A STUDY OF THE EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON VEGETATIVE GROWTH AND SEED PRODUCTION OF LEAF LETTUCE (*LACTUCA SATIVA* L.)

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LETTUCE SEED HEAD

ABSTRACT

Three leaf lettuce (Lactuca sativa L.) cultivars, Thai, Grand Rapids and Slobolt were grown in a controlled environment at either 25/15°C or 30/20°C day/night temperatures and at 10, 12 or 14 hours daylength. Leaf fresh weight, dry weight, leaf area and leaf number all increased with increasing temperature and photoperiod. Slobolt produced a higher vegetative yield than Thai and Grand Rapids. Long days and high temperatures hastened stem elongation. Flowering in Thai and Grand Rapids was mainly influenced by high temperature whereas Slobolt required both high temperatures and long days. Slobolt however, was considerably delayed in bolting and flowering compared with the other two cultivars.

Lettuce plants showed two definite flowering peaks over a 50 -day flowering period. Slobolt produced only one peak at 25/15°C due to its slow bolting character.

Seed development studies were carried out on plants grown in both the 25/15°C and 30/20°C temperature regimes and at 12 hours daylength. The higher temperature regime hastened seed maturity, germination and shattering. Lettuce seed reached physiological maturity 11 days after anthesis at 30/20°C and 13 days after anthesis at 25/15°C, when the seed head had just begun to turn brown-green. Germination capacity also reached its maximum at this stage. Shattering however, occurred about two days after seed maturity at 20% moisture content at 30/20°C and 4 - 5 days later at 25/15°C.

The three lettuce cultivars used in this study produced seed successfully in all treatments. Optimum time of harvest was found to occur when the majority of seed heads had turned slightly brown in colour and was also reduced by higher temperatures and longer daylengths due to earlier bolting and flowering. Highest seed yield was obtained under long days (14 hours). Grand Rapids produced higher seed yields than Thai and Slobolt.

High seed yield was related to increased branch and flower numbers, percentage of seed set or seed numbers per head and time of harvest. Good seed set was obtained only under longer daylengths at high temperature while at 25/15°C, daylength was relatively unimportant. Final seed germination was unaffected by temperature or daylength. Practical application of the results which are relevant to Thailand conditions are discussed.

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INTRODUCTION

Leaf lettuce is the most popular salad crop in Thailand. It is grown commercially throughout the year and is produced for both the local market and for home use in areas throughout the country. Its production and consumption have risen markedly over recent years in line with population increases.

Leaf lettuce is early maturing and easy to grow. It develops best during the cool months when the rainfall is moderate. The cool months are always associated with the "dry season" in Thailand, making them also suitable for seed production. However, profit is a major concern to Thai farmers, who prefer to concentrate on growing lettuce for market consumption with its associated quick financial return, rather than for seed. Most of the lettuce seed sown in Thailand is imported, although some small quantities of seed are produced in the country.

Since leaf lettuce is not adapted to long distance shipment or transport, those areas at great distance from the market are possibly better suited to seed production rather than attempting to supply the fresh market. Some seed growers have tried to produce lettuce seed but have generally been discouraged by low seed yields and quality. It is likely that this disappointing return from seed production in leaf lettuce has occurred through lack of information about the desirable agronomic conditions and requirements for maximising seed yield. If seed growers could overcome these difficulties, lettuce seed production in Thailand might be more socially acceptable and financially successful.

A number of investigators have studied lettuce production from the view point of enhancing seed stalk formation and flowering or devising methods of treating lettuce plants to make them flower. Although early observations suggested a photoperiodic effect in lettuce (Garner and Allard, 1920; Tincker, 1933), it has been subsequently shown that the photoperiod response is conditioned by temperature (Robert and Struckmeyer, 1938). Higher temperatures accelerate bolting and flowering while long days promote and short days delay reproductive development (Thompson and Knott, 1933; Krickl, 1954; Rappaport and Wittwer, 1956,a,b; Raleigh, 1959; Ito et al., 1963; Cytovic, 1967a; Hiraoka, 1967, 1969).

