05) 101 days after sowing
Shoot height (cm)
30.0
20.0
10.0
0
14
24
34
44
54
101
Days from sowing

Fig. 15 (Exp. 2) Effects of night temperatures and radiant exposure on development of first flower bud. (18 plants per treatment. 10.1.78)


High night temperatures (20 °C), natural day light with supplementary lighting
Low night temperatures (13°C), natural day light with supplementary lighting
High night temperature (20°C), natural day light
Low night temperature (13°C), natural day light
indicates time of anthesis
Stages of flower development
8
7
6
5
4
3
1
0
50
57
64
71
78
85
92
99
Days from sowing

By the time the experiment was ended, plants grown at a high night temperature had produced a greater number of generations of branches than plants at a low night temperature and associated with the increases in the number of branches there were increases in the number of flowers formed (Table 26b). No flower abortion was observed.

Effects of using artificial lighting to supplement natural day light were in general similar to those reported in Chapter 4. Growth in dry weight, leaf area and plant height were significantly increased by the treatment (Figs. 12, 13 and 14) while flower initiation was promoted (Table 24b). As in Exps. 1 and 8 (Chapter 4), supplementary lighting caused a reduction in the number of leaves formed on the primary shoot below the terminal flowers (Table 25a).

Appearance of flower buds (Table 25b) and opening of the first flower (Table 26a) occurred earlier in plants growing in supplementary lighting than in those grown in natural day light only. It appeared that these effects were attributable to earlier flower initiation rather than any hastening of subsequent flower development. The number of flowers formed by the end of the experiment was increased significantly by supplementary illumination (Table 26b).

5.2 (Exp. 21) Effects of night temperatures and shading on flowering

In the previous experiment (Exp. 2) treatments were given from the time the cotyledons had become fully expanded. In the present experiment, treatments were not applied until flower buds

Table 26a (Exp. 2) Effects of night temperature and radiant exposure on first anthesis. 18 plants per treatment (10.1.78)

Number of days from sowing to opening of flowers at tip of primary shoot

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Natural day light	97.9	77.1	87.5
Natural day light with supplementary lighting	90.6	70.3	80.45
Mean	94.25	73.7	

LSD (P=0.05) to compare temperature means = 1.9
LSD (P=0.05) to compare radiant exposure means = 1.1
Night temperature x radiant exposure interaction (P=0.05) NS

Table 26b (Exp. 2) Effects of night temperature and radiant exposure on flower formation. 18 plants per treatment (10.1.78)

Number of flowers formed per plant (95 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Natural day light	34.6	57.1	45.85
Natural day light with supplementary lighting	40.1	63.2	51.65
Mean	37.35	60.15	

LSD (P=0.05) to compare temperature means = 10.5
LSD (P=0.05) to compare radiant exposure means = 6.0
Night temperature x radiant exposure interaction (P=0.05) NS

had become visible and the objective was to examine effects on post-initiation stages of flower development.

The night temperature treatments (low 13°C and high 20°C) were the same as in the previous experiments but radiant exposure was varied by shading instead of by supplementary lighting. Some plants were grown in natural day light (9.00h-17.00h) while others were grown under shading that cut out about 60 percent of solar radiation at plant level.

A 2 x 2 factorial split-plot, completely randomised design was used. Treatments were replicated four times. The timing of experiment is shown in Table 23.

Results

Table 27a shows that growth in dry weight of the shoot was significantly increased by a high night temperature. As in the previous experiment the higher growth rate promoted by high temperature was associated with a more rapid production of branches. A flower was produced on each branch so that more flowers were produced at high than at low night temperatures (Table 27b). When the experiment was ended (102 days after sowing) more flowers had opened in the high temperature treatments than in the low temperature treatments (Table 28a). This applied only to the unshaded plants; in shaded plants all the flowers aborted in both of the temperature treatments.

High night temperature hastened flower development towards anthesis. In unshaded plants, flowers formed at the tip of the primary shoot opened earlier when the night temperature was maintained at about 20°C rather than at 13°C (Table 28b); these

Table 27a (Exp. 21) Effects of night temperature and shading on total shoot dry weight. 16 plants per treatment (4.9.79)

Total shoot dry weight (g) per plant (102 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Shaded	12.66	14.81	13.74
Unshaded	29.69	33.52	31.61
Mean	21.18	24.17	

LSD (P=0.05) to compare shading means = 2.8
LSD (P=0.05) to compare temperature means = 5.3
Shading x night temperature interaction (P=0.05) NS

Table 27b (Exp. 21) Effects of night temperature and shading on flower formation. 16 plants per treatment (4.9.79)

Number of visible flower buds produced per plant up to 99 days after sowing

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Shaded	10.8	27.3	19.1
Unshaded	30.8	54.8	42.8
Mean	20.8	41.1	

LSD (P=0.05) to compare shading means = 4.7
LSD (P=0.05) to compare temperature means = 6.6
Shading x temperature interaction (P=0.05) NS

Table 28a (Exp. 21) Effects of night temperature and shading on flower opening. 16 plants per treatment (4.9.79)

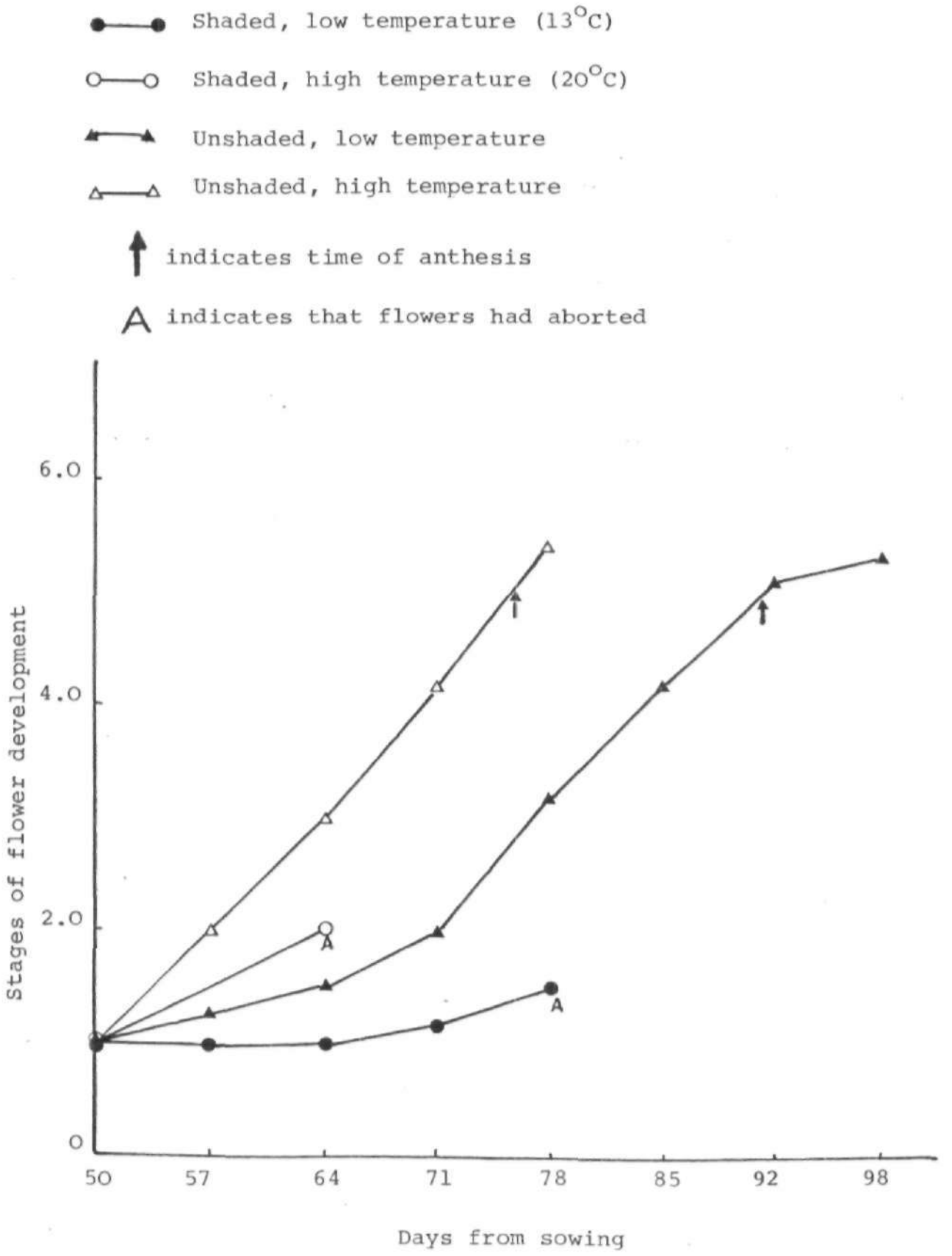
Number of flowers, per plant that had opened (102 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Shaded	0	0	0
Unshaded	3.6	16.7	10.2
Mean	1.8	8.9	

Table 28b (Exp. 21) Effects of night temperature and shading on opening of flower at tip of the primary shoot. 16 plants per treatment (4.9.79)

Days from sowing to opening of flowers at tip of the primary shoot

Radiant exposure	Low night temp. 13°C	High night temp. 20°C
Shaded	All first flowers aborted	All first flowers aborted
Unshaded	86.6	73.4


Shaded, low temperature (13°C)
Shaded, high temperature (20°C)
Unshaded, low temperature
Unshaded, high temperature
indicates time of anthesis
A indicates that flowers had aborted
Stages of flower development
6.0
4.0
2.0
0
A
A
50
57
64
71
78
85
92
98
Days from sowing

flowers had just become visible as small buds when the treatments started. Weekly observation of stage of development of the first formed flowers showed that when the night temperature was high, successive stages were reached earlier (Fig. 16).

The present experiment differed from the previous one (Exp. 2) in that large numbers of flowers aborted before they reached anthesis. This was probably because unlike previous experiment plants were growing when daily radiant exposures were increasing in spring while in the present experiment they were subjected to the declining radiant exposures of autumn; at the end of the experiment in December solar radiation levels would have been at their lowest. The suggestion is supported by the observation that shading in the present experiment increased the incidence of flower abortion (Tables 29a and 29b). Flower abortion was also increased by high night temperatures; this effect was apparent when the incidence of abortion was assessed whether in terms of the number of flowers per plant that aborted (Table 29a) or in terms of the percentage of flowers formed that aborted (Table 29b).

Although plants were kept after flowers had opened no fruit set was observed in the experiment; all of the flowers were shed with abscission layers forming at the bases of the pedicels (Plate 2b). It appeared probable that the low levels of solar radiation in December were unfavourable for pollination.

Shading, like low night temperatures, caused a reduction in the growth in dry weight of the shoot system (Table 27a) and also a reduction in the number of flowers that had been formed by the end of the experiment (102 days after sowing). The lower flower

Table 29a (Exp. 21) Effects of night temperature and shading on incidence of flower abortion. 16 plants per treatment (4.9.79)

Number of flowers that had aborted per plant (99 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Shaded	7.0	25.8	16.4
Unshaded	4.4	14.9	9.7
Mean	5.7	20.4	

LSD (P=0.05) to compare shading means = 3.8
LSD (P=0.05) to compare temperature means = 5.4
Shading x temperature interaction (P=0.05) NS

Table 29b (Exp. 21) Effects of night temperature and shading on the proportion of flowers that aborted. 16 plants per treatment (4.9.79)

Percent flowers aborted per plant (99 days after sowing)

Radiant exposure	Low night temp. 13°C	High night temp. 20°C	Mean
Shaded	64.8	94.5	79.7
Unshaded	14.3	27.2	20.8
Mean	39.6	60.9	

number appeared to reflect the smaller number of generations of branches that had been produced. In the shaded plants all of the flowers formed at the tips of the primary shoots aborted and the incidence of abortion was also high in later formed flowers (Tables 29a and 29b).

5.3 (Exp. 25) Effects of night temperatures, shading and shoot pruning on flowering and fruit set

In this experiment night temperature (high and low night temperatures) and shading treatments were started when the flower buds first became visible as in Exp. 21. In addition to these treatments effects of limiting the number of branches on each plant were examined. It appeared that "shoot pruning" to reduce the number of branches might reduce the incidence of flower abortion by reducing intra-plant competition for metabolites

Night temperature and shading treatments were provided as previously described in Exp. 21. Shoot pruning was effected by removing small developing branches to leave two shoots to continue the growth of the plant. The procedure used is described in Chapter 7. The amount of tissue removed was small and never more than 700 mg in dry weight.

Commencement of treatments and duration of the experiment are shown in Table 23. Plants were grown in 15.2 cm diameter plastic pots.

Treatments were arranged in a 2 x 2 x 2 factorial split-plot design, completely randomised and replicated 9 times. One plant was used per replicate.

Results

As in Exp. 21 the number of flower buds formed was increased by the high night temperature treatment (Table 30). The increase was greater in pruned plants as it was to be expected reducing the number of branches on the plants led to marked reductions in the number of flower buds that were formed. Shading reduced flower formation in unpruned plants but had little effect on flower number in plants reduced to only two leading shoots (Table 30).

The number of flowers that opened during the course of the experiment varied widely with the treatments and was not affected significantly by either night temperature or shading (Table 31). In nearly all of the treatments a large proportion of the flowers aborted before they reached anthesis. The number and percentage of flowers aborting was increased by shading (Tables 32a and 32b). Effects of night temperature appeared to vary with the other conditions imposed but in shaded plants high night temperatures led to increases in the incidence of flower abortion (Table 32a).

Where the number of branches was reduced flower abortion still occurred, and in terms of the percentage of flowers that aborted, it was generally as high or higher in pruned as in unpruned plants. This incidence of abortion, together with the reduction in the number of flower buds formed due to pruning meant that the number of flowers that opened during the experiment was significantly less in pruned plants than in plants allowed to remain intact.

In this experiment plants were kept in the treatments until

Table 30 (Exp. 25) Effects of night temperature, shading and shoot pruning on flower formation. 9 plants per treatment (15.11.79)

Number of flower buds counted per plant up to 141 days after sowing

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13	Shaded	40.1	12.4	26.3	30.4
	Unshaded	56.2	12.7	34.5	
20	Shaded	64.3	14.7	39.5	42.0
	Unshaded	72.9	16.2	44.6	
Shoot pruning means		58.4	14.0		

LSD (P=0.05) to compare shading means = 2.8
LSD (P=0.05) to compare shoot pruning means = 3.0
LSD (P=0.05) to compare temperature means = 4.3
Shading x shoot pruning interaction (P=0.05) Significant
Shading x shoot pruning x night temperature interactions (P=0.05) NS

Table 31 (Exp. 25) Effects of night temperature, shading and shoot pruning on flower opening. 9 plants per treatment (15.11.79)

Number of flowers, per plant that had opened (141 days after sowing)

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13	Shaded	2.9	2.1	2.5	3.4
	Unshaded	5.7	2.9	4.3	
20	Shaded	4.7	3.6	4.2	7.9
	Unshaded	15.7	7.5	11.6	
Shoot pruning means		7.3	4.0		

LSD (P=0.05) to compare shading means NS
LSD (P=0.05) to compare shoot pruning means = 3.0
LSD (P=0.05) to compare temperature means NS
Shading x shoot pruning interaction (P=0.05) Significant
Shading x shoot pruning x night temperature interactions (P=0.05) NS

Table 32a (Exp. 25) Effects of night temperature, shading and shoot pruning on incidence of flower abortion. 9 plants per treatment (15.11.79)

Number of flowers that had aborted per plant (141 days after sowing

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13	Shaded	3.7	2.9	3.3	2.0
	Unshaded	0	1.3	0.7	
20	Shaded	24.9	6.9	15.9	9.1
	Unshaded	4.2	0.2	2.2	
Shoot pruning means		8.2	2.8		

Table 32b (Exp. 25) Effects of night temperature, shading and shoot pruning on proportion of flower abortion. 9 plants per treatment (15.11.79)

Percent flowers that aborted per plant (141 days after sowing)

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13	Shaded	9.2	23.4	16.3	10.7
	Unshaded	0	10.2	5.1	
20	Shaded	38.7	46.9	42.8	23.2
	Unshaded	5.8	1.2	3.5	
Shoot pruning means		13.4	20.4		

some of the flowers at the tips of the primary shoots and on the lower branches had set fruit. The weight and volume of fruit per plant was always greater in unshaded plants than in shaded plants (Tables 33a and 33b). In shaded plants a few fruits were set when night temperatures were low but no fruits were produced at high night temperatures (Table 33a). In unshaded plants there was no clear effect of temperature on the weight or volume of fruits produced; it appeared that the number of fruits set per plant was greater at low than at high night temperatures but that their total weight was not necessarily greater presumably because the individual fruits were larger in the high night temperature treatments.

Dissection of the fruits at the end of the experiments showed that most of those produced at low night temperatures were parthenocarpic while those produced at high temperatures all contained seeds (Tables 34a and 34b). Among the plants grown at low night temperature, those that were shaded produced only parthenocarpic fruits while those that were unshaded produced somewhere between 20 and 30 percent seeded fruits.

The removal of shoots from the plants did not cause any obvious reduction in the weight or volume of fruit produced. The greatest weight and volume of fruits were produced by plants pruned to two leading shoots and grown unshaded at high night temperatures.

5.4 (Exp. 4) Effects of night temperatures on fruit set and development

In this experiment, plants were subjected to a range of

Table 33 (Exp. 25) Effects of night temperatures, shading and shoot pruning on fruit size. 9 plants per treatment (15.11.79)

(a) Fruit fresh weight (g) per plant with no. of fruits set per plant in brackets (141 days after sowing)

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13 (low)	Shaded	1.41 (0.3)	1.14 (0.2)	1.28 (0.3)	7.67 (0.7)
	Unshaded	14.82 (2.0)	13.3 (1.7)	14.06 (1.9)	
20 (high)	Shaded	No fruit set	No fruit set	-	11.27 (0.6)
	Unshaded	9.9 (0.8)	35.18 (1.4)	22.54 (1.1)	
Shoot pruning means		6.53 (0.8)	12.41 (0.8)		

(b) Fruit volume (cm^3) per plant (141 days after sowing)

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13 (low)	Shaded	2.67	1.67	2.17	14.53
	Unshaded	27.11	26.67	26.89	
20 (high)	Shaded	No fruit set	No fruit set	-	20.13
	Unshaded	15.89	64.61	40.25	
Shoot pruning means		11.42	23.24		

Table 34 (Exp. 25) Effects of night temperatures, shading and shoot pruning on parthenocarpy. 9 plants per treatment (15.11.79)

(a) Percent fruits, per plant, that were parthenocarpic

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13 (low)	Shaded	100.0	100.0	100.0	89.6
	Unshaded	72.2	86.5	79.4	
20 (high)	Shaded	No fruit set	No fruit set	-	0
	Unshaded	0	0	0	
Shoot pruning means		43.1	46.6		

(b) Seed fresh weight (g) with number of seeds per fruit in brackets (141 days after sowing)

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13 (low)	Shaded	0 (0)	0 (0)	0 (0)	0.08 (2.0)
	Unshaded	0.21 (3.0)	0.11 (0.9)	0.16 (2.0)	
20 (high)	Shaded	No fruit set	No fruit set	-	0.69 (60.3)
	Unshaded	1.29 (99.4)	1.48 (141.9)	1.39 (120.7)	
Shoot pruning means		0.38 (25.6)	0.4 (35.7)		

night temperatures at about the time flowers were opening and the temperature treatments were maintained for 10 days only. The main object of the experiment was to examine the effects of night temperatures on fruit set in individual flowers.

Two lots of plants were grown in the glasshouse until flowers on the first generation of branches in the first lot (Exp. 4a) and flowers on the second generation of branches (Exp. 4b) in the second lot were about to open. Any flowers formed on the lower branches had been removed.

Temperatures were set at 5^{o} or $10^{o}C \pm 1.5$ in two cold rooms. A third growth room was maintained at $25^{o}C \pm 1.5$. Further plants were grown in a glasshouse maintained at a night temperature of $18^{o}C \pm 2.5$.

Plants were grown in the glasshouse during the day (9.00h-17.00h) and were transferred to the rooms maintained at temperatures of 5^{o}, 10^{o} and $25^{o}C$ at night (17.00h-9.00h). Further plants remained in the glasshouse with a night temperature of $18^{o}C$ throughout.

Treatments were arranged in completely randomised blocks and replication was done in time due to lack of space in the rooms at which night temperatures were maintained. Timing of the experiments is shown in Table 23.

Results

Flower opening was delayed in plants growing at the lower night temperatures (5^{o} and $10^{o}C$), consequently fruit set was delayed as well. In Exp. 4a the incidence of fruit set was highest in plants subjected to the 10^{o} night temperature treatment

Plate 4 (Exp. 4) : Effects of night temperature on size and shape of fruits. 12 plants per trearment (24.3.78)

(a) Fruits set at 10°C.

(b) Fruits set at 18°C.



(a)



(b)

or grown in the glasshouse throughout (Table 35a). In Exp. 4b where plants were at a later stage of development (flowers on the second generation of branches about to open) nearly all the flowers set fruit (Table 35b) and no significant effect of night temperature treatments on fruit set was observed.

In both experiments almost all the fruits formed in the $5^{o}C$ and $10^{o}C$ treatments were apparently parthenocarpic (Tables 35c and 36a). The highest number of seeds per fruit was observed in the $25^{o}C$ treatment (Tables 36b and 36c). Whereas parthenocarpic fruits were generally small, flat and irregularly shaped, seeded fruits appeared to be bigger and more regularly shaped (Plate 4).

Some abnormalities in morphological features of parthenocarpic fruits were observed. Length of pedicel of fruit was greater in parthenocarpic fruits than in seeded fruits by about 1.2 cm (Table 37a). Growth of structures like "florets" or "fruit-lets" was observed in all parthenocarpic fruits. Number of these internal growths was greater in fruits formed at lower night temperatures than in fruits formed at high night temperatures (Table 37b). No effect of shoot pruning was observed on development of abnormal growths in fruit whereas shading increased the occurrence of such growths.

5.5 Discussion

In the experiments reported here vegetative development was measured in terms of growth in dry weight of the shoot system, leaf area and shoot height. Growing plants at a night temperature of $20^{o}C$ as compared with $13^{o}C$ markedly promoted

Table 35a (Exp. 4a) Effects of night temperature on fruit set. 12 plants per treatment (24.3.78)

Number of flowers that set fruit (2 flowers per plant)

5°C	10°C	18°C	25°C
0.8	2.0	1.8	1.3

LSD (P=0.05) 0.4

Table 35b (Exp. 4b) Effects of night temperature on fruit set. 12 plants per treatment (24.3.78)

Number of flowers that set fruit (4 flowers per treatment)

5°C	10°C	18°C	25°C
3.8	3.8	4.0	3.9

LSD (P=0.05) NS

Table 35c (Exp. 4a) Effects of night temperatures on parthenocarpy. 12 plants per treatment (24.3.78)

	5°C	10°C	18°C	25°C
Total number of fruits set per treatment	10.0	24.0	21.0	18.0
Number of parthenocarpic fruits per treatment (12 plants)	10.0	14.0	3.0	1.0
Percent parthenocarpy	100.0	58.3	14.3	5.6

Table 36a (Exp. 4b) Effects of night temperatures on parthenocarpy. 12 plants per treatment (24.3.78)

	5°C	10°C	18°C	25°C
Total number of fruits set per treatment	46.0	46.0	48.0	47.0
Number of parthenocarpic fruits per treatment	46.0	45.0	0	0
Percent parthenocarpy	100.0	97.8	0	0

Table 36b (Exp. 4a) Effects of night temperatures on seed formation. 12 plants per treatment (24.3.78)

Number of seeds formed per fruit

5°C	10°C	18°C	25°C
0	0.5	60.8	133.3

Table 36c (Exp. 4b) Effects of night temperatures on seed formation. 12 plants per treatment (24.3.78)

Number of seeds formed per fruit

5°C	10°C	18°C	25°C
0	0.3	47.0	129.2

Table 37 (Exp. 25) Effects of night temperature, shading and shoot pruning on growth of fruit pedicel and internal abnormal growths in fruit plants per treatment (15.11.79)

(a) Length (cm) of fruit pedicel (140 days after sowing)

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13 (low)	Shaded	1.13	0.69	0.91	2.0
	Unshaded	3.48	2.69	3.09	
20 (high)	Shaded	No fruit set	No fruit set	-	0.79
	Unshaded	1.17	1.98	1.58	
Shoot pruning means		1.45	1.34		

(b) Number of internal abnormal growths per fruit

Night temperature (°C)	Radiant exposure	All shoots (control)	2 shoots	Radiant exposure means	Night temperature means
13 (low)	Shaded	0.9	0.7	0.8	1.3
	Unshaded	2.1	1.5	1.8	
20 (high)	Shaded	No fruit set	No fruit set	-	0
	Unshaded	0	0	0	
Shoot pruning means		1.5	1.1		

vegetative development by increasing the number of internodes which extended. This contrasts with the promotion of shoot height due to the marked elongation of internodes on the primary shoot when the day length is extended with tungsten filament lamps (see Chapter 4).

Effects of night temperature on flowering appeared to depend upon the developmental stage of the plant at which treatments were imposed and also on the duration of the treatments. Subjecting plants to a night temperature of 20°C at cotyledon expansion hastened flower initiation and caused a small reduction in the number of leaves formed before flower initiation occurred. Similar effects on flower initiation were obtained with supplementary lighting both here and in Exps. 1 and 8 previously reported (Chapter 4).

Associated with this earlier flower initiation was an increase in growth in terms of dry weight, leaf area and shoot height. The hypothesis that the time of flower initiation depends on the preceding vegetative growth rate (Lang, 1952) seems to be supported by these results.

Evidence from workers on the influence of night temperature on leaf formation prior to flower initiation in sweet pepper is conflicting. Whereas Rylski (1972) obtained an increased number of leaves at a low night temperature, Deli and Tiessen (1969) reported that a low night temperature reduced the number of leaves formed before flower initiation. The discrepancy between results of experiments here and those obtained by Rylski on one hand and reports of Deli and Tiessen on the other may be explained by the differences in the time the

temperature treatments were imposed and the duration of the treatments. Deli and Tiessen (1969) subjected plants to temperature treatments after 3 to 5 leaves had expanded and only for a period of 25 days whereas night temperature treatments here and in Rylski's experiments were imposed at cotyledon expansion and lasted for several weeks. Rylski (1972) could not obtain any effect of night temperature on the number of leaves formed before initiation of the first flowers when treatments were given for only 3 weeks after the cotyledons had fully expanded.

Flower formation was markedly influenced by night temperature. Experimental results showed that plant development measured by the number of generations of branches produced per plant was more rapid at 20^{o}C than at 13^{o}C night temperature. An increase in the number of branches formed means an increase in the number of flowers formed since each branch is terminated by a flower. There is evidence that the rate of flower formation was increased by high night temperature. The increase in the number of flowers formed and the rate at which flowers were formed due to a high night temperature of 20^{o}C is attributable to the greater availability and more efficient utilization of metabolites at a high night temperature rather than at a low night temperature.

Contrasting effects of night temperatures on flower formation to those obtained here have been reported. Deli and Tiessen (1969) obtained increases in the number of flowers formed in sweet pepper due to a low night temperature of 12^{o}C. They attributed the increase to a profuse branching that occurred

at the low night temperature. In the experiments undertaken by Deli and Tiessen (1969) plants were transplanted out of doors after they had been exposed to night temperatures of 12^{o} or $18^{o}C$ for 25 days in the glasshouse. It is possible that vegetative development had slowed down in plants exposed to a high temperature due to flowering, whereas active vegetative development continued in plants grown at a low night temperature, in which case profuse branching could occur in the plants. Vegetative and reproductive development have been reported to continue in a cyclic pattern in peppers (Wells, 1966; Kato and Tanaka, 1971; Song and Park, 1976).

Development of flower buds from their first appearance to opening stage was hastened by high night temperature. The reason for this is not clear. However, plants grown at high night temperature had a larger leaf area than the low temperature plants. This larger leaf area exposed to the available light might have favoured flower development. The effects of high night temperature in promoting flower development were limited to pre-anthesis stages of development.

The experiments reported here indicated that high night temperature induced post-anthesis shedding of flowers. The increase in the numbers of flowers shed due to high night temperature might be explained on the basis of competition for available assimilates (Hussey, 1963a; Calvert, 1969). It is possible that in the pre-anthesis stages reserves of assimilates were sufficient to maintain development of flowers. Later, when the number of flower buds had increased, reserves were insufficient resulting in the abscission of a number of open

flowers. It is possible that failure of pollination at the high night temperature contributed to increased flower shedding.

The increase in post-anthesis shedding could also be attributed to increased transpiration at the high night temperature (Cochran, 1936) or a decrease of sugar in plants grown at high night temperatures (Dorland and Went, 1947). Whether or not respiration contributed to flower shedding at high night temperature is not clear.

Fruit set was affected by night temperature. Little fruit set occurred in plants grown at the high night temperature due to increased post-anthesis shedding of flowers. However, low night temperatures of 10° and 13°C increased fruit set. Size of fruit, as measured by fresh weight and volume, was reduced at these low night temperatures. This decrease was probably due to a lack of seeds in fruits set at low night temperatures.

It is generally believed that post-anthesis shedding of flowers is due to lack of pollination and fertilization. The fact that parthenocarpic fruits have been reported to occur in peppers shows that failure of fertilization and seed growth does not necessarily lead to failure of fruit set.

Results of Exps. 4 and 5 here showed that parthenocarpy was markedly promoted by low night temperatures. The role of low night temperatures in promoting formation of parthenocarpic fruit is not clear. However, the occurrence of parthenocarpy at low night temperatures could be attributed to a reduction in pollen viability (Rylski, 1972 and 1973). Cochran (1936) believed that parthenocarpy in pepper was caused by lack of fertilization as a result of slow growth of the pollen tube

down the style at low temperatures. Similar effects of low temperatures in promoting parthenocarpic fruit development have been reported in tomato (Went, 1957).

Growth and development were found to be retarded in the parthenocarpic fruits; their shape was irregular compared with seeded fruits set at high night temperatures. Also associated with parthenocarpic fruits were internal abnormal growths which were morphologically similar to fruit or flowers. Similar abnormalities had been observed in pepper fruits developed without fertilization (Cochran, 1934 and 1936). The cause of these abnormal growths is not known. It is possible, however, that the growths developed instead of seeds, since very few of these abnormal growths were observed in seeded fruits.

There is evidence that a combination of high night temperature and high light flux densities hastened flower initiation, enhanced flower development and promoted fruit set. This favourable interaction may be due to a greater availability and utilization of carbohydrates under these conditions compared with the situation under the less favourable conditions of low night temperatures and low light flux densities.

Effects of reducing the number of branches on flowering are not clear. Flower abortion occurred in both pruned and unpruned plants. Fruit set was not affected by shoot pruning, but fresh weight of fruit increased in plants pruned at two leading shoots.

Further effects of shoot pruning on flowering and fruit set are considered in Chapter 7.

5.6 Summary

(1) Effects of growing pepper plants at night temperatures of 20°C and 13°C were studied. Growth measured in terms of dry weight, leaf area ard shoot height was promoted by increasing the night temperature from 13° to 20°C.

(2) In plants grown at a night temperature of 20°C flower initiation occurred earlier, rates of flower development were more rapid and anthesis occurred earlier than in plants grown at a night temperature of 13°C.

(3) The incidence of flower abortion was greater at high night temperatures than at low night temperatures and in shaded plants than in unshaded plants.

(4) The proportion of flowers that were shed after opening was increased when night temperatures were high or when plants were shaded. High night temperatures and shading also led to small reduction in the number of fruits that were set per plant.

(5) The weight of early fruit produced was greater at high than at low night temperatures and in unshaded than in shaded plants.

(6) Parthenocarpy was promoted by low night temperatures.

Chapter 6

Effects of Growth Substances on Flowering, Fruit Set and Subsequent Fruit Development (Exps. 9, 15, 11, 17 and 23)

Results of previous experiments indicated that a high proportion of flowers of sweet pepper might fail to set fruit. The object of experiments described in this chapter was to explore the possibility of increasing fruit set by the application of growth substances. There was also interest in how far the growth of parthenocarpic fruits that were observed to form when night temperatures were low (Chapter 5) might be promoted by treatments with growth substances.

There is evidence that beta-naphthoxy acetic acid (NOA) and gibberellic acid (GA_3) can influence fruit set in some species belonging to the Solanaceae. An increase in fruit set was observed in eggplant and in tomato as a result of application of NOA (Nothmann and Koller, 1975; Kepcka, 1966). An increase in fruit set in tomato in response to application of GA_3 was reported by Yamaguchi, Takahashi and Sugiyama (1962).

In view of these reports, interest was attached to effects of NOA and GA_3 in fruit set in sweet pepper and these growth substances were selected for study in the experiments described here.

6.1 Methods of preparation and application of growth substances

Beta—naphthoxyacetic acid (NOA) and gibberellic acid (GA_3)

were used. 10^{-4}M concentrations of NOA and GA_3 were prepared by dissolving a measured weight of each chemical in 2 ml ethanol and then adding the required volume of de-ionised water. Tween 20 was used as a wetting agent at 0.1 percent by volume. Concentration of growth substances used was as follows:

Growth substance	Parts per million (ppm)
NOA	30, 60, 120
GA_3	100

The growth substances were applied as a fine spray either to entire open flowers or to emasculated flowers (see 2.5 in Chapter 2). In some experiments they were also supplied as a foliar spray applied to run-off. Control plants were sprayed with de-ionised water containing the same quantity of Tween 20 and ethanol. Applications were always made at the same time in the morning (about 11.00h).

Emasculation of flowers was carried out as previously described in Chapter 2.

Replicated randomised block design was employed in all experiments.

Timing of individual experiments is shown in Table 38.

6.2 (Exp. 9) Effects of NOA and night temperture on fruit set and subsequent fruit development

Plants in this experiment were grown at two night

Table 38 Detail of experiments described in Chapter 6

Exp. number	Title of Exp.	Date of sowing seed	Date treat-ments commenced	Stage of plant development at which treatments commenced	Date Exp. was terminated
9	Effects of NOA and night temperature on fruit set and subsequent fruit development (12 plants per treatment)	14.3.79	25.5.79	2-3 days before anthesis of flowers on the first generation of branches	2.7.79 (110 days after sowing)
15	Effects of NOA and emasculation on fruit set and subsequent fruit development (10 plants per treatment)	12.4.79	14.6.79	2-3 days before anthesis of flowers on the first generation of branches	16.7.79 (95 days after sowing)
11	Effects of NOA, GA_3 and emasculation on fruit set and subsequent fruit development (16 plants per treatment)	12.4.79	28.6.79	2-3 days before anthesis of flowers on the first generation of branches	7.8.79 (117 days after sowing)
17	Effects of NOA, GA_3 and emasculation on fruit set and subsequent fruit development (12 plants per treatment)	23.5.79	2.8.79	2-3 days before anthesis of flowers on the first generation of branches	11.9.79 (111 days after sowing)
23	Effects of NOA and GA_3 on flowering fruit set and subsequent fruit development (8 plants per treatment)	31.8.79	12.12.79	Anthesis of flowers formed on the third generation of branches	31.1.80 (153 days after sowing)

temperatures, 10° or 18°C for a period of 14 days starting 2 to 3 days before anthesis of the flowers formed on the first generation of branches. NOA at 30 ppm or 60 ppm was applied to these flowers as they opened. Subsequently plants were grown in the glasshouse maintained at 18 ± 1.5°C night temperature until the experiment was terminated 110 days after sowing the seed.

Results

Flower opening was observed to be delayed by two days in plants grown at 10°C night temperature. All the flowers on the particular branches selected for treatment set fruit whether they were sprayed with NOA or with water.

Growth in size of the fruits was determined by measuring their diameter at weekly intervals from anthesis until the experiment was terminated. The fresh weight of fruit, on per fruit basis, was also determined at the end of the experiment. Fig. 17 shows that rate of growth of fruit was not affected by the growth substance. Similarly, no effect of NOA was obtained on fresh weight of fruit up to 110 days after sowing (Table 39a).

Rate of fruit development and size of fruit were affected by night temperatures. Subjecting plants to a night temperature of 18°C for 14 days from anthesis increased both diameter of fruit and fresh weight of fruit (Fig. 17; Table 39a).