Jones (1927) and Soffer and Smith (1974a) reported that lettuce showed a definite peak flowering and suggested that either temperature or light intensity might influence the flowering pattern. Best seed set has been observed at night temperatures between 17 - 23°C under short days after induction under long days (Koller, 1962), although seed maturity is hastened by high temperatures (Jones, 1927; Globerson, 1981). Difficulties in the germination of lettuce seeds have also been reported by Borthwick and Robbins (1928) and by Harrington and Thompson (1952) but can be overcome by using only fully mature seed (Thompson, 1936), since maximum seed germination capacity is normally reached one or two days before seed maturation (Globerson, 1981).

Although these factors undoubtedly affect seed yield and quality, the time of harvest can also be important. Seeds produced from early-formed flowers are heavier than those produced later in the season (Soffer and Smith, 1974a). By delaying harvest much of the seed yield can be lost because of shattering (Hawthorn and Pollard, 1954). Larger seeds also emerge faster and produce more vigorous seedlings (Smith et al., 1973b).

Under commercial harvesting conditions, the entire crop is handled at the one time. As a result, plants have a seed population that has been exposed to different weather conditions for varying periods of time and also bear seeds which are at different stages of seed maturity. This can result in significant differences in seed quality.

Little work has been carried out on the effect of environment on lettuce seed production, particularly with leaf lettuce. However, the environment includes so many interrelated factors that it is often difficult to determine the major factor or factors affecting plant growth and development. This suggests that in attempting to separate and analyse these environmental factors effectively, it is often necessary to conduct experiments under controlled environment conditions.

The objectives of this study were to determine how variation in temperature and photoperiod affected vegetative growth, flowering and flowering pattern, seed development, seed yield and seed quality in leaf lettuce cultivars. The alternating temperatures and ranges of daylength used were chosen to simulate as closely as possible the types of environmental range likely to be experienced in Thailand. Attempts were also made to determine the optimum time of harvest to ensure high seed yield and quality. The cultivars used in this experiment were chosen because of their similarity to local lettuce cultivars used in Thailand. Three cultivars (Thai, Grand Rapids and Slobolt) were chosen for further study following initial screening trials on a number of different leaf lettuce cultivars.

CHAPTER 1

REVIEW OF LITERATURE

The amount of work on lettuce cited in the literature is quite large. The majority of this work, however, has concentrated on the reaction of lettuce plants to environmental factors - particularly to daylength and to temperature. Much of this work has critically examined the reaction of lettuce to these variables during vegetative growth and their effect on the determining the onset of floral initiation.

Comparatively little work has been published which has critically evaluated the influence of environment on seed development or effects of environmental conditions on seed yield, yield components and seed quality.

A knowledge of the conditions which predetermine flowering and seed formation is useful in the successful production of lettuce seed. Bolting or premature seeding in lettuce is a common source of loss since it destroys market acceptability and therefore the value of the vegetative plant. Nevertheless this characteristic is a natural one which is essential for the production of seed.

Lettuce growing demands close attention to detail as regards cultural methods, while climatic conditions also play a very important part. The culture of lettuce for market use does not involve the production of the inflorescence and seed. Seed growers, by contrast, have to carry their crops through a further stage of growth in order to obtain a saleable product (Hawthorn and Pollard, 1954).

1. General Description of Lettuce (*Lactuca sativa* L.)

Lettuce has been in cultivation for at least 2500 years. Its origin is believed to be in inner Asia Minor, Iran and Turkistan (Durst, 1915; Hedrick, 1919). It is an annual which belongs to the sunflower family or Compositae family (McCollum, 1980) and is one of about 300 species (Koster, 1976) in the genus Lactuca (milk-forming).

There are six morphological types of lettuce; crisphead, butterhead, cos, leaf, stem and latin (Thompson, 1944; Rodenburg, 1960). The leaf or bunching cultivars (*Lactuca sativa* var. crispa) are grown principally in the tropics. They do not form heads but develop a more open type of growth. They are early producers, and are easy to grow under adverse conditions especially in summer (Herklots, 1972; Ryder, 1979). Better known cultivars in this group include Black Seeded Simpson, Grand Rapids, Prize Head, Domineer, Ruby, Salad Bowl and Slobolt (Shoemaker, 1953; Herklots, 1972; McCollum , 1980).

Lettuce requires a long warm growing season and a low rainfall at harvest time. Most cultivars grow best at mean maximum day temperatures of about 22°C, but cool nights are essential (Whitaker *et al.*, 1974). The leaf lettuce, however, grows more successfully all year round and is not heat sensitive (Herklots, 1972; Ryder, 1979).