Formation of parthenocarpic fruits was influenced by NOA and night temperatures. As in Exp. 4 (Chapter 5) the incidence of parthenocarpic fruits was increased by subjecting plants to a low night temperature. The incidence of parthenocarpy was also

Fig. 17 (Exp. 9) Effects of NOA and night temperature on fruit growth (12 plants per treatment. 14.3.79)

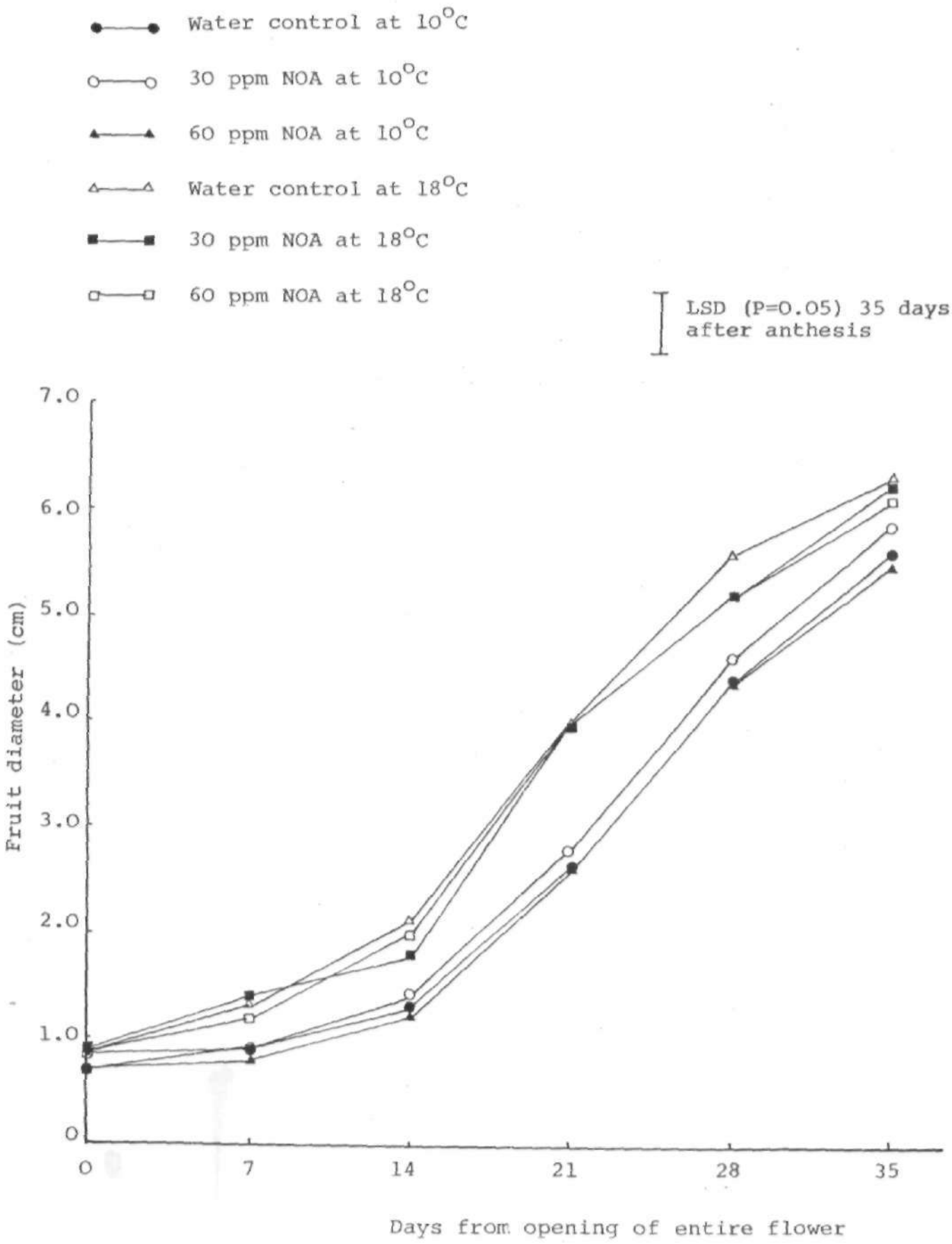

Water control at 10°C
30 ppm NOA at 10°C
60 ppm NOA at 10°C
Water control at 18°C
30 ppm NOA at 18°C
60 ppm NOA at 18°C
LSD (P=0.05) 35 days after anthesis
Fruit diameter (cm)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
7
14
21
28
35
Days from opening of entire flower

Table 39a (Exp. 9) Effects of NOA and night temperature on fresh weight of fruit. 12 plants per treatment (14.3.79)

Mean fruit fresh weight (g)(110 days after sowing)

Night temperature (°C)	0 ppm NOA (control)	30 ppm NOA	60 ppm NOA	Mean
10	57.9	56.4	59.1	57.8
18	66.1	65.1	68.2	66.5
Mean	62.0	60.8	63.7	

LSD (P=0.05) to compare NOA means NS
LSD (P=0.05) to compare night temperature means = 7.1
NOA x night temperature interaction (P=0.05) NS

Table 39b (Exp. 9) Effects of NOA and night temperatures on formation of seeds. 12 plants per treatment (14.3.79)

Number of seeds formed per fruit (110 days after sowing)

Night temperature (°C)	0 ppm NOA (control)	30 ppm NOA	60 ppm NOA	Mean
10	10.8	6.4	6.0	7.7
18	125.4	48.4	8.4	60.7
Mean	68.1	27.4	7.2	

LSD (P=0.05) to compare NOA means = 25.5
LSD (P=0.05) to compare night temperature means = 27.6
NOA x night temperature interaction (P=0.05) Significant

increased by application of NOA (Tables 40a and 40b). NOA at 60 ppm was more effective in increasing percentage parthenocarpy than NOA at 30 ppm. When the incidence of parthenocarpy was already high due to the low night temperature treatment effects of NOA were less apparent than in the high night temperature treatment.

Associated with the promotion of parthenocarpic fruit development by application of NOA and by low night temperatures there were reductions in the mean number of seeds formed per fruit (Table 39b).

6.3 (Exp. 15) Effects of NOA and emasculation on fruit set and subsequent fruit development

The object of the experiment reported here was to study effects of NOA on fruit set in emasculated and entire flowers.

Two flowers carried on the first generation of branches and at similar stages of development were selected on each plant. One of them was emasculated at stage 4 of flower bud development (see Plate 1) and one was left entire. When the entire flower had opened, both flowers were sprayed with 0, 30, 60 or 120 ppm NOA.

Plants were grown in the glasshouse and growth of individual fruits was determined by measuring the diameter at weekly intervals until experiment was terminated 95 days after sowing.

Results

Fruit set in the sense of retention and growth of the ovary

Table 40a (Exp. 9) Effects of NOA and night temperatures on parthenocarpy. 12 plants per treatment (14.3.79)

Number of parthenocarpic fruits (out of 24 fruits per treatment)

Night temperature (°C)	0 ppm NOA (control)	30 ppm NOA	60 ppm NOA	Mean
10	16.0	18.0	22.0	18.7
18	2.0	12.0	19.0	11.0
Mean	9.0	15.0	20.5	

LSD (P=0.05) to compare NOA means = 7.1
LSD (P=0.05) to compare night temperature means = 5.6
NOA x night temperature interaction (P=0.05) Significant

Table 40b (Exp. 9) Effects of NOA and night temperatures on percent parthenocarpy. 12 plants per treatment (14.3.79)

Percentage of parthenocarpic fruits (out of 24 fruits per treatment

Night temperature (°C)	0 ppm NOA (control)	30 ppm NOA	60 ppm NOA	Mean
10	66.7	75.0	91.7	77.8
18	8.3	50.0	79.2	45.8
Mean	37.5	62.5	85.5	

occurred in both emasculated and non-emasculated flowers in all plants. The formation of fruits from emasculated flowers indicated that pollination or fertilization was not necessary for fruit growth to occur in sweet pepper.

In this experiment emasculation was not completely effective in preventing pollination precisely because some anther dehiscence had occurred before stamens were removed or because some cross pollination occurred. Of the fruits formed from emasculated flowers and sprayed with water, two out of ten contained a small number of seeds (Tables 41a and 41b).

Effects of NOA on the growth in diameter of the fruit were small (Fig. 18). There was evidence that the rate of fruit growth in the early stages was increased by application of NOA to the flowers but any effect of treatment was no longer apparent 3 weeks from the time of flower opening.

No significant effect of NOA on the growth in fresh weight of fruit either from entire or emasculated flowers was observed (Table 42a). The fresh weight allowed by fruits formed from entire flowers was greater than that allowed by fruits from emasculated flowers (Table 42a).

The formation of parthenocarpic fruits was markedly influenced by spraying the flowers with NOA. Tables 41a and 41b show that no parthenocarpic fruits developed from entire flowers sprayed with water while all of the fruits formed from entire flowers which had been sprayed with 120 ppm NOA were parthenocarpic. The effectiveness of NOA in inducing parthenocarpy increased with increasing concentration from 30 ppm to 120 ppm.

Fig. 18 (Exp. 15) Effects of NOA and emasculation on fruit growth (10 plants per treatment. 12.4.79)

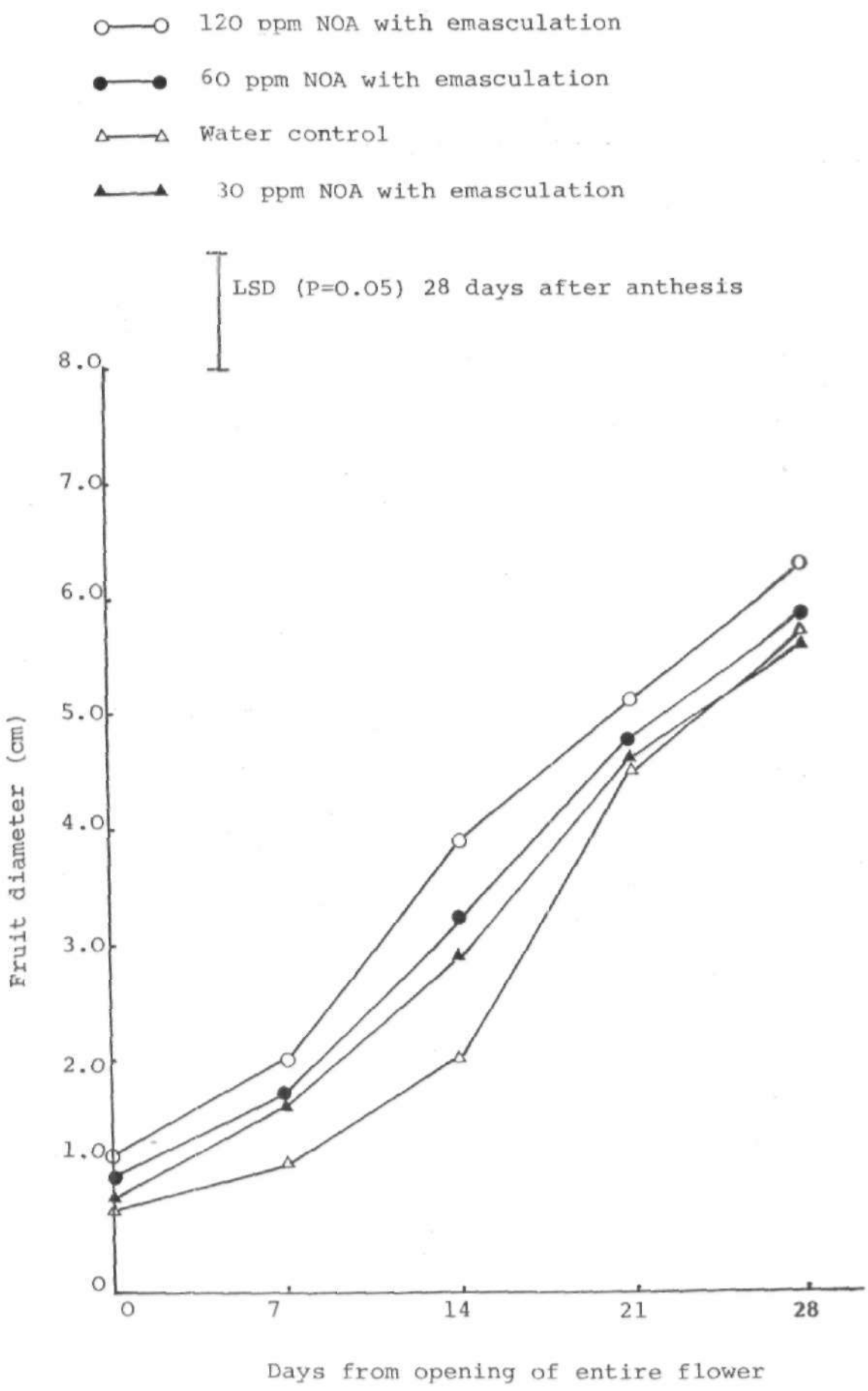

120 ppm NOA with emasculation
60 ppm NOA with emasculation
Water control
30 ppm NOA with emasculation
LSD (P=0.05) 28 days after anthesis
Fruit diameter (cm)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
7
14
21
28
Days from opening of entire flower

Table 41a (Exp. 15) Effects of NOA and emasculation on parthenocarpy. 10 plants per treatment (12.4.79)

Number of parthenocarpic fruits (out of 10 fruits per treatment)

Emasculation	Concentration of NOA (ppm)				
	0 (control)	30	60	120	Mean
Emasculated	8.0	8.0	8.5	10.0	8.6
Non-emasculated	0	6.5	9.0	10.0	6.4
Mean	4.0	7.3	9.0	10.0	

Table 41b (Exp. 15) Effects of NOA and emasculation on formation of seeds . 10 plants per treatment (12.4.79)

Number of seeds per fruit (10 fruits per treatment)

Emasculation	Concentration of NOA (ppm)				
	0 (control)	30	60	120	Mean
Emasculated	6.3	7.8	5.5	0	4.9
Non-emasculated	173.3	20.7	8.3	0	50.6
Mean	98.8	14.3	6.9	0	

Table 42a (Exp. 15) Effects of NOA and emasculation on fresh weight of fruit. 10 plants per treatment (12.4.79)

Mean fresh weight (g) of fruit (95 days after sowing)

Emasculation	Concentration of NOA (ppm)				
	0 (control)	30	60	120	Mean
Emasculated	72.4	64.5	70.7	85.2	73.2
Non-emasculated	112.5	96.3	98.8	102.6	102.6
Mean	92.5	80.4	84.8	93.9	

LSD (P=0.05) to compare NOA means NS
LSD (P=0.05) to compare emasculation means = 17.9
NOA x emasculation interaction (P=0.05) NS

Table 42b (Exp. 15) Effects of NOA and emasculation on development of internal growths. 10 plants per treatment (12.4.79)

Number of internal abnormal growths per plant (95 days after sowing)

Emasculation	Concentration of NOA (ppm)				
	0 (control)	30	60	120	Mean
Emasculated	5.4	4.6	5.0	6.2	5.3
Non-emasculated	0.7	4.5	6.1	6.5	4.5
Mean	3.1	4.6	5.6	6.4	

In fruits formed from entire flowers application of NOA to the flower reduced the number of seeds formed (Table 41b). When entire flowers were sprayed with water, a mean of 173 seeds per fruit was produced. With application of the lowest concentration of NOA (30 ppm) only 21 seeds per fruit were formed while following application of the highest concentration (120 ppm) no seeds were present.

When fruits were cut open in order to count number of seeds present, it was observed that in some, abnormal growth of the fruit wall had occurred resulting in the presence of irregular protuberances that extended into the loculi (Plate 5). Counts of these protuberances indicated that this incidence was higher in parthenocarpic fruits than in normally seeded fruits. Few protuberances were observed in fruits developed from entire flowers that had not been sprayed with NOA (Table 42b).

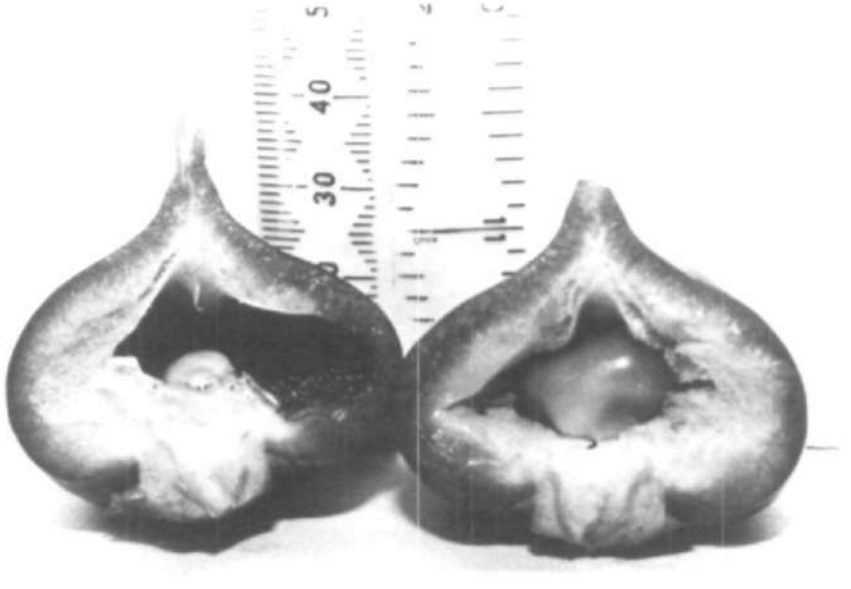
6.4 (Exps. 11 and 17) Effects of NOA, GA_3 and emasculation on fruit set and subsequent fruit development

These experiments were carried out to compare effects of NOA and GA_3 on fruit set and subsequent fruit development from emasculated and non-emasculated flowers formed on the first generation of branches. Interest was attached to any interactions between NOA and GA_3.

One flower per plant was emasculated 2 or 3 days before opening and after a non-emasculated flower had also opened, both were sprayed with NOA, GA_3, a combination of NOA and GA_3 or with de-ionised water. Diameter of the developing fruits were measured at weekly intervals from anthesis.

Plate 5 (Exp. 23) : L.S. parthenocarpic fruit showing abnormal growths of the fruit wall resulting in irregular protuberances which also extend into the loculi

(2.2.80)


5
40
30

The thermostat in the glasshouse was set to give a minimum night temperature of 16°C.

Results

As in the previous experiments, all the flowers selected for treatment set fruit, although in some of the treatments some or all of the fruits were parthenocarpic (Tables 44a and 44b). As in Exp. 15 emasculation was not entirely effective in preventing pollination and in both experiments (Exps. 11 and 17) a few fruits developed from emasculated flowers were found to contain a few seeds (Tables 45a and 45b).

In Exp. 11 there was no marked effect of the growth substance treatments on growth in diameter of the fruits either from emasculated or entire flowers (Fig. 19). The growth in fresh weight of fruits from emasculated flowers was not increased significantly as a result of the growth substance applications (Table 43a). The fresh weight of fruits from entire flowers was reduced where the flowers were sprayed with growth substances; the extent of the reduction was similar for all the growth substance treatments.

In Exp. 17, there was some increase in the growth in diameter and fresh weight of fruits developed from emasculated flowers due to application of NOA. GA_3 was apparently ineffective in promoting growth under the conditions of this experiment. "Control" fruits developed from emasculated flower sprayed with water grew less in diameter (Fig. 20) and in fresh weight (Table 43b) than in Exp. 11. In exp. 17 as in Exp. 11 the fresh weight of fruits developed from entire flowers was

Fig. 19 (Exp. 11) Effects of NOA, GA_3 and emasculation on fruit growth (16 plants per treatment. 12.4.79)

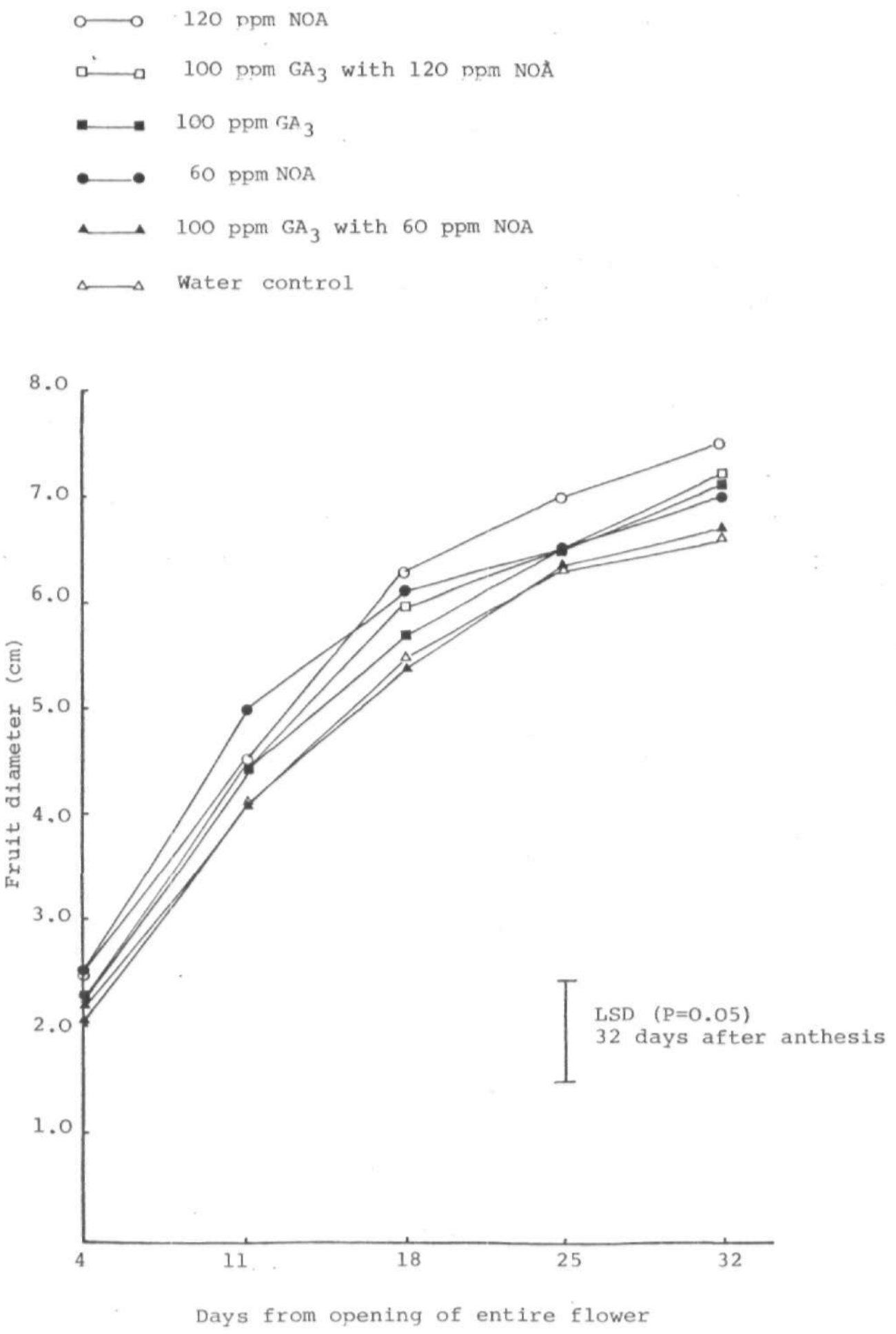

120 ppm NOA
100 ppm GA3 with 120 ppm NOA
100 ppm GA3
60 ppm NOA
100 ppm GA3 with 60 ppm NOA
Water control
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
Fruit diameter (cm)
LSD (P=0.05)
32 days after anthesis
4
11
18
25
32
Days from opening of entire flower

Fig. 20 (Exp. 17) Effects of NOA, GA_3 and emasculation on fruit growth (12 plants per treatment. 23.5.79)

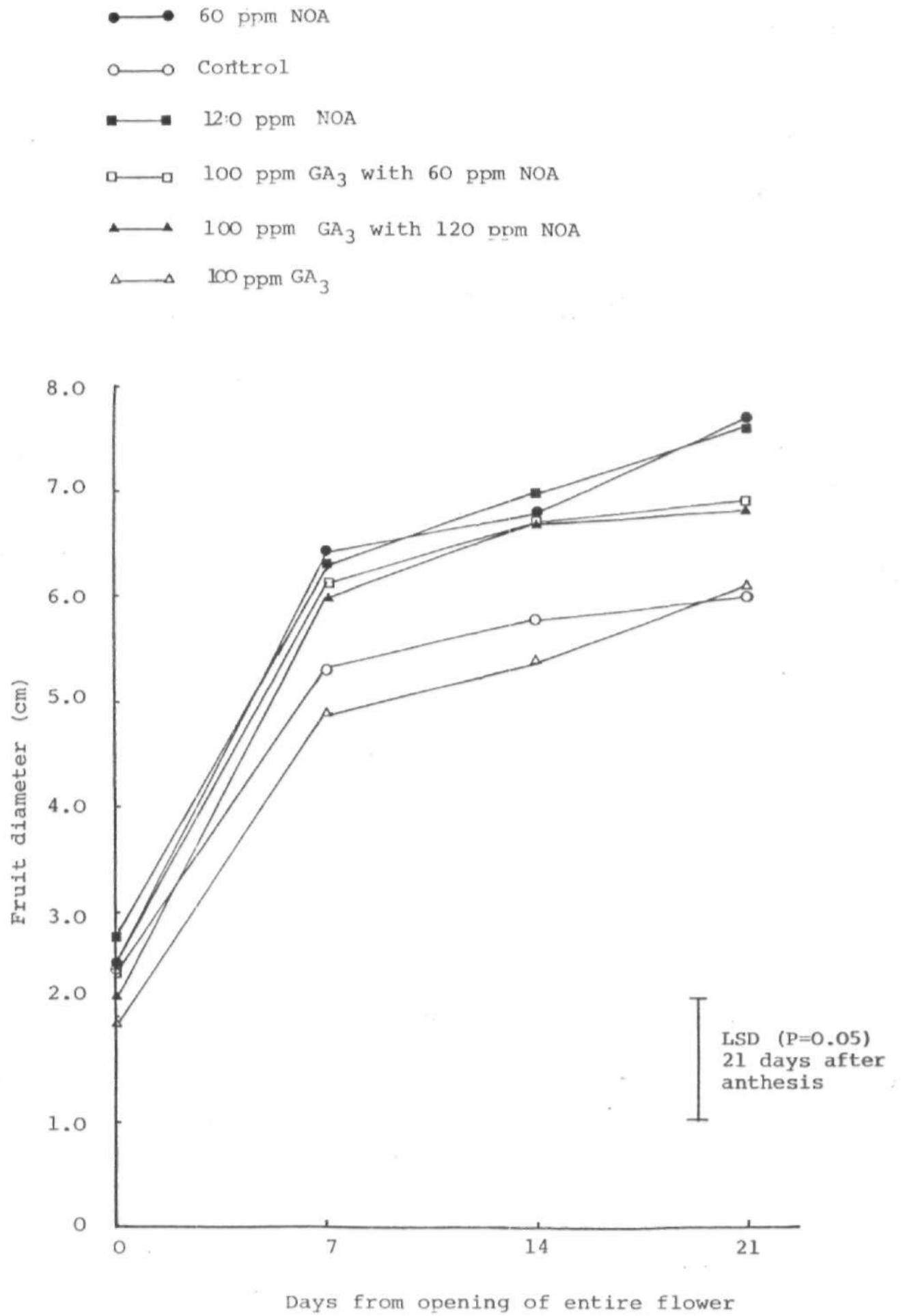

60 ppm NOA
Control
120 ppm NOA
100 ppm GA3 with 60 ppm NOA
100 ppm GA3 with 120 ppm NOA
100 ppm GA3
Fruit diameter (cm)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
7
14
21
LSD (P=0.05)
21 days after
anthesis
Days from opening of entire flower

Table 43a (Exp. 11) Effects of NOA, GA_3 and emasculation on fresh weight of fruit. 16 plants per treatment (12.4.79)

Mean fresh weight (g) of fruit (16 fruits per treatment) (110 days after sowing)

Emasculation	0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 60 ppm NOA	100 ppm GA_3 + 120 ppm NOA
+	73.4	87.4	88.5	76.2	77.4	90.8
-	120.9	81.9	82.5	73.0	75.5	86.9

LSD (P=0.05) to compare growth substances = 22.8
Growth substances x emasculation interaction (P=0.05) Significant

Table 43b (Exp. 17) Effects of NOA, GA_3 and emasculation on fresh weight of fruit. 12 plants per treatment (23.5.79)

Mean fresh weight (g) of fruit (12 fruits per treatment) (110 days after sowing)

Emasculation	0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 60 ppm NOA	100 ppm GA_3 + 120 ppm NOA
+	38.0	57.2	93.8	46.1	73.7	76.2
-	153.6	109.8	115.8	113.9	102.4	112.4

LSD (P=0.05) to compare growth substances = 23.5
Growth substances x emasculation interaction (P=0.05) Significant

reduced by spraying the flowers with growth substances.

As in previous experiments (Exps. 9, 15) application of NOA to the entire flowers was found to increase the number of parthenocarpic fruits that developed and to reduce the mean number of seeds developed per fruit (Tables 44a, 44b, 45a and 45b). While the two experiments (Exp. 11 and 17) were consistent in showing this effect of NOA they appeared to differ in how far application of GA_3 affected parthenocarpy.

In Exp. 11 (Table 44a) there appeared to be no effect of GA_3 on the proportion of fruits that developed parthenocarpically while in Exp. 17 (Table 44b) GA_3 like NOA appeared to be effective in inducing parthenocarpic development from entire flowers. Examination of data on number of seeds developed per fruit (Tables 45a and 45b) however, shows that application of GA_3 (100 ppm) to entire flowers produced very marked reductions in seed numbers per fruit in both experiments. It may be concluded that application of GA_3 like application of NOA was interferring with normal fruit development, probably by inhibiting pollination, fertilization or seed development. The treatments with GA_3 and with NOA did not appear to be additive in their effects on seed number.

6.5 (Exp. 23) Effects of NOA and GA_3 on flowering, fruit set and subsequent fruit development

The object of this experiment was to investigate how far the application of growth substances might affect fruit set in winter conditions. Growth substances were applied as sprays to the whole shoot system while in previous experiments they had

Table 44a (Exp. 11) Effects of NOA, GA_3 and emasculation on parthenocarpy. 16 plants per treatment (12.4.79)

Number of parthenocarpic fruits (out of 16 fruits per treatment)

Emasculation	0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 60 ppm NOA	100 ppm GA_3 + 120 ppm NOA
+	13.0	15.0	16.0	14.0	13.0	15.0
-	1.0	10.0	14.0	1.0	10.0	13.0

LSD (P=0.05) = 1.0
Growth substances x emasculation interaction (P=0.05) NS

Table 44b (Exp. 17) Effects of NOA, GA_3 and emasculation on parthenocarpy. 12 plants per treatment (23.5.79)

Number of parthenocarpic fruit (out of 12 fruits per treatment)

Emasculation	0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 60 ppm NOA	100 ppm GA_3 + 120 ppm NOA
+	11.0	10.0	12.0	11.0	11.0	11.0
-	0	8.0	11.0	7.0	7.0	5.0

Table 45a (Exp. 11) Effects of NOA, GA_3 and emasculation on formation of seed. 16 plants per treatment (12.4.79)

Number of seeds formed per fruit (116 days after sowing)

Emasculation	0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 60 ppm NOA	100 ppm GA_3 + 120 ppm NOA
+	37.3	4.0	0	1.3	0	0
-	398.3	30.8	13.9	26.4	31.4	40.4

Table 45b (Exp. 17) Effects of NOA, GA_3 and emasculation on formation of seed. 12 plants per treatment (23.5.79)

Number of seeds formed per fruit (112 days after sowing)

Emasculation	0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 60 ppm NOA	100 ppm GA_3 + 120 ppm NOA
+	6.2	0	0	5.7	0	0
-	308.3	80.7	47.6	68.4	93.1	89.6

been applied as localised sprays to the flowers.

NOA, GA_3 or a combination of both was sprayed on the whole plants to run-off after the flowers formed on the third generation of branches had opened. Emasculation of flowers was not carried out. Data were collected on flower formation, flower abortion, fruit set and subsequent fruit growth.

Results

Flower formation was determined by counting the number of flower buds that became visible during the period of the experiment. Table 46a shows that the number of flower buds that had become visible by the end of the experiment, 153 days after sowing was increased as a result of application of NOA at 120 ppm. No effect of GA_3 or a combination of NOA and GA_3 on flower formation was observed.

Flower abortion was reduced by the application of either NOA alone, GA_3 alone or a combination of the two growth substances. Both the number of flowers that aborted (Table 46b) and the percentage of flowers that aborted (Table 46c) were reduced by application of the growth substances. It appeared that when supplied alone NOA was somewhat more effective in reducing abortion than GA_3; when the two substances were applied together they were not additive in their effects.

Fruit set was generally better in the present experiments than in previous experiments conducted in the winter and reported in Chapters 4 and 5. Whereas no effect of either NOA at 60 ppm alone; GA_3 (100 ppm) alone or NOA (120 ppm) and GA_3 (100 ppm) together was observed, a significant increase in fruit

Table 46 (Exp. 23) Effects of NOA and GA_3 on flowering behaviour. 8 plants per treatment (31.8.79)

(a) Number of visible flower buds counted per plant (153 days after sowing)

0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 120 ppm NOA
56.4	63.9	75.8	54.1	51.4

LSD (P=0.05) = 8.8

(b) Number of flowers aborted per plant (153 days after sowing)

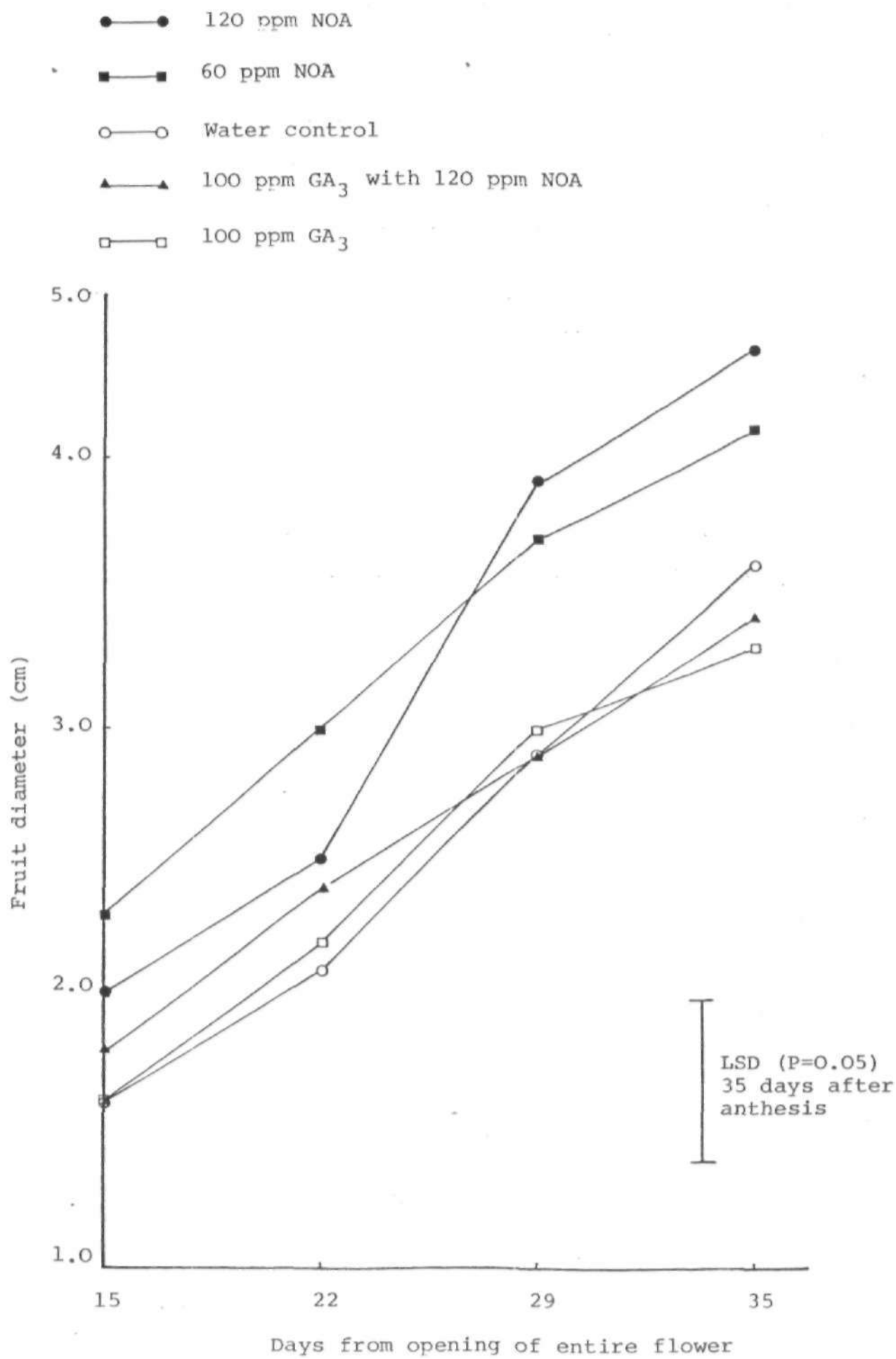
0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 120 ppm NOA
18.8	9.8	11.0	14.0	13.8

LSD (P=0.05) = 2.2

(c) Percent flower abortion per plant (153 days after sowing)

0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 120 ppm NOA
33.3	15.3	14.5	25.9	26.8

Fig. 21 (Exp. 23) Effects of NOA and GA_3 on fruit growth (8 plants per treatment. 31.8.79)


120 ppm NOA
60 ppm NOA
Water control
100 ppm GA3 with 120 ppm NOA
100 ppm GA3
5.0
4.0
3.0
2.0
1.0
Fruit diameter (cm)
LSD (P=0.05)
35 days after
anthesis
15
22
29
35
Days from opening of entire flower

set (Table 47a) was obtained with application of NOA at 120 ppm.