Cultivated lettuce (*Lactuca sativa* L.) is a quantitative long-day plant at high temperature and is day neutral at low temperatures (Vince-Prue, 1975). Seed-stalk development is influenced primarily by high temperature (21-26° C) and photoperiod is less effective in affecting seed formation (Thompson and Knott, 1933). Long days (16 h) promote seed-stalk development while short days (9 h)delay it in Great Lakes head lettuce (Rappaport and Wittwer, 1956a).

The inflorescence is a panicle consisting of a cluster of heads, each containing from 15 to 25 or more florets. The head which terminates the inflorescence is the oldest. Secondary or lateral heads arise later in the axils of the leaves (Hawthorn and Pollard, 1954). The lateral branches also have terminal flowers which are the first to open on their respective branches. Position on the inflorescence is generally not related to flowering time (Soffer and Smith, 1974a).

The flowers are perfect and the yellow corolla is sympetalous and five lobed. There are five stamens, each attached separately at the base of the corolla tube. The anthers are united to form a sheath. The ovary is one-celled, inferior, and contains two carpels. The style is bi-lobed. The fruit is a one-seeded achene with a tuft of hairs attached (Jones, 1927). The seed is a spindle form with a number of longitudinal ribs on the surface (Isely, 1947).

Cultivated lettuce is almost entirely self-pollinated but 1 - 6 percent cross pollination by insects has been reported (Thompson, 1934). The flowers are generally open for only 1-2 h each day. However, on bright days they may only be open for half an hour whereas on cool cloudy morning they may remain open for several hours (Jones, 1927).

Flowering continues on a single plant over a fairly long period and shows definite peaks. Over 90% of the seed yield comes from flowers which open during the first 35 days (d) Soffer and Smith, 1974a). Seeds are ripe within 12-13 and 17 d after anthesis from plants harvested at 20°C and 25°C, respectively (Jones, 1927; Globerson, 1981). Best seed set has been reported at night temperatures between 17 and 23°C under short day (8 h) conditions (Koller, 1962). The number of normally developed achenes averaged 16.2 seeds/head (Jones, 1927).

In general, the leaf types of lettuce produce much more seed than do the heading types. Respective average seed yields of 500 kg/ha and 100 kg/ha have been reported (Hawthorn and Pollard, 1954).

Germination of lettuce seed is inhibited by high temperatures. The optimum for germination is a constant temperature of about 24°C. Above 26°C germination is increasingly inhibited (Borthwick and Robbins, 1928).

2. Temperature and Photoperiod Effects on Growth and Development

Since the cultivation of lettuce under glass is of great importance during the winter period, many experiments have been carried out with the purpose of obtaining optimal growth under variable conditions of temperature, photoperiod and light intensity. Major emphasis in this research has been placed on butterhead lettuce.

Brouwer and Huyskes (1968) studied the behaviour of plants of the cultivar Rapide and the hybrid Rapide x Hamadan, grown in controlled climate rooms, at a temperature of 20°C and under two daylengths (8 or 16 h) each combined with three light intensity levels, and under a 12 h daylength with one light intensity. Both cultivars responded to increasing light intensity more effectively when grown under long day conditions than short days. Growth rates increased with increasing light intensities in all cases. Bensink (1958, 1961, 1971) explored the influence of temperature, daylength, light intensity and other factors on the growth of butterhead cultivars Meikoningen and Rapide in growth rooms. Leaf production was approximately constant, the rate of production increased with increasing light intensity at a constant temperature and with increasing temperature at a constant light intensity. Leaf width and length both responded positively to increasing daylength and light intensity but leaf length was more responsive than leaf width to changes under low light levels or under short days. Subsequent development under high light intensity or under long day conditions, resulted in the leaves becoming successively broader. Low light intensity and short days tended to maintain the production of relatively long narrow leaves. The effect of temperature was also dependent upon light intensity. At high light levels, there was a positive effect on leaf width with inceasing temperature and negative effect at low light intensity. Likewise, Bierhuizen et al. (1973) demonstrated that a rapid linear rise in fresh weight occurred with an increase in radiation and high temperature. Time to full plant development which makes it suitable for harvest also depended on subsequent total radiation. In contrast leaf numbers and leaf area of head lettuce cv. Blondie were not different between that at 25/17°C and 21/13°C if radiant energy was maintained at a low level of 12.8 W/m^2 (Verkerk and Spitters, 1973).