The rate of growth in diameter of fruits was increased by the application of NOA alone at either 60 ppm or 120 ppm. Fig. 21 shows that diameter of fruit was markedly increased by NOA at 120 ppm. There appeared to be no effect of GA_3 applied alone while GA_3 applied in presence of NOA (120 ppm) reduced the rate of growth in diameter of the fruits. Growth in fresh weight of fruit (Table 47b) was increased by NOA at 120 ppm; GA_3 applied alone had no significant effect on the fresh weight of fruit produced; when NOA (120 ppm) and GA_3 (100 ppm) were applied together the fresh weight of fruits produced was less than when NOA was applied alone.

As in the previous experiments, effect of growth substances was to increase parthenocarpy and to greatly reduce the number of seeds per fruit (Tables 47c and 48a). Application of either NOA or GA_3 led to marked reduction in the number of seeds. There were abnormal internal growth of the fruit wall in most of the fruits that contained few or no seeds (Table 48b).

6.6 Discussion

Experimental results show that formation of flowers was influenced by NOA. Promotion of flower formation due to NOA must mean that development of successive generation of branches was increased by the growth substance. The mechanism of effects of NOA to increase flower formation is not clear but it is possible that application of NOA increased translocation of metabolites to the growing points in plant.

Overbeek (1953) suggested the possibility that auxin

Table 47a (Exp. 23) Effects of NOA and GA_3 on fruit set. 8 plants per treatment (31.8.79)

Number of fruits set per plant up to 153 days after sowing

0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 120 ppm NOA
2.6	3.9	8.3	4.0	3.6

LSD (P=0.05) = 3.7

Table 47b (Exp. 23) Effects of NOA and GA_3 on fresh weight of fruits. 8 plants per treatment (31.8.79)

Mean fresh weight (g) of fruit (153 days after sowing)

0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 120 ppm NOA
49.0	78.3	109.8	77.1	68.7

LSD (P=0.05) = 40.4

Table 47c (Exp. 23) Effects of NOA and GA_3 on parthenocarpy. 8 plants per treatment (31.8.79)

Number of parthenocarpic fruits per plant (153 days after sowing)

0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm NOA	100 ppm GA_3 + 120 ppm NOA
0.4	3.4	7.1	3.5	2.5

Table 48a (Exp. 23) Effects of NOA and GA_3 on formation of seed. 8 plants per treatment (31.8.79)

Number of seeds formed per fruit

0 ppm	60 ppm NOA	120 ppm NOA	100 ppm NOA	100 ppm GA_3 + 120 ppm NOA
141.5	5.1	1.9	4.6	2.3

Table 48b (Exp. 23) Effects of NOA and GA_3 on development of abnormal growths. 8 plants per treatment (31.8.79)

Number of internal abnormal growths per fruit

0 ppm (control)	60 ppm NOA	120 ppm NOA	100 ppm GA_3	100 ppm GA_3 + 120 ppm NOA
0	3.2	5.1	3.3	2.8

may be a required factor for synthesis of florigen which may promote flower formation in plants. If this theory is true, any increase in auxin content in plant may increase flower formation and this may explain why exogenous application of NOA in this experiment increased number of flower buds formed.

The effect of NOA to reduce incidence of flower abortion in Exp. 23 carried out in winter is important because failure of fruit set which must be associated with flower abortion has been reported to be a major problem in pepper (Mote *et al.*, 1975 and Park and Jeong, 1976).

Flower abortion when total radiation was poor could be due to intra-plant competition for nutrients; insufficient nutrients could lead to reductions in supply of auxin to the abscission layer of developing buds which may induce their abortion. This explanation is supported by the fact that incidence of flower abortion was reduced by 50 percent with application of NOA.

Any influence of the application of growth substances on fruit set could not be easily assessed because fruit set occurred in the control and treated plants in most experiments. However, in experiment conducted in the winter there was evidence that NOA significantly increased fruit set. It is clear that when GA_3 was applied alone or in combination with NOA, it did not affect fruit set in sweet pepper.

The significance of auxin in fruit setting has been recognized by several workers. Overbeek (1953) suggested that promotion of fruit set due to auxin may be attributed to induced changes in the ovary, duplicating those normally brought about by pollination. Crane (1964) attributed promotion of fruit set

by auxin to its presence in pollen, its production in the style and its stimulation of growth of ovary. Further evidence that auxin influences fruit set has been provided by the use of auxin extracts from plants to increase fruit set. Wittwer (1943) and Redemann *et al.* (1951) obtained fruit set in pepper and tomato with extracts of immature maize kernels, Luckwill (1948) obtained it in tomatoes with extracts of immature apple seeds.

Synthetic auxins have also been reported to increase fruit set in some vegetable crops. Gustafson (1942), Odland and Chan (1950), Osborne and Went (1953) and Kepcka (1966) had obtained increases in fruit set with exogenous application of NOA to open flowers. In the egg plant Muthukrishnan and Srinivasan (1963) and more recently Nothmann and Koller (1975) and Olympios (1976) reported that NOA increased fruit set. However, little has been reported on effects of NOA to increase fruit set in sweet pepper. Rylski (personal communication) could not obtain any increase in fruit set in sweet pepper as she obtained in tomato and the egg plant with application of growth substances. She attributed different responses to growth regulators in relation to fruit set between pepper and tomato or egg plants partly to morphological differences in the fruit.

Results from experiments show that growth in diameter and fresh weight was greater in fruits formed from entire flowers than emasculated flowers. Any effect of NOA on size of fruit formed by emasculated flowers was inconsistent and small while NOA had little effect on size of fruits formed from the entire flowers. Neither GA_3 nor combinations of NOA and GA_3 had any significant effect on fruit size.

One suggestion from the results may be that growth in seeded fruit could occur naturally without exogenous application of growth substances. It appeared that presence of seed in fruit may increase growth in its size and that NOA may replace seed effect in emasculated ovary. It has been established (Gustafson, 1939; Crane, 1964; Nitsch, 1951 and 1965) that auxin concentration is high in seed. Since auxin has been known to promote cell expansion, it is probable that any application of auxin to seedless fruit may increase growth in size of fruit.

There is evidence that parthenocarpy occurs in pepper (Charles *et al.*, 1979). Evidence here and from Chapter 5 indicates that parthenocarpy can also be induced in pepper. Application of growth substances markedly increased number of parthenocarpic fruits formed in plant. Both NOA and GA_3 were found to promote parthenocarpy.

The cause of parthenocarpy in sweet pepper is not fully known. Whereas Cochran (1936) believed that parthenocarpy was due to lack of fertilization caused by slow growth of pollen tube down the style, more recently Rylski (1974) attributed parthenocarpic fruit development to non-viability or lack of production of pollen. Both Cochran (1936) and Rylski (1974) obtained parthenocarpy at low night temperatures. Gustafson (1936) however, obtained parthenocarpy in many plants with application of auxins to flower buds. He suggested that parthenocarpy might have been caused due to increase of auxin content in the ovary. Gustafson (1939) further strengthened his previous suggestion when he found that flower buds of seedless oranges, lemons and grapes contain more free auxin than flower

buds of comparable seeded species.

More recently Nitsch *et al.* (1960) found that up to about 8 days after anthesis the growth substance content was higher in the seedless strain than in the seeded one when they compared two strains of *Vitis labrusca* var. "Concord".

A high percentage of parthenocarpic fruits here was found to contain internal abnormal growths (Plate 5) which could not be found in pollinated fruits; the internal wall of the fruit had developed to form some protuberances. Occurrence of similar internal growths in parthenocarpic fruits had been reported in the previous chapter (Chapter 5). Cochran (1934 and 1936) had observed similar abnormalities in peppers and noted that such abnormal growths occurred widely in the genus *Capsicum*. The cause of such abnormal development in fruit is not clear. Whereas Cochran (1934 and 1936) observed a few seeds in such fruits, no seeds were found in fruits with abnormal growths here. It is possible that a high concentration of auxin in parthenocarpic fruits may induce development of the internal abnormal growths which seem to have developed instead of seeds around the placenta.

Any practical significance of parthenocarpic fruit development in sweet pepper is doubtful, especially since such fruits are reduced in size compared with pollinated fruits. Any improvement in size of parthenocarpic fruit may be acceptable in its use as a salad vegetable.

There is evidence that some parthenocarpic fruits are similar in size and shape to their pollinated counterparts while others are not. Crane (1964) reported that parthenocarpic

fruits of egg plant, grape and tomato are not greatly different in size and development to their pollinated counterparts whereas apple, apricot, avocado and pear fail to grow to normal size.

6.7 Summary

(1) When night temperatures were low fruits that developed were either parthenocarpic or contained very few seeds. Localised application of beta-naphthoxyacetic acid (NOA) or gibberellic acid (GA_3) to open flowers under these conditions had little or no effect on fruit growth.

(2) When plants were grown in a "normal" temperature regime with night temperatures of 16°C, localised application of NOA or GA_3 to the flowers caused marked reductions in the number of seeds produced per fruit and often caused a reduction in the growth in fresh weight of the fruits.

(3) The emasculation of flowers generally led to the development of parthenocarpic fruits of lower fresh and dry weight than fruits developed from entire flowers. Application of NOA or GA_3 to emasculated flowers had little or no effect on fruit growth.

(4) Under winter conditions where the incidence of fruit set was low, the application of NOA as a spray applied to run-off increased the number of fruits produced. GA_3 was not effective in increasing fruit set under these conditions. Application of either NOA or GA_3 affected fruit development in that the number of seeds per fruit was markedly reduced.

Chapter 7

Further Effects of Shoot Pruning and Shading on Flowering and Fruit Set (Exps. 22, 24 and 26)

A relatively small proportion of the flowers formed in pepper develops into fruit. Mote *et al*. (1975) observed that only 6 percent of the flowers produced in many varieties of pepper in India develop to set fruit. This was confirmed by Park and Jeong (1976).

It is possible that flower abortion and failure of fruit set occur as a result of intra-plant competition for assimilates between the branches that are produced. From a previous experiment (Exp. 25, Chapter 5) it appeared that limiting the numbers of shoots growing on the plant may affect flower development and fruit set. Poor light conditions have also been shown to affect flower development. Experiments in this chapter were designed to examine any influence that shoot pruning and shading may exert on post-initiation development of the flower and on fruit set. The possibility of any interactions between pruning and shading was also investigated.

7.1 Methods of shoot pruning

The number of shoots on the plant was limited to one, two or four leaders by removing the growing tips of unwanted shoots. The control plants were allowed to grow intact (see Plate 6).

Plate 6 (Exp. 24) : Effects of shoot pruning on flowering and fruit set (12.1.80)

(a) A photograph showing an unpruned (control) plant on the left and a plant pruned to one leading shoot on the right.

(b) A photograph showing an unpruned (control) plant on the left and a plant pruned to two leading shoots on the right (Note stumps on the pruned plant).

↑ indicates stumps on the pruned plant



a



b

The quantity of tissue removed was small, usually not greater than 700 mg in total dry weight per plant.

In Exps. 22 and 24 pruning was stated after the first and second branches had extended; stumps were left in some treatments (see Plate 6). Any flowers formed on the stumps were not removed. However, in Exp. 26 no stumps were left because pruning was started as soon as flowers were visible on the main laterals.

When the shoots were removed, the leaf subtending the previous branch was left intact so that only the flower bud and the two unfolded leaves which would grow to subtend the next generation of branches were removed. Pruning was done at approximately weekly intervals until the experiment was terminated. In Exps. 22 and 24 flowers formed at the tips of the primary shoots and those on the main branches had been removed before pruning treatments commenced.

7.2 Experimental designs

Four treatments were used in Exp. 22. Pruning was carried out to leave one, two or four leading shoots while further plants were left intact as "controls". Treatments were arranged in a randomised block design with one plant per plot, replicated ten times. In Exp. 24 the same treatments were again arranged in randomised blocks, but this time with four replicates and containing 4 plants. In Exp. 26 the same four treatments were combined with two shading treatments (shaded with non-shaded), in a split-plot randomised block design in factorial combination. They were replicated six times with 2

plants per sub-plot. The timing of individual experiments is shown in Table 49.

Shading was provided by two layers of green "Netlon" plastic netting used to reduce the incident solar radiation by 60 percent.

7.3 Results

7.3.1 Effects of shoot pruning on flowering and fruit set (Exps. 22 and 24)

There were no consistent effects of shoot pruning on shoot growth in terms of dry weight accumulation. Total dry weight of the shoot system was unaffected by shoot pruning in Exp. 22 (Table 50a).but was significantly increased by pruning to leave one or two leading shoots in Exp. 24 (Table 50b). By the time the experiments had ended growth in dry weight of the shoot systems was greater below the point at which pruning commenced than above it (Tables 50a and 50b).

Flowering behaviour was influenced by shoot pruning. The higher number of flower buds formed in the unpruned plants compared with the pruned plants (Line a, Tables 51 and 52) was due to the greater number of branches that developed where no pruning was carried out.

Experimental evidence shows that flower abortion was affected by shoot pruning. Both the number and percentage of flowers aborted (Lines b and c, Tables 51 and 52) was markedly higher in the unpruned plants. Within the pruning treatments the incidence of flower abortion decreased as the number of

Table 49 Detail of experiments 22, 24 and 26

Exp. number	Title of experiment	Date of sowing	Date treatments commenced	Stage of plant development at which treatments commenced	Date exp. was terminated
22	Effects of shoot pruning on flowering and fruit set	31.8.79	21.11.79	When the flowers formed on the third generation of branches had reached stage 3	17.1.80 (139 days after sowing)
24	Effects of shoot pruning on flowering and fruit set	5.10.79	24.1.80	When the flowers formed on the second generation of branches had reached stage 3	7.3.80 (154 days after sowing)
26	Effects of shoot pruning and shading on flower and fruit set	20.1.80	27.3.80	When the flowers formed on the first generation of branches had reached stage 3	13.5.80 (114 days after sowing)

Table 50a (Exp. 22) Effects of shoot pruning on the growth in dry weight of the shoot system. 10 plants per treatment (31.8.79)

Dry weight (g) per plant (137 days after sowing)

	All shoots (control)	4 shoots	2 shoots	1 shoot
Dry weight of shoots below 2nd generation of branches	15.00	12.88	11.7	13.68
Dry weight of shoots above 2nd generation of branches	3.54	5.60	4.88	6.09
Total shoot dry weight	18.54	18.48	16.58	19.77

LSD (P=0.05) for total shoot dry weight NS

Table 50b (Exp. 24) Effects of shoot pruning on the growth in dry weight of the shoot system. 16 plants per treatment (5.10.79)

Dry weight (g) per plant (123 days after sowing)

	All shoots (control)	4 shoots	2 shoots	1 shoot
Dry weight of shoots below 2nd generation of branches	7.42	8.16	8.51	9.18
Dry weight of shoots above 2nd generation of branches	2.00	2.35	2.92	2.08
Total shoot dry weight	9.42	10.51	11.43	11.25

LSD (P=0.05) for total shoot dry weight = 1.7

Table 51 (Exp. 22) Effects of shoot pruning on flowering behaviour. 10 plants per treatment (31.8.79)

	All shoots (control)	4 shoots	2 shoots	1 shoot	LSD (P=0.05)
(a) Number of flowers formed per plant up to 136 days after sowing	68.2	29.5	25.5	21.5	8.7
(b) Number of flowers that aborted per plant, up to 136 days after sowing	54.6	21.1	16.6	11.6	8.6
(c) Percent flowers that aborted per plant up to 136 days after sowing	80.1	71.5	65.1	54.0	
(d) Number of flowers that opened per plant up to 136 days after sowing	14.6	11.1	8.8	8.2	2.5
(e) Number of flowers shed per plant up to 136 days after sowing	12.9	8.2	5.9	4.5	2.4
(f) Percent of post-anthesis shedding per plant up to 136 days after sowing	88.4	73.9	67.0	54.9	

Table 52 (Exp. 24) Effects of shoot pruning on flowering behaviour. 16 plants per treatment (5.10.79)

	All shoots (control)	4 shoots	2 shoots	1 shoot	LSD (P=0.05)
(a) Number of flowers formed per plant up to 121 days after sowing	148.0	28.3	20.9	12.4	14.7
(b) Number of flowers that aborted per plant up to 121 days after sowing	100.5	12.3	8.1	0.8	2.5
(c) Percent flowers that aborted per plant up to 121 days after sowing	67.9	43.5	38.8	6.5	
(d) Number of flowers that opened per plant up to 121 days after sowing	17.3	10.0	9.4	7.5	4.0
(e) Number of flowers shed per plant up to 121 days after sowing	15.4	7.5	4.9	2.6	3.6
(f) Percent of post-anthesis shedding per plant up to 121 days after sowing	89.0	75.0	52.1	34.7	

shoots growing on the plants was reduced. The smallest proportion offlower abortion occurred in the one-shoot plants.

Flower opening was markedly influenced by the number of shoots growing on the plant. The number of flowers that had opened by the time experiments ended was greatest in unpruned plants (line d, Tables 51 and 52) while the proportion of flowers formed which opened was greatest in plants pruned to one leading shoot. It is evident that the proportion of flowers that opened increased as the number of shoots growing on the plant decreased.

Generally, only a small number or a low proportion of flowers that opened developed beyond anthesis. Post-anthesis shedding both in ter. m of numbers and percentage increased as the numbers of shoots growing on the plants increased (lines e and f, Tables 51 and 52). How far this increase was due to a promotion of flower development in pruned plants is not known.

Fruit set was generally poor in both experiments. It is possible that this was due to environmental conditions in late winter and early spring. However, number of fruits set was consistently smaller on the control plants than on pruned plants (Tables 53 and 54). Any difference in number of fruits set per plant within pruning treatments was not significant (Tables 53 and 54). A few fruits were set on the stumps in two and four-shoot plants; any effects exerted by these stumps on fruit set could not be easily assessed. Fresh weight of fruits was recorded in Exp. 22 and it was significantly increased in the pruned plants. Fresh weight of fruits was significantly greater in one shoot-plant than in two-shoot plants (Table 53). The

Table 53 (Exp. 22) Effects of shoot pruning on fruit set and fresh weight of fruits. 10 plants per treatment (31.8.79)

	All shoots (control)	4 shoots	2 shoots	1 shoot	LSD (P=0.05)
Number of fruits set per plant up to 136 days after sowing	1.4	2.5	2.7	2.9	1.5
Fresh weight (g) of fruits per plant up to 136 days after sowing	36.3	76.7	65.7	82.6	9.5

Table 54 (Exp. 24) Effects of shoot pruning on fruit set. 16 plants per treatment (5.10.79)

Numbers of fruits set per plant, up to 121 days after sowing

All shoots (control)	4 shoots	2 shoots	1 shoot
0.5	1.3	2.3	2.3

LSD (P=0.05) = 1.2

effect of shoot pruning to increase fresh weight of fruits was significantly greater in one-shoot plants than in four-shoot plants.

7.3.2 Effects of shoot pruning and shading on flowering and fruit set (Exp. 26)

In Exp. 26 it was observed that growth of the dry weight of the shoot system was greater in the plants pruned to two leading shoots than control plants (Table 55a).

It appeared that flower formation was affected by pruning treatments. Table 55b and Fig. 22 show that numbers of flowers formed per plant up to 100 days after sowing were significantly greater in the control than in the pruned plants. The increase was associated with the greater number of shoots that developed in the control plants.

The incidence of flower abortion was smaller in the present experiments than the previous experiments. The number and the percentage (Tables 56a and 56b) of flowers that had aborted up to 100 days after sowing was greater in the control than pruned plants. Table 56a indicates the increase in the number of flowers aborted in the control as compared with any pruning treatments was significant. Within the pruning treatments, flower abortion was significantly reduced as the number of leading shoots allowed to remain on the plants decreased.

The time that a flower first opened in the plant was not affected by the pruning treatments. Table 57b shows that first flowers opened at about the same time in all plants.

Fig. 22 (Exp. 26) Effects of shoot pruning and shading on flower formation (12 plants per treatment. 20.1.80)

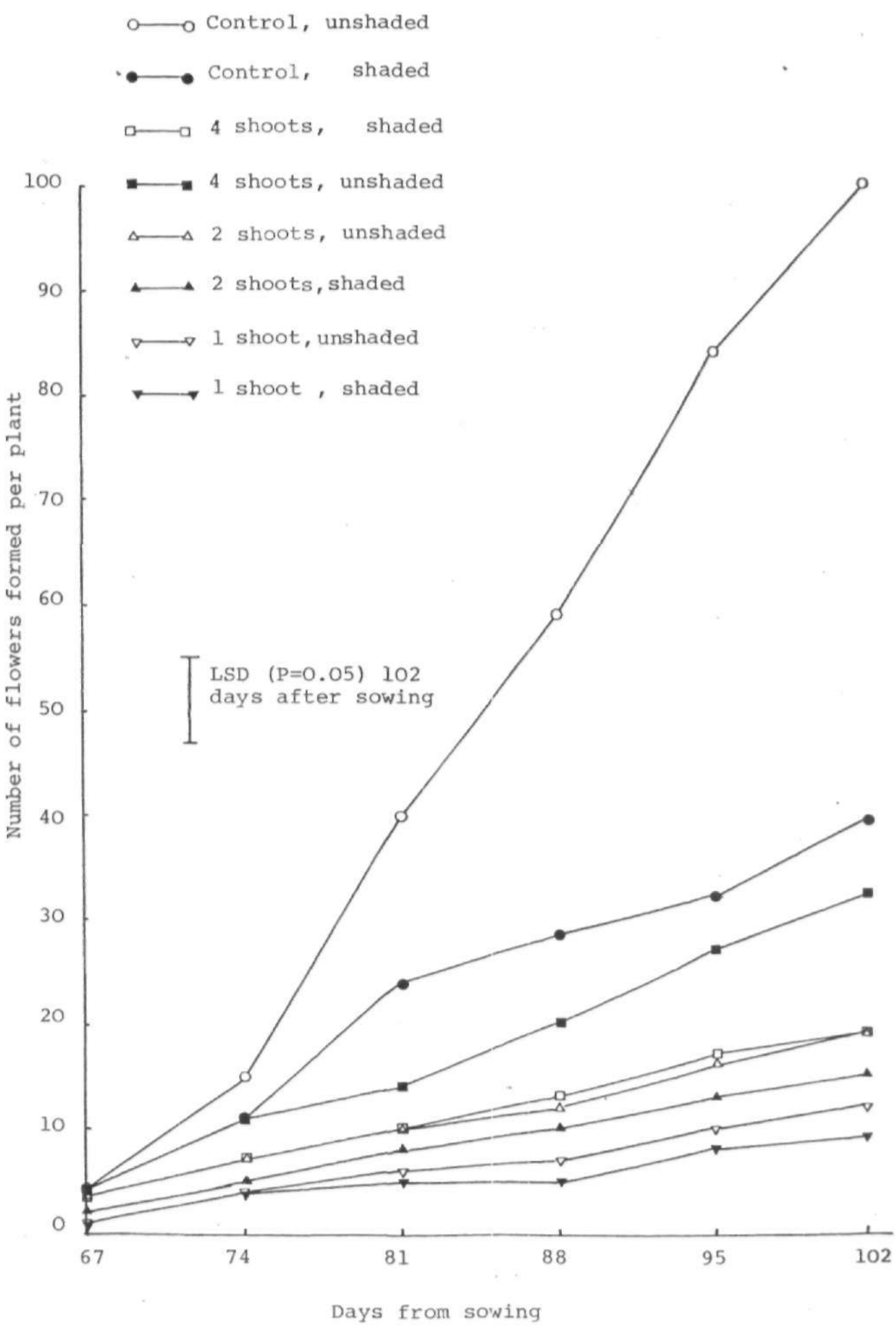

Control, unshaded
Control, shaded
4 shoots, shaded
4 shoots, unshaded
2 shoots, unshaded
2 shoots, shaded
1 shoot, unshaded
1 shoot , shaded
LSD (P=0.05) 102 days after sowing
Number of flowers formed per plant
100
90
80
70
60
50
40
30
20
10
0
67
74
81
88
95
102
Days from sowing

Table 55a (Exp. 26) Effects of shoot pruning and shading on total shoot dry weight. 12 plants per treatment (20.1.80)

Dry weight (g) of shoot system per plant (102 days after sowing)

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	6.52	9.75	10.24	8.32	8.71
Unshaded	17.55	18.17	19.07	17.76	18.14
Shoot pruning mean	12.04	13.96	14.66	13.04	

LSD (P=0.05) to compare shading means = 2.5
LSD (P=0.05) to compare pruning means = 2.4
Shading x pruning interactions (P=0.05) NS

Table 55b (Exp. 26) Effects of shoot pruning and shading on flower formation. 12 plants per treatment (20.1.80)

Number of flower buds formed per plant up to 100 days after sowing

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	39.3	18.8	14.5	8.7	20.3
Unshaded	99.9	32.3	19.1	11.6	40.7
Shoot pruning means	69.6	25.6	16.8	10.2	

LSD (P=0.05) to compare shading means = 4.6
LSD (P=0.05) to compare pruning means = 5.9
Shading x pruning interactions (P=0.05) Significant

Table 56 (Exp. 26) Effects of shoot training and shading on flower abortion. 12 plants per treatment (20.1.80)

(a) Number of flowers aborted per plant up to 100 days after sowing

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	20.3	6.3	3.8	2.4	5.7
Unshaded	3.3	1.2	1.5	0.4	1.6
Shoot pruning means	6.8	3.8	2.6	1.4	

LSD (P=0.05) to compare shading means = 1.4
LSD (P=0.05) to compare shoot training means = 1.0
Shading x shoot training interaction (P=0.05) Significant

(b) Percent flowers that aborted per plant up to 100 days after sowing

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	51.7	33.5	26.2	27.6	34.8
Unshaded	3.3	3.7	7.9	3.4	4.6
Shoot pruning means	27.5	18.6	17.1	15.5	

Table 57a (Exp. 26) Effects of shoot pruning and shading on flower opening. 12 plants per treatment (20.1.80)

Number of flowers that opened per plant up to 100 days after sowing

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	3.3	4.5	4.8	3.2	4.0
Unshaded	17.3	10.8	7.2	4.8	10.0
Pruning means	10.3	7.7	6.0	4.0	

LSD (P=0.05) to compare shading means = 1.4
LSD (P=0.05) to compare pruning means = 1.2
Shading x pruning interaction (P=0.05) Significant

Table 57b (Exp. 26) Effects of shoot pruning and shading on first anthesis in the plant. 12 plants per treatment (20.1.80)

Number of days from sowing to first anthesis in the plant

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	88.8	89.3	87.8	88.7	88.7
Unshaded	87.7	85.2	86.5	86.7	86.5
Pruning means	88.3	87.3	87.2	87.7	

The number of flowers that opened up to 100 days after sowing was significantly greater in control plants than in pruned plants (Table 57a), but the proportion of flower buds that opened increased as the number of leading shoots allowed to remain on the plants decreased.

A decrease in post-anthesis shedding due to pruning shoots was observed. Number and percentage of flowers shed per plant was significantly reduced by pruning shoots (Tables 58a and 58b). Pruning plants to a single shoot was significantly more effective in reducing incidence of post-anthesis shedding than pruning to two or four leading shoots (Tables 58a and 58b).

As reported in Exp. 25 (Chapter 5) and Exps. 22 and 24, fruit set was low in the present experiment. However, the number of fruits set per plant was increased by about one to two in pruned plants as compared with unpruned plants (Table 59a). Accompanying the increases in fruit set there were increases in the fresh weight of fruits produced per plant (Table 59b).

Parthenocarpy occurred but it appeared that pruning had no consistent effect on number of parthenocarpic fruits (Table 60a). Similarly any effect of shoot pruning on formation of seed was not consistent (Table 60b).

Effects of shading in the present experiment were generally similar to effects due to shading previously reported in Exp. 3 (Chapter 4) and Exps. 21 and 25 (Chapter 5). In the present experiment, however, shading produced a marked reduction in the growth in dry weight of shoots (Table 55a).

Effects of shading in reducing the number of flowers formed per plant were highly significant (Table 55b). Fig. 22

Table 58 (Exp. 26) Effects of shoot pruning on post-anthesis shedding. 12 plants per treatment (20.1.80)

(a) Number of flowers shed per plant up to 100 days after sowing

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading means
Shaded	1.8	0.8	1.7	0.3	1.2
Unshaded	1.2	0.7	0.7	0.3	0.7
Pruning means	1.5	0.8	1.2	0.3	

LSD (P=0.05) to compare shading means NS
LSD (P=0.05) to compare pruning means = 0.4
Shading x pruning interaction (P=0.05) NS

(b) Percent of flowers that had shed per plant (100 days after sowing)

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	54.5	17.8	35.4	9.4	29.3
Unshaded	6.9	6.5	9.7	6.3	7.4
Pruning means	30.7	12.2	22.6	7.9	

Table 59 (Exp. 26) Effects of shoot pruning and shading on fruit set. 12 plants per treatment (20.1.80)

(a) Number of fruits set per plant up to 100 days after sowing

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	0	1.2	1.4	1.4	1.0
Unshaded	2.7	4.5	3.8	2.5	3.4
Pruning means	1.4	2.9	2.6	2.0	

(b) Fruit fresh weight (g) per plant (100 days after sowing)

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	0	7.0	5.4	13.6	6.5
Unshaded	31.5	60.3	55.5	52.6	50.0
Pruning means	15.8	33.7	30.5	33.1	

Table 60a (Exp. 26) Effects of shoot pruning and shading on parthenocarpy. 12 plants per treatment (20.1.80)

Percent parthenocarpy (out ot total fruits set per plant)

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	No fruit set	16.7	69.2	21.4	35.8
Unshaded	8.7	4.7	9.1	11.1	8.4
Pruning means	8.7	10.7	39.2	16.3	

Table 60b (Exp. 26) Effects of shoot pruning and shading on seed formation and seed fresh weight. 12 plants per treatment (20.1.80)

Number of seeds per fruit (100 days after sowing)

	All shoots (control)	4 shoots	2 shoots	1 shoot	Shading mean
Shaded	No fruit set	9.7	13.3	23.2	15.4
Unshaded	126.8	174.0	99.7	105.9	126.6
Pruning means	126.8	91.9	56.5	64.6	

shows that relatively high number of flowers formed in unshaded plants was associated with the production of relatively high numbers of branches.

The incidence of flower abortion was markedly increased by shading treatment. Shading to reduce total solar radiation by 60 percent significantly increased number of flowers that had aborted (Tables 56a and 56b).

Opening of the first flowers occurred at a similar time in shaded and unshaded plants (Table 57b). However, the number of flowers that had opened by the time the experiment ended was reduced by about 6 in shaded plants (Table 57a).

Post-anthesis shedding was not influenced by shading treatment, but shading affected fruit set. In the unpruned plants, the shading treatment prevented fruit set and reduced it by 44 to 73 percent in the pruned plants (Table 59a).

Shading in the present experiment as in the previous experiment (Exp. 25) appeared to induce parthenocarpy (Table 60a). The fresh weight of fruits produced per plant up to 100 days after sowing was affected by shading treatment. Table 59b shows a decrease of 31 to 53g per plant due to the shading treatment.

Seed formation was adversely affected by shading. In the few non-parthenocarpic fruits, number of seeds per fruit was 10 to 23 whereas up to 174 seeds were counted per fruit in the unshaded plants (Table 60b).

7.4 Discussion

In the experiments reported here any effects of shoot

pruning on growth in dry weight of the shoot system were small. Pruning did not lead to any reduction in the dry weight of the shoot system and in each of the experiments reported here significant increases in shoot growth were observed in response to a reduction in the number of leading shoots to two. It is likely that pruning reduced mutual shading of the leaves and it is possible that the interception of radiation was greater in pruned than unpruned plants.

The proportion of flower buds that aborted was higher in intact plants than in plants pruned to reduce the number of leading shoots to one, two or four.

It is possible that the relatively high incidence of flower abortion in intact plants was due to intra-plant competition for assimilates between the developing branches.

At the time the experiments were terminated, only a few fruits had been formed per plant. However, an influence of reducing the number of leading shoots on fruit set was apparent. The pruning of shoots led to increases in the number of fruits set of the order of one to two per plant. Associated with the increases in the number of fruits set there were increases in the fresh weight of fruits produced per plant. The extent to which the increased fresh weight of fruit is attributable to increased growth of individual fruits is not known.

Little is known concerning effects of pruning in pepper. However in commercial production of the crop, pruning to two shoots in a plant has produced greater and earlier yields than other systems (Uffelen, 1976). Quality of fruits was better

and labour costs were reduced in pruned than unpruned plants (Uffelen, 1976). Similar effects of pruning on fruit set were obtained in sweet pepper by Price (1978).

The amount of tissue removed in plant by Uffelen (1976) and Price (1978) is not known; it is likely that tissue was removed at a more advanced stage of plant development than the experiments here. However, it appeared that by limiting the number of shoots per plant it was possible to increase fruit set. The increases in fruit set may have been due to reductions in competition for assimilates between branches in pruned plants This view seems to be confirmed by an observation (Price, 1978) that within pruning system fruit yields were further increased when side shoots were removed.

The incidence of post-anthesis shedding was generally small in the experiments here and observation showed that shedding of flowers occurred in upper branches after flowers on lower branches had set fruits. This is consistent with the hypothesis that fruit is the greatest sink for carbohydrates in sweet pepper plant (Hall, 1977; Hall and Brady, 1977).

Shading appeared to retard development in the plants; in response to shading there were significant decreases in growth in dry weight and increases in incidence of flower abortion and shedding. Fruit set was decreased or inhibited in shaded plants.

Effects of shading were greater in the intact than in pruned plants. These effects of shading (see Chapters 4 and 5) may be attributable to reductions in production, distribution and utilization of assimilates due to a decrease in levels of

total radiant exposure.

There appeared to be an interaction between shading and pruning treatments; the greater the number of shoots growing in the plant, the more adverse the effects of shading on flower opening and fruit set. No fruit set occurred in shaded, intact plants and where a few fruits were set in pruned plants, they were largely parthenocarpic.

The increased number of parthenocarpic fruits that developed in shaded plants may have been due to a reduction of temperature by shading.

7.5 Summary

(1) The pruning treatments adopted here were carried out in order to reduce the number of leading shoots on each plant; they did not result in any decrease in the growth in dry weight of the shoot systems.

(2) The proportion of flower buds that aborted and the proportion of open flowers that were shed were reduced by the pruning treatments.

(3) Pruning produced small but significant increases in the number of fruits set per plant. Pruning to reduce the number of leading shoots to one or two was more effective than pruning to reduce the number of leading shoots to four.

(4) Shading the plants retarded their growth and development. Shading also produced increases in the incidence of flower abortion and post-anthesis shedding and reduced the number of fruits set per plant.

Chapter 8

Effects of Water Stress on Flowering and Fruit Set (Exps. 7, 13 and 16)

In Nigeria pepper is cultivated mainly in the northern states where rainfall is often erratic; failure of fruit set has been attributed to excessive wetness in the rainy season and to excessive dryness in the dry season. Information on the responses of sweet pepper plants to different watering regimes might help the planning programmes for this region. A primary object of the experiments described in this chapter was to examine effects of water stress on flowering and fruit set. Interest was also attached to how responses to different watering regimes might vary with the stage of development of the plants.

8.1 Methods and experimental designs

The three treatments used here provided wet, medium and dry regimes. For the wet regime the plants were allowed to lose 5 percent of pot weight at field capacity, medium 20 percent and dry 33 percent. The potted plants were allowed to lose water until appropriate weight was reached and the medium was then brought back to field capacity. Treatments continued until the first-formed fruits had become mature.

Plants in Exps. 7 and 16 were grown in 15.2 cm diameter pots while those in Exp. 13 were grown in 20.3 cm diameter pots. Pots were filled with John Innes potting compost no. 2 (see

Table 61 Detail of experiments described in Chapter 8

Exp. number	Title of experiment	Date of sowing	Size of pots (cm) in which plants were grown	Date treatments commenced	Stage of plant development at which treatments commenced	Date exp. was terminated
7	A preliminary investigation on effects of water stress on flowering and fruit set (10 plants per treatment)	15.2.78	15.2	7.4.78	First flower bud visibility stage	15.6.78 (120 days after sowing)
13	Effects of water stress and night temperature on flowering and fruit set (10 plants per treatment)	6.6.78	20.3	10.7.78	First flower bud visibility stage	11.9.78 (97 days after sowing)
16	Effects of water stress and stage of plant development on flowering and fruit set (12 plants per treatment)	23.5.79	15.2	27.7.79	Older plants (at anthesis)	(121 days after sowing)
		5.6.79			Younger plants (14 days to anthesis)	21.9.79 (108 days after sowing)

Chapter 2 for composition of composts).