Scaife (1973) also showed that the relative growth rate of Cobham Green was not affected significantly by temperature over the range 10 to 14°C. Soffe et al. (1977) found that dry weight and leaf area of lettuce cv. Kloek was increased by extending the daylength from 12 h (115 W/m^2) to 16 h with 4 h of low intensity (3 W/m^2) when grown at 15°C.

Cracker and Seibert (1983) reported that the vegetative dry weight and leaf number of Grand Rapids lettuce was primarily influenced by the length of photoperiod, with most growth occurring under long photoperiods. By 59 d after sowing, plants grown at the highest irradiance level (113 W/m^2) with 24 hours photoperiod produced over three times more dry matter than with 8h. The highest total leaf area was formed under the lowest irradiance level (14.1 W/m^2).

3. Temperature and Photoperiod Effects on Flowering

Flowering in many plants is not determined solely by genetic constitution, but is controlled by environmental factors which interact with genetic constitution in a specific manner (Zeevaart, 1963). The two main climatic factors which control flowering in lettuce are temperature and photoperiod (Garner and Allard, 1920; Robert and Struckmeyer, 1938).

Daylength is of primary importance in the growth and development of many plants, particularly with respect to flowering (Garner and Allard, 1920).

Tincker (1933) observed that Early Paris and Stanstead Park lettuce plants responded to increased photoperiods by a more rapid development of flower stalks, and responded to a decrease in daylength by increased vegetative development. Rudorf and Stelzner (1934) grew six varieties of lettuce, and exposed them to different periods of daylengths, 16.5, 12 and 8 h. The summer cultivars did not respond, but the other cultivars showed a diminished tendency to shoot to seed with short daylength.

Thompson and Knott (1933) reported that high temperature during the early stages of growth was responsible for the production of seed-stalks later. They also suggested that temperature (21-26°C) was an important factor involved in premature seeding in head lettuce cultivar White Boston. In this cultivar, plants went to seed under high temperature even under relatively short days (10 to 12 h). Seed-stalks elongated more rapidly in plants that had been grown continuously at 21-26°C temperature and long days (15 h).

Likewise, Rappaport and Wittwer (1956b) showed that Bibb, required long photoperiods (16 h) and warm nights (21°C) for seed-stalk development. Grand Rapids flowered on either warm nights or in long photoperiods, while the Tendergreen cultivar flowered primarily in long photoperiods.

Raleigh (1959) also found that seed-stalk elongation was enhanced by higher temperatures in head lettuce. The seed-stalk was significantly longer at 26/21°C than at 26/15°C; at 21/21°C than 26/15°C and 21/15°C than at 26/10°C.

Subsequently Ito et al. (1963) suggested that high temperatures above 20°C are effective for flower induction. At 30°C, lettuce plants need fewer days of exposure for flower induction than at 23°C. At 17°C both stem elongation and flower induction are delayed. Long days (16 h) with high temperatures led to flower induction but photoperiods less than 8 h together with high temperatures result in the failure of flower induction. Full sunlight, long days, and abundant nitrogen supply hasten plant growth, being followed by earlier flower induction. Shading, short days, poor nitrogen supply and defoliation all retard both plant growth and flower induction.

Cytovic (1967a) studied five lettuce cultivars grown at 8, 10, 12 or 24 h daylength. The leafy cultivars Moskovskij, Parnikovyi and Boul and the head lettuce Bibb reacted strongly to reduced daylength. In particular, 8 to 12 h daylength also reduced the number of plants affected by bacterial diseases. Hiraoka (1967a, 1967b) showed that high temperature (25°C) and long days (16 h) accelerated bolting, budding and flowering whereas short days (8 h) at lower temperature encouraged heading and delayed bolting. The Premier Great Lakes and Great Lakes 366 cultivars were apparently less sensitive to photoperiod than was the Edogowa strain of the cv. Wayahead but the number of branches was higher at high temperatures and an 8 h daylength. Hiraoka (1969) also confirmed that the higher the temperature, the longer was the seed-stalk and the earlier was flower bud differentiation.

Several studies have indicated that cultivated lettuce can be induced to bolt by treatment with certain growth regulators (Franklin, 1948; Clark and Wittwer, 1949; Wittwer and Bukovac, 1957; Thomas, 1968; Northmann, 1973; Gutterman et al., 1975). Gibberellic acid (GA_3) is most effective in promoting flowering and seed yield (Harrington, 1960; Hillman, 1962; Hiraoka, 1967a; Cytovic, 1967b; Globerson and Ventura, 1973). Bukovac and Wittwer (1958) found that GA_3 promoted flowering in Great Lakes, head lettuce and the effects were additive to those of long days

(18 h), high temperature (19-21°C) and seed vernalization. Gibberellin treated plants formed no vegetative heads and produced elongated stems prior to the appearance of visible flower primordia. Furthermore, Cytovic (1967b) reported that double stalk formation was found in 60% of the GA_3 treated plants of Premier Great Lakes and that, following treatment, plants immediately bolted, producing flowers and seeds. GA_3 sprayed at the rate of 3 to 10 µl/l on lettuce plants at the 4 and 8 leaf stages of growth significantly increased seed yield in Great Lakes head lettuce. Harrington (1960) also reported that the seed crop matured about two weeks earlier, with extremely uniform maturity among treated plants. Similarly, Globerson and Ventura (1973) applied 5 µl/l of GA_3 at the 2, 4 and 6 leaf stages to butterhead No. 615 and crisphead No. 923 (both bolting resistant cultivars) in a commercial field. The GA_3 treated plants flowered earlier and were more uniform than the controls. Seed yield was also higher in treated plots, with maximum yields of 564 kg/ha in No. 615 and 260 kg/ha in No. 923.

4. Temperature and Photoperiod Interactions with Vernalization on Flowering

Milthorpe and Horowitz (1943) investigated the effect of a low temperature treatment at 5°C for 10 to 20 d during the period of germination and early growth. They found that such conditions stimulated seed-stalk development in lettuce provided that they were followed by high temperatures and a long photoperiod. This effect has been similarly demonstrated in White Boston, head lettuce (Knott et al., 1937) and in Imperial (Gray, 1942). Andrew (1953) also reported a consistent promotion of seed-stalk development and flowering in lettuce 456 and Great Lakes when plants were grown under long day and at a temperature of 15°C following seed vernalization.

With Great Lakes cultivar, Rappaport and Wittwer (1965a) found considerable interaction between vernalization and the photoperiod and temperature during subsequent growth. In 16 h days, and at a minimum glasshouse temperature of 21°C, vernalization caused a reduction of 28 d in the time from sowing to anthesis. In 16 h days and at 16°C, the reduction was 22 d and in 9 h days at 21°C, it was 7 d. In 9 h days at 16°C, vernalization caused no significant reduction in time to anthesis. Clearly, flowering was hastened by vernalization, but its expression could be subsequently reduced by short days and prevented by low temperature.

Prince (1980) concluded that vernalization of seeds in most Lactuca sativa L. cultivars provided a means of hastening seed production, as long as other conditions, particularly daylength and temperature, were suitable for flowering. The greatest response was found among the crisphead lettuce cultivars but the varieties which showed little response to vernalization tended to have an extreme requirement for long days in order to flower. Vernalization did not hasten bolting in Slobolt and Cos 3288 cultivars (Thompson and Kosar, 1948).

5. Seed Quality and Germination

Germination, purity and health are the three main criteria of seed quality which are well established by the International Seed Testing Association (ISTA., 1976). Seed quality can be affected by a number of distinct, but often interacting factors including genetic factors (species and varietal), physiological factors (premature harvest of the seeds) and pathological factors (seed-borne diseases and mechanical damage) (Heydecker, 1969).

Lettuce seed quality was explored by Scaife and Jones (1970) who showed that under uniform conditions, and in the absence of interplant competition, the fresh weight of lettuce cultivar Borough Wonder at harvest was directly and linearly related to the weight of the seeds.

Smith et al. (1973a) developed a slant test for seed vigour, in which seeds were germinated until maximum radicle extension was reached. The seeds of Calmar cultivar were germinated on slanted blotters immersed in water in the dark, eliminating the effects of nutrition supply outside the seed itself. With this method seed weight was found to be more important than seed width or thickness in predicting vigour. An air column separator was shown to be an effective way of separating seeds varying in weight. Smith et al. (1973b) showed in field trials that light (low vigour) seeds emerged slower, with less total emergence, and produced smaller seedlings at thinning time, than heavy (high vigour) seeds. Head size at harvest and the proportion of marketable heads in the crop were greater from high vigour seeds.