Treatments were arranged in simple randomised blocks, replicated three times with 10 plants per treatment in Exp. 7. In Exp. 13 plants in the different watering regimes were grown at night temperatures of 18° or 25°C otherwise "normal" temperature regimes were maintained in the glasshouse (see Chapter 2). Treatments were arranged in completely randomised blocks with 5 replicates and 10 plants were used per treatment in Exp. 13. Plants in Exp. 16 were subjected to the water stress treatments at anthesis stage (older plants) or 14 days before anthesis (younger plants). Treatments were arranged in 2 x 3 factorial randomised blocks, replicated 4 times with 12 plants per treatment.

8.2 Determination of water content of the plants (Exp. 16)

Relative turgidities of the plants in the different watering regimes were determined by a leaf disc technique after Weatherly (1950 and 1962). A modification of the technique was also adapted by Catsky (1965). Samples were taken from second leaves on the primary shoot using one cm diameter leaf punchers. Two samples of identical discs were cut from each leaf with punchers a and b. Fresh weight of sample a was determined and dried in an oven for 48h at 80°C. A second sample b was weighed and allowed to float on water covered with plastic sheet to maintain saturation, under a low light flux density supplied from a warm white fluorescent lamp for 24h. The sample was then weighed and dried in an oven set at 80°C for 48h. Relative turgidity of the whole plant was calculated

as follows:-

$$\text{Relative turgidity} = \frac{FWa - DWa}{FWt - DWb} \times 100$$

where FWa = fresh weight disc sample a

DWa = dry weight disc a

FWt = weight disc b after floating on water for 24h

DWb = dry weight disc sample b

The plant water content was recorded in Table 62.

Total solar radiation in the glasshouse throughout the duration of the experiment was recorded with a Kipp's solarimeter. The daily mean radiation was found to be 13.8 MJ m^{-2} during the period of the experiment (Exp. 16).

8.3 (Exp. 7) Effects of water stress on flowering and fruit set

This experiment was a preliminary investigation to examine effects of water stress at three levels of watering, wet, medium and dry. Plants were subjected to treatments at the first appearance of the flowers formed at the tip of the primary shoot.

Results

Growth in dry weight of plant was markedly influenced by the watering regime adopted. Frequent watering significantly increased dry weight (Table 63b). No difference in the growth of dry weight due to medium watering and dry treatments was observed. A small but significant increase in diameter of stem was obtained with frequent watering (Table 63a).

Flowering behaviour was affected by water stress. A

Table 62 (Exp. 16) Water content of plants as determined by leaf-disc technique after Weatherley (1950 and 1962)

Relative turdigity (percent) of plants

Stage of plant development	Wet	Medium	Dry	Field capacity
Older	90.0	74.1	65.5	95.5
Younger	95.6	78.3	68.3	99.4

Table 63a (Exp. 7) Effects of water stress on diameter of stem. 10 plants per treatment (15.2.78)

Stem diameter (cm) (120 days after sowing)

Wet	Medium	Dry
1.5	1.2	1.2

LSD (P=0.05) = 0.2

Table 63b (Exp. 7) Effects of water stress on total plant dry weight. 10 plants per treatment (15.2.78)

Dry weight (g) of plant systems (120 days after sowing)

	Wet	Medium	Dry
Root dry weight (g)	14.3	10.44	6.05
Dry weight (g) of stem and leaves	25.98	15.96	20.18
Fruit dry weight (g)	7.02	3.5	1.57
Total plant dry weight (g)	47.3	29.9	27.8

LSD (P=0.05) total plant dry weight = 3.9

greater number of flowers was formed in plants receiving the wet treatment than the medium or dry treatments. Table 64a shows that the wetter the regime the greater the number of flower buds formed. The increase due to the wet treatment must have been due to a more rapid rate of development of successive generations of branches. Development of flowers from the time of their first appearance to opening was not affected by water stress since opening of the flowers at the tip of the primary shoot occurred at similar time in all plants.

Flower abortion was increased by water stress. Tables 64b and 64c indicate that the number and the percentage of flowers that aborted was markedly increased in the dry treatment.

The incidence of flower shedding was markedly reduced by frequent watering. A greater number of flowers opened in wet than medium or dry treatments (Table 64d), but fewer number of flowers were shed in wet than dry treatments (Table 64e). Table 64f shows that only 6.9 percent of flowers that opened were shed in plants in wet regime, whereas 39 and 36 percent of flowers in plants in the medium and dry regimes respectively were shed after opening. It is possible that failure of pollination due to non-viability of pollen may cause post-anthesis shedding in plants receiving infrequent watering.

Fruit set was influenced by the watering regimes. A greater number and percentage of flowers that opened in the wet regime set fruits than in the medium or the dry regime (Tables 65a and 65b). Fresh weight of fruits per plant was measured and Table 65c shows that fruit fresh weight was significantly increased in plants receiving frequent watering. Any difference

Table 64 (Exp. 7) Effects of water stress on flowering behaviour. 10 plants per treatment (15.2.78)

(a) Number of visible flower buds counted up to 115 days after sowing

Wet	Medium	Dry
209.7	93.0	40.3

LSD (P=0.05) = 45.5

	Wet	Medium	Dry	LSD (P=0.05)
(b) Number of flowers aborted per plant	1.7	13.7	16.9	3.6
(c) Percentage of flowers aborted per plant	1.0	14.7	41.9	

	Wet	Medium	Dry	LSD (P=0.05)
(d) Number of flowers opened per plant	33.3	19.7	14.7	8.1
(e) Number of flowers shed per plant	2.3	7.7	5.3	3.0
(f) Percentage of flowers shed per plant	6.9	39.1	36.1	

Table 65 (Exp. 7) Effects of water stress on fruit set and fresh weight of fruits. 10 plants per treatment (15.2.78)

	Wet	Medium	Dry	LSD (P=0.05)
(a) Number of fruits set per plant	14.3	3.3	1.9	4.1
(b) Percent of opened flowers that set fruit per plant	42.9	16.8	12.9	-
(c) Fresh weight (g) of fruits per plant	560.5	106.4	88.0	139.3

Table 66 (Exp. 13) Effects of water stress and night temperature on dry weight of shoot system. 10 plants per treatment (6.6.78)

Dry weight (g) of total shoot system per plant (97 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	32.37	20.62	18.21	23.73
25	24.13	17.09	12.24	17.82
Mean	28.25	18.86	15.23	

LSD (P=0.05) to compare watering means = 3.3
LSD (P=0.05) to compare temperature means = 2.7
Watering x night temperature interactions (P=0.05) Significant

between the fresh weight of fruit in the medium regime and in the dry regimewas not significant.

8.4 (Exp. 13) Effects of water stress and night temperature on flowering and fruit set

Results of the preliminary experiment (Exp. 7) indicated that flowering and fruit set were affected by frequency of watering plants. In the present experiment, effects of water stress whenplants were grown in 18° or 25°C night temperature on flowering and fruit set were investigated.

The timing of the experiment is shown in Table 61.

Results

Effects of water stress on growth in dry weight were similar to those reported in the previous experiment. Table 66 shows that growth in dry weight of shoot system up to 97 days after sowing was significantly greater in the wet than in the medium or the dry regime. An increase in leaf area due to frequent watering was obtained (Table 67b). It is not clear whether the increase was due to an increase in number of leaves or the size of leaves. Growing plant in the wet regime increased growth in diameter of the primary shoot as compared with medium or dry treatment (Table 67a).

As in Exp. 7, flower formation was affected by water stress and the effect of the wet regime in increasing number of flower buds formed was consistent. Table 68a shows that the number of flowers formed per plant was significantly increased by the wettest regime; the increase in number of flowers formed

Table 67a (Exp. 13) Effects of water stress and night temperature on diameter of stem. 10 plants per treatment (6.6.78)

Stem diameter (cm) (90 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	1.5	1.1	0.77	1.1
25	1.3	0.97	0.82	1.0
Mean	1.4	1.0	0.79	

LSD (P=0.05) to compare watering means = 0.12
LSD (P=0.05) to compare temperature means NS
Watering x night temperature interaction (P=0.05) NS

Table 67b (Exp. 13) Effects of water stress and night temperature on leaf area. 10 plants per treatment (6.6.78)

Leaf area (cm^2) per plant (95 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	3020.5	1283.5	854.8	**1719.6**
25	3159.0	1326.6	1246.4	**1910.7**
Mean	3089.8	1305.1	1050.6	

LSD (P=0.05) to compare watering means = 465.1
LSD (P=0.05) to compare temperature means NS
Watering x night temperature interaction (P=0.05) NS

Table 68a (Exp. 13) Effects of water stress and night temperature on flower formation. 10 plants per treatment (6.6.78)

Number of flower buds formed per plant (95 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	181.8	110.4	78.2	123.5
25	176.0	99.6	68.4	114.7
Mean	178.9	105.0	73.3	

LSD (P=0.05) to compare watering means = 25.7
LSD (P=0.05) to compare temperature means NS
Watering x night temperature means (P=0.05) NS

Table 68a (Exp. 13) Effects of water stress and night temperature on flower abortion. 10 plants per treatment (6.6.78)

Number of flowers aborted per plant (95 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	0.13	6.6	5.8	4.2
25	1.9	18.1	9.6	9.9
Mean	1.0	12.4	7.7	

in the medium regime as compared with the dry regime was significant.

The incidence of flower abortion was lower in the present experiment than in the previous experiment. Whereas only one or two flowers per plant failed to open in the wet treatment (Table 68b), 12 and 8 flowers aborted per plant in medium and dry treatments respectively. However, post-anthesis shedding was greater in the present experiment than in Exp. 7. Table 69a shows that the smallest number of flowers was shed in plants growing in the wet regime while the largest number was shed in dry regime. No effect of watering regime on fruit set was obtained (Table 69a). Table 69a shows that fresh weight of fruits was increased in the wet and the medium regimes as compared with the dry regime.

There was evidence that growing plants at a night temperature of 18°C as compared with 25°C resulted in an increase in growth. This was indicated by growth in dry weight of the shoot system which was smaller at 25°C than at 18°C (Table 66). No effect of night temperature on growth in diameter of the stem, leaf area (Tables 67a and 67b), flower formation (Table 68a) or flower development.

At a high night temperature of 25°C the incidence of post-anthesis flower shedding was greater than at a low night temperature of 18°C (Table 69b) except in the dry regime where no effect of night temperature on flower shedding was obtained. Fruit set was not affected by night temperatures but growth in fresh weight of fruits was markedly increased at 18°C night temperature (Table 69a).

Table 69a (Exp. 13) Effects of water stress and night temperature on fruit fresh weight. 10 plants per treatment (6.6.78)

Fresh weight (g) of fruits per plant with number of fruits set in brackets (95 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	248.1 (3.5)	107.3 (1.5)	27.9 (1.0)	127.8 (2.0)
25	34.6 (2.4)	29.1 (1.0	0	21.2 (1.6)
Mean	141.4 (3.0)	68.2 (1.3)	14.0 (0.5)	

Table 69b (Exp. 13) Effects of water stress and night temperature on post-anthesis shedding. 10 plants per treatment (6.6.78)

Number of flowers shed per plant (95 days after sowing)

Night temperature (°C)	Wet	Medium	Dry	Mean
18	9.8	31.0	50.4	30.4
25	31.5	46.2	46.0	41.2
Mean	20.7	38.6	48.2	

LSD (P=0.05) to compare watering means = 4.8
LSD (P=0.05) to compare temperature means = 8.3
Watering x night temperature interaction (P=0.05) NS

8.5 (Exp. 16) Effects of water stress and stage of plant development on flowering and fruit set

The results of previous experiments (Exps. 7 and 13) indicated that flowering and fruit set could be influenced by water stress. What was not known was the stage of development at which any effects of water stress became most critical. In the present experiment plants at anthesis of the first flowers (older plants) or 14 days before anthesis of first flowers (younger plants) were subjected to three regimes of watering for 15 days. Any effects of water stress and stages of plant development on flowering behaviour and fruit set were examined.

Results

Effects of watering treatments on flower development and fruit set were similar to those reported in Exps. 7 and 13. Tables 70a and 70b indicate a significant increase in flower abortion and post-anthesis shedding as the frequency of watering decreased. Whereas the number of flowers that aborted was reduced to about one in plants receiving the wet treatment, this number was increased to about 8 in the dry treatment and to about 5 in the medium treatment.

Frequent watering increased the number of fruits set (Table 71a) while both the medium and the dry regimes reduced the number of fruits set per plant by about 3. Any increase in fresh weight of fruits (Table 71b) due to the wet treatment was attributable to the increase in the number of fruits set rather than an increase in the rate of growth of individual fruits.

Table 70a (Exp. 16) Effects of water stress and stage of plant development on flower abortion. 12 plants per treatment (25.5.79, 5.6.79)

Number of flowers aborted per plant (15 days after treatments had commenced)

Stage of plant development	Wet	Medium	Dry	Mean
Older	0.33	2.8	6.1	3.1
Younger	0.77	7.5	9.3	5.9
Mean	0.55	5.2	7.7	

LSD (P=0.05) to compare watering means = 0.8
LSD (P=0.05) to compare plant age means = 0.6
Watering x plant age interaction (P=0.05) = 1.1

Table 70b (Exp. 16) Effects of water stress and stage of plant development on post-anthesis shedding. 12 plants per treatment (23.5.79, 5.6.79)

Number of flowers shed per plant (108 days after sowing)

Stage of plant development	Wet	Medium	Dry	Mean
Older	0.67	6.3	6.8	4.6
Younger	1.3	6.6	7.4	5.1
Mean	0.99	6.45	7.1	

LSD (P=0.05) to compare watering means = 0.8
LSD (P=0.05) to compare plant age NS
Watering x plant age interaction (P=0.05) NS

Table 71a (Exp. 16) Effects of water stress and stage of plant development on fruit set. 12 plants per treatment (23.5.79, 5.6.79)

Number of fruits set per plant (108 days after sowing)

Stage of plant development	Wet	Medium	Dry	Mean
Older	7.2	2.5	2.6	**4.1**
Younger	1.8	0.75	0.36	**0.97**
Mean	4.5	1.6	1.5	

LSD (P=0.05) to compare watering means = 0.5
LSD (P=0.05) to compare plant age means = 0.4
Watering x plant age interaction (P=0.05) = 0.8

Table 71b (Exp. 16) Effects of water stress and stage of plant development on fresh weight of fruits. 12 plants per treatment (23.5.79, 5.6.79)

Fresh weight (g) of fruits per plant (108 days after sowing)

Stage of plant development	Wet	Medium	Dry	Mean
Older	421.4	213.7	216.0	**283.7**
Younger	255.7	83.5	43.0	**127.4**
Mean	338.6	148.6	129.5	

LSD (P=0.05) to compare watering means = 37.2
LSD (P=0.05) to compare plant age means = 30.4
Watering x plant age interaction (P=0.05) NS

The effects of water stress were greater in the younger than the older plants. Table 70a shows that number of flowers that aborted per plant up to 15 days after watering treatments had commenced was greater in the younger than the older plants. This increase in flower abortion was significant at the medium and the dry regimes.

Fruit set was generally low in the present experiment and as it would be expected, the number of fruits set per plant was greater in the older than in the younger plants (Table 71a); there was little evidence that water stress was more effective in reducing fruit set in the younger than the older plants. A significant effect of the dry treatment as compared with the wet regime to reduce fresh weight of fruits was observed to be greater in the younger than the older plants (Table 71b).

8.6 Discussion

The results of experiments reported here indicated that growth in dry weight of the shoot system was greatest in a wet regime. The reductions in dry weight due to the medium and dry regimes is not consistent with the view of some previous workers (Veihmeyer and Hendrickson, 1950) that plant growth is unaffected by soil moisture stress until the permanent wilting percentage is attained.

Watering regimes that keep the soil close to field capacity have been shown to favour growth in dry weight of plants of tomato (Salter, 1954, 1957 and 1958; Gates, 1955; Abdelhafeez and Verkerk, 1969), snap beans (Maurer, Ormrod and Scott, 1969) and sugar beet (Milford and Lawlor, 1975). However, Chmela and

Vlcek (1974) could not obtain any increase in dry weight of sweet pepper plants grown in a wet regime and Owen (1958) could not obtain any significant reduction in dry matter production when sugar beet, broad beans and lettuce plants were grown in dry regimes in the glasshouse.

The increase in growth in dry weight of plants grown close to the field capacity may be attributable partly to an increase in water-use efficiency. A support for this view was provided by Manning, Miller and Teare (1977) who reported that maintaining plants of peas at constant low moisture regimes, significantly reduced the water-use efficiency. They concluded that reductions in total plant growth accounted for the decline in water-use efficiency.

Any increase in the rate of production of successive branches in sweet pepper means that number of flower buds formed will be increased. The promotion of flower bud formation due to the wet treatment must be attributed to the more rapid formation of branches. A similar effect of the high moisture treatment to increase the number of flower buds formed in pepper was obtained in the glasshouse by Cochran (1936).

It is evident that the incidence of flower abortion was markedly affected by water stress. Greatest abortion occurred in the driest regime. Similarly post-anthesis shedding was increased as moisture content decreased. Failure of pollination due to reduced moisture content in plant may have caused dropping of flowers shortly after they had opened. Abdelhafeez and Verkerk (1969) found that the numbers of shed flowers were higher at the dry than the wet regimes.

Fruit set was influenced by water stress. The number of fruits set per plant was consistently increased by the wet treatment. Increases in the number of fruit set were accompanied by increases in growth in dry weight of the shoot, leaf area and plant height. These results suggest that increase in vegetative development may promote fruit set by increasing the availability of assimilates. In his work on the effects of different water regimes on vegetative growth and fruit development in the tomato, Salter (1958) could only obtain a small fruit set with greatest vegetative growth under conditions of high soil moisture.

The stage of development at which the plant was subjected to water stress had marked effects on flower development. Although there was only 14 days between the younger and the older plants, the incidence of flower abortion and post-anthesis shedding was more marked in the younger plants grown in the dry regime than in the older plants grown in the same watering regime. Effect of the dry treatment on fruit set in the younger and older plants was not clear, but growth in the fresh weight of fruits was significantly reduced in the younger plants grown in the medium and dry regimes as compared with the older plants grown in the medium and dry regimes.

A high percentage of flower abortion and post-anthesis shedding occurred at 18^{o} or $25^{o}C$ night temperature especially at the dry regimes. It is possible that increases in flower abscission were due to excessive respiration. This view was strengthened by the increase in flower abscission which was accompanied by a reduction in the growth of dry weight. Similar

effects of high night temperatures to increase incidence of flower abscission have been reported in tomato (Abdelhafeez and Verkerk, 1969).

8.7 Summary

(1) Growth in shoot dry weight, leaf area and stem diameter were increased by frequent watering.

(2) The incidence of flower abortion and of post-anthesis shedding were increased as water stress increased.

(3) The number of fruits set per plant was greater in a wet than in a dry regime.

Chapter 9

General Discussion

The purpose of this discussion is to consider together results of experiments reported in the previous chapters. The objective of the experiments was to study stages of reproductive development in sweet pepper including the onset of flower initiation, post-initiation development of flowers and fruit set.

The methods adopted for growing the plants were designed to allow control of a number of environmental conditions including night temperature and photoperiod. During the daytime plants were grown in the glasshouse in pots on trolleys; during the "night" period they could be moved to dark rooms in which different temperatures could be maintained and different photoperiodic lighting treatments imposed. These methods allowed plants to be grown up to the time that fruits were developing at the tip of the primary shoot and on the first one or two generations of branches (3-5 months after sowing the seed). The experiments were terminated at this stage or earlier in order to avoid too great a limitation of growth due to the size of pot used and in order to allow adequate numbers of plants to be grown in the space available in the glasshouse. It followed that data obtained on fresh weight or dry weight of fruit produced in the experiments could indicate the potential yield from the plant in the earlier stages of reproductive development but could not be accepted as indicative of potential total yield

over the normal duration of a pepper crop. The experiments allowed direct examination of factors affecting the change from vegetative to reproductive development that occurred with the initiation of flowers at the tip of the primary shoot, of factors leading to abortion of the flowers before they reached anthesis and of treatments that affected fruit set in the first few flowers to open on the plants.

The time of initiation of flowers at the tip of the primary shoot, as determined by dissection and microscopic examination, was affected by radiant exposure and by night temperature. High radiant exposures and high night temperatures reduced the duration of the vegetative phase of development. The use of high flux artificial illumination to supplement day light in the winter hastened flower initiation by 20-30 days while shading to reduce total radiation by about 60 percent in the summer delayed the initiation of flowers by about 10 days.

Evidence was consistent that the time to the first appearance of flower buds was increased by low radiant exposures while the number of leaves formed before initiation of the first flowers was generally increased by one or two. Night temperatures of 20°C as compared with 13°C hastened flower initiation, reduced the number of leaves formed before flowers were initiated by one or two and hastened the first appearance of flower buds.

The treatments providing relatively high radiant exposure and a relatively high night temperature had in common that they promoted the growth in dry weight of the shoot system, increase in leaf area and growth in height. Thus it was possible that the treatments affected the duration of the vegetative phase

through effects on growth rates or growth relationships within the plant. This hypothesis assumes an internal mechanism controlling the onset of flowering such that flower initiation occurs when the plant attains a particular size or when a particular relationship is established between the growth of different parts. The experimental evidence suggested that the number of leaves formed might be important in determining the onset of flowering in that this number did not vary by more than one or two with the treatments applied. Nevertheless a high night temperature and high radiant exposures generally produced small reductions in leaf number to flower so it is unlikely that the number of leaves formed represented a simple determining factor. It appears more probable that some other aspect of development related to increase in leaf number and increase in dry weight exerted a controlling influence on flower initiation. Increases in apical size (Hussey, 1963a; Calvert, 1969) or increases in photosynthetic leaf area might be of importance. Klapwijk and de Lint (1975) observed that in tomato plants grown under conditions where water and nutrients were unlikely to be limiting to growth, stages of reproductive development were correlated with growth in fresh weight of the shoot system, but how far such a correlation occurred in sweet pepper was not determined.

Differences in photoperiod had less effect on the duration of the vegetative phase than did differences in radiant exposure or night temperature. Extension of the day by low intensity illumination from tungsten filament lamps delayed flower initiation by a few days and generally increased the

number of leaves formed on the primary shoot by one or two. This result was consistent with the observations reported by Cochran (1936) but not with those reported by Rylski (1972). Rylski found that pepper plants grown in short days of 7h duration produced more leaves below the first formed flowers than plants grown in long days of 17h duration. One explanation of the apparent difference in results is that Rylski employed a relatively high irradiance (2700 lux from fluorescent and incandescent lamps) for her long day treatment so that effects of photoperiod and effects of total incident radiation could have been confounded.

On the basis of the results obtained in the experiments employing tungsten filament lamps to extend the day it might have been concluded that sweet pepper was a quantitative short day plant. Wittwer (1963) classified tomato as a facultative short day plant because extension of a 9h photoperiod by low intensity artificial illumination led to small increases in the number of leaves formed below the first inflorescence. However, further experiments conducted here with pepper indicated that the quality of light used to extend the day was important in determining the effects of photoperiod.

Extension of the day with "warm-white" fluorescent lamps failed to produce any delay in flower initiation or any increase in the number of leaves on the primary shoot. Furthermore night break treatments of 2h duration employing either tungsten filament lamps or warm white fluorescent lamps were also ineffective in delaying flowering. These results were not typical of short-day plants in general (Vince-Prue, 1975) and in view of

the importance of radiant exposure and temperature in determining the onset of flowering it can be argued that sweet pepper is best classified as a day-neutral plant.

Once flowers had been initiated at the tip of the primary shoot branching of the plants occurred and further flowers were produced at the tips of successive generations of branches. During this phase of development it appeared that high rates of growth in dry weight were associated with the rapid production of branches and of flowers. High rates of growth in dry weight of the shoot produced by high radiant exposures, by high night temperatures or by frequent watering of the growing medium were generally associated with a relatively rapid appearance of flower buds. Long photoperiods involving extension of the day by the use of tungsten filament lamps had little or no effect on the rate of formation of flowers once the vegetative phase of growth had been completed.

Flowers, once initiated, did not necessarily continue their development to anthesis; a proportion stopped growing in the bud stage and aborted. It appeared that for continued development the flowers were dependent on a supply of carbon assimilates and that a shortage of assimilates led to flower abortion. The incidence of abortion was always very high when plants were shaded during the summer. Presumably under these conditions rates of photosynthesis were limited by the low radiation levels while the relatively high temperatures then occurring would have led to increased rates of utilisation of assimilates in respiration and in synthetic processes. High night temperatures led to increases in the incidence of flower

abortion and it is possible that this again reflected a shortage of carbon assimilates due to relatively high rates of utilisation in the floral tissues.

Pruning treatments that limited the number of branches on each plant reduced the number of flower buds that formed but increased the percentage of buds that continued development to full opening. This effect may be explained if in the early stages of their development branches compete for carbon assimilates supplied from leaves below. Pruning would have the effect of reducing this competition and increasing the supply of carbon assimilates available to each branch. Long day treatments that employed lighting from tungsten filament lamps may have also affected flower abortion through effects on competition for assimilates. Increases in the incidence of flower abortion due to these treatments were accompanied by increased growth in length of the stems. The promotion of stem growth may have diverted assimilates away from the flowers. It has been suggested that flower abortion in tomatoes occurs as a result of competition for carbon assimilates between the inflorescence and vegetative organs of the plant (Cooper and Hurd, 1968; Calvert, 1969; Kinet, 1977a).

An alternative explanation of the effect of the long day treatments is suggested by experiments concerned with flower abortion in *Phaseolus vulgaris* (Ojehomon *et al.*, 1968, 1973; Bentley *et al.*, 1975; Zehni and Morgan, 1970, 1976). It has been claimed that in this plant, illumination from tungsten filament lamps may promote the formation of growth inhibiting substances and possibly abscisic acid, which can induce abortion

of the flower. In the experiments conducted here flower abortion in sweet pepper increased when high moisture tensions were allowed to develop in the growing media. In other plants shortage of water has been shown to lead to increases in levels of endogenous abscisic acid (Hsiao, 1973). It is possible that water stress affected flower abortion in sweet pepper by acting on levels of endogenous growth substances and in particular of abscisic acid.

The study of fruit set in sweet pepper is complicated by the common occurrence of parthenocarpy in this plant (Rylski, 1974; Charles, Amirouche and Malaoui, 1979). In the experiments reported here as in those reported by Rylski (1974) the incidence of parthenocarpy was found to be high when plants were grown at low night temperatures about the time of anthesis. Thus in sweet pepper failure of pollination and fertilization did not necessarily mean failure of fruit set; even in the normal temperature regime of the glasshouse (16^{o}C at night) emasculation of flowers did not prevent fruit growth and development although the parthenocarpic fruits produced were generally smaller than those produced from entire flowers.

Under some conditions flowers opened and were then shed with the formation of an abscission layer at the base of the pedicel. Presumably these were conditions unfavourable for pollination or fertilization and also for parthenocarpic fruit development. The percentage of open flowers that were shed was high when radiant exposures were low (see Exps. 21, 25 or 26), when night temperatures were high and when high moisture tensions were allowed to develop in the growing medium. Increased flower

shedding in tomato has been observed in response to high night temperatures and shortage of water (Abdalla and Verkerk, 1968; Abdelhafeez and Verkerk, 1969).

Under winter conditions when the number of flowers that set fruit was low an application of β-naphthoxyacetic acid as a spray applied to run off increased the number of fruits set. NOA has been found to be effective in increasing fruit set in a number of other plants under conditions unfavourable to pollination (Kepcka, 1966; Nothmann and Koller, 1975).

When sweet pepper plants were pruned to limit the number of branches that developed, the proportion of flowers that set fruits was increased and, more surprising, the number of fruits that set per plant was also increased. An increase in the proportion of flowers that set fruit might have been expected in view of the reduced number of flowers that were allowed to develop but the increases in the number of fruits set per plant suggests that the pruning treatments may have produced conditions favourable to fertilization. The possibility of pruning acting through intraplant competition for assimilates has already been discussed in relation to flower abortion. A reduction in this competition could have favoured pollination perhaps by leading to the production of larger quantities of viable pollen. In tomato plants grown in the winter fruit set has been found to be limited by the amount of viable pollen produced (Verkerk, 1957).

It has already been pointed out that the experiments conducted here did not continue beyond the time when the first few fruits were reaching maturity. Within the limited periods studied the fresh weight of fruits produced was found to be

increased by high radiant exposures, high night temperatures, frequent watering of the growing media and by pruning the plant to reduce the number of leading shoots. The experiments concerned with the effects of these various treatments indicated that high radiant exposures probably increased the early yield of fruit through effects on all stages of reproductive development. These included hastening of first flower initiation, increasing the rate of formation of further flowers (Keyes, 1940), reducing the incidence of flower abortion and increasing the incidence of fruit set. How far rates of growth of individual fruits were increased was not determined. Osborne and Went (1953) observed that a reduced light intensity was generally unfavourable for maximum fruit set and fruit growth in the tomato.

There was evidence that water stress might limit early yield of fruit by reducing the rate of formation of flowers (Cochran, 1936), by increasing flower abortion (Addicott and Lynch, 1955) and reducing fruit set (Abdelhafeez and Verkerk, 1969). Effects of different watering regimes on the time of change from vegetative to reproductive growth were not studied.

Delays in the formation and opening of flowers were probably a major factor in determining the reduction in fruit production brought about by low night temperatures. Reductions in rates of fruit growth may also have been important but this probability was not discussed in the experiments here. Kato and Tanaka (1971) found that the higher the night temperature in the range 16^{o}-22^{o}C, the more rapid the rates of fruit growth. Increases in the weight of fruit produced due to pruning appeared

to be associated with increases in the number of flowers per plant that set fruit.

General Summary

A study was made of factors affecting flowering and fruit set in sweet pepper plants grown from seed. The duration of the initial vegetative phase of growth was prolonged when radiant exposures were low, as in the winter or when shading was used in the summer. The change from vegetative to reproductive development was also delayed by a reduction in night temperature from 20°C to 13°C. It is suggested that radiant exposure and night temperature affected flower initiation through effects on the rate of growth and development of the whole plant rather than on processes specific to the control of flowering.

In experiments designed to increase the responses of sweet pepper plants to differences in photoperiod, results varied with the sources and timing of illumination used to provide the long-day treatments. Extension of an 8h day to 18h by the use oflow intensity illumination from tungsten filament lamps delayed flower initiation by a few days but when warm-white fluorescent lamps were used to extend the day the time to flower initiation was unaffected.

A proportion of the flowers initiated stopped growing in the bud stage and aborted. Conditions found to be conducive to flower abortion were low radiant exposures, high night temperatures, long-day treatments produced by the use of tungsten filament lamps and infrequent watering.

Pollination and fertilization were not prerequisities for fruit set since parthenocarpic fruit development could occur.

The incidence of parthenocarpy was high when night temperatures were low. Low radiant exposures, high night temperautres and infrequent watering were unfavourable to fruit set and led to increases in the proportion of flowers that were shed after opening. Under some conditions the proportion of open flowers that set fruits could be increased by pruning plants to reduce the number of leading shoots or by spraying with β-naphthoxy-acetic acid.

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APPENDIX

Statistical Analyses

Examples of the analysis of variance used to test the significance of treatment effects are presented here. Least significant differences between treatment means were calculated to assess the significance of the effects of various levels of the applied treatments.

Abbreviations used in the appendix are as follows:

d.f	Degrees of freedom
s.s	Sums of squares
m.s	Mean square
F	Variance ratio
*	Significant at the 0.05 level of probability
**	" " " 0.01 " " "
***	" " " 0.001 " " "
n	Number of replicates of treatments
LSD	Least significant difference between two means
NS	Not significant

(Exp. 8) Effects of photoperiod, radiant exposure and pot size

Total shoot dry weight (g) per plant

	Source of variation	d.f	s.s	m.s	F
1	Blocks	3	294.42	98.14	1.33 NS
2	Radiant exposure	1	2079.02	2079.02	28.2*
	Error A	3	221.52	73.84	
4	Pot size	1	2971.71	2971.71	106***
5	Photoperiod	2	342.50	171.25	6.12*
6	Radiant exposure x pot size	1	498.07	498.07	17.8***
7	Radiant exposure x photoperiod	2	26.49	13.24	0.47 NS
8	Pot size x photoperiod	2	80.42	40.21	1.44 NS
9	Radiant exposure x pot size x photoperiod	2	1.79	0.79	0.03 NS
	Error B	30	839.91	28.00	
	Total	47	7355.85		

Standard error for comparing any two treatment means:

$$= \sqrt{\frac{2 \times \text{error B m.s}}{n}}$$

$$= \sqrt{\frac{2 \times 28.00}{4}}$$

$$= 3.74$$

LSD:

"t" value 30 d.f P=0.05 = 2.04

LSD = 3.74 x 2.04

= 7.63

(Exp. 8) Effects of photoperiod, radiant exposure and pot size

Number of days from sowing to the first appearance of the flower buds

Source of variation	d.f	s.s	m.s	F
Blocks	3	69.51	23.17	2.17 NS
Radiant exposure	1	3445.77	3445.77	322.0***
Error A	3	32.06	10.69	
Pot size	1	0.0088	0.0088	0.003 NS
Photoperiod	2	597.31	298.65	81.6***
Radiant exposure x pot size	1	0.15	0.15	0.04 NS
Radiant exposure x photoperiod	2	75.87	37.93	10.4**
Pot size x photoperiod	2	0.502	0.25	0.07 NS
Radiant exposure x pot size x photoperiod	2	1.76	0.88	0.24 NS
Error B	30	109.73	3.66	
Total	47	4332.66		

Standard error for comparing any two treatment means:

$$\sqrt{\frac{2 \times \text{error B m.s}}{n}}$$

$$= \sqrt{\frac{2 \times 3.66}{4}}$$

$$= 1.35$$

LSD:

"t" value d.f 30 P=0.05 = 2.04

LSD = 1.35 x 2.04

= 2.8

(Exp. 3) Effects of photoperiod and shading

Number of flower buds formed per plant

Source of variation	d.f	s.s	m.s	F
Blocks	2	0.447	0.22	0.084 NS
Photoperiod	1	306.84	306.84	114.86***
Shading	1	1916.73	1916.73	717.49***
Photoperiod x shading	1	22.2	22.2	8.31*
Error	6	16.03	2.67	
Total	11	2262.24		

Standard error for comparing any two treatment means:

$$\sqrt{\frac{2 \times \text{error m.s}}{n}}$$

$$= \sqrt{\frac{2 \times 2.67}{3}}$$

$$= 1.33$$

LSD :

"t" value d.f. 6 P=0.05 = 2.45

LSD = 1.33 x 2.45

= 3.26

(Exp. 2) Effects of night temperature and radiant exposure

Number of days from sowing to opening of the flowers at the tip of the primary shoot

Source of variation	d.f	s.s	m.s	F
Blocks	2	0.22	0.11	0.19 NS
Night temperature	1	1275.14	1275.14	200.0***
Radiant exposure	1	149.11	149.11	260.0***
Night temperature x radiant exposure	1	0.301	0.301	0.52 NS
Error	6	3.44	0.57	
Total	11	1428.21		

Standard error for comparing any two treatment means:

$$\sqrt{\frac{2 \times \text{error m.s}}{n}}$$

$$= \sqrt{\frac{2 \times 0.57}{3}}$$

$$= 0.62$$

LSD:

"t" value d.f 6 P=0.05 = 2.45

LSD = 0.62 x 2.45

= 1.51

(Exp. 25) Effects of night temperature, shading and shoot pruning

Mean fresh weight (g) of fruit

Source of variation	d.f	s.s	m.s	F
Night temperature	1	233.64	233.64	0.54 NS
Shading	1	5616.23	5616.23	13.1*
Error A	1	428.76	428.76	
Shoot pruning	1	621.28	621.28	4.61*
Night temperature x pruning	1	824.86	824.86	6.12*
Shading x pruning	1	649.8	649.8	4.82*
Temperature x shading x pruning	1	792.68	792.68	5.88*
Error B	64	8620.98	134.7	
Total	71	17788.23		

Standard error for comparing any two treatment means:

$$\sqrt{\frac{2 \times \text{error B m.s}}{n}}$$

$$= \sqrt{\frac{2 \times 134.7}{9}}$$

$$= 5.47$$

LSD:

"t" value d.f 64 P=0.05 = 2

LSD = 5.47 x 2

= 10.94

(Exp. 26) Effects of shoot pruning and shading

Number of flowers that aborted per plant

Source of variation	d.f	s.s	m.s	F
Blocks	5	7.98	1.6	0.45 NS
Shading	1	200.08	200.08	56.6***
Error A	5	17.67	3.53	
Shoot pruning	3	189.94	63.31	40.4***
Shading x pruning	3	49.29	16.43	10.5***
Error B	30	47.02	1.57	
Total	47	511.98		

Standard error for comparing any two treatment means:

$$\sqrt{\frac{2 \times \text{error B m.s}}{n}}$$

$$= \sqrt{\frac{2 \times 1.57}{6}}$$

$$= 0.72$$

LSD:

"t" value d.f 30 P=0.05 = 2.04

LSD = 2.04 x 0.72

= 1.47