Soffer and Smith (1974a) studied the flowering pattern in lettuce and its relation to seed yield and quality. Over 90% of the seed yield was from flowers opening during the first 35 d of a 70 d flowering period. Seeds produced during the first of two flowering peaks were heavier than later produced seeds. Seed size was unrelated to number of seeds per head. Seed yield and quality were unaffected by early harvest or by withholding water or nutrients during the latter half of the flowering period. Flowering rate, seed yield and quality were not related to air temperature in the range 20 to 35°C.

Soffer and Smith (1974b) showed that the magnitude of correlation between seed weight and seedling vigour ranged widely among seeds from different mother plants. Correlations between individual seed measurements and embryo physical parameters to seedling vigour were significant but seed size and seedling vigour were not associated with either head weight or uniformity. Soffer and Smith (1974c) also studied nutritional effects; increased nutrients supplied to plants grown in soil resulted in increased seed yield but no seed vigour. However, hydroponically grown seed was heavier than soil grown seed, but it lacked vigour. Nevertheless there was a linear increase in seed yield, weight/seed and seedling vigour with increase in nitrogen. The results showed that the relationship between seed size and vigour was dependable only within seed lots.

Renard (1978) reported that the middle grades of lettuce seeds (from six grades) gave the best germination capacity and the shortest germination time. The largest seeds were sometimes damaged, and often showed reduced germination properties but produced larger plants. The smallest seeds were the worst from all points of view.

Many factors have been shown to influence lettuce seed germination including area of production, seed age, cultivar, physiological age of plant at time of seed harvest, nutrition of the parent plant, light, temperature, carbon dioxide and oxygen etc. (Borthwick and Robbins, 1928; Thornton, 1936; Thompson, 1936, 1938; Harrington and Thompson, 1952; Koller, 1962; Gutterman, 1973). Light and temperature are the two aspects which have been studied most extensively (Toole, 1973; Vanderwoude and Toole, 1980 and Vanderwoude, 1982).

Flint (1934) and Flint and McAlister (1935) showed that the greatest promotive response to lettuce seed germination from a given irradiance occurred in the red region (600-700 nm) of the spectrum. Maximum inhibition occurred from irradiances in the far-red range (720-760 nm). The action spectrum curve for the promotion and inhibition of germination of Grand Rapids lettuce has been defined by Borthwick et al.(1952, 1954).

In terms of temperature, lettuce seed germination is satisfactory at 15 to 20°C. At 26°C or above, germination is inhibited, depending upon cultivar (Thompson and Horn, 1944; Borthwick and Robbins, 1928). This sensitivity to temperature is most pronounced with freshly harvested seed (Harrington and Thompson, 1952).

Thompson (1936) found that fully matured seeds of Grand Rapids germinated in diffused light at 15 to 20°C and in darkness at 10 to 15°C but that germination capacity dropped significantly when the temperature in darkness was increased to 25°C. Immature seeds failed to germinate in the absence of light at either 10 to 15°C or 25°C. The Hilde cultivar also germinated satisfactorily at 15-20°C in darkness (Krestchmer, 1978).

Gray (1977) in work with seeds of cultivars Hilde, Feltham King and Avon crisp showed that the first 4 h of imbibition and the phase between the onset of mitosis and radicle emergence were not sensitive to high temperature. These findings agree with similar work by Ikuma and Thimann (1964) with Grand Rapids.

Hadnagy (1979) recommended the need to prechill lettuce seeds of cultivars Attraction, Nansen and Soroksari at 4-6°C for 2 d followed by germination at 20°C with light to obtain full germination capacity.

In the cultivar Slobolt, germination is apparently accelerated by exposure of seed to fluorescent light for 24 h either alone or followed by 24 h dark/light periods at 20-25°C but was delayed when seed was germinated at 30°C (Verma and Pujari, 1977) compared with a similar effect in Great Lakes at 32°C (Dunlap and Morgan, 1977).

Light effects can be modified by the addition of chemicals. GA_3 overcomes the effect of far-red light (Kahn et al., 1957). However, Burdett and Vidaver (1971) have shown the effects of ethylene and gibberellin together in promoting germination in far-red light over that of gibberellin alone. These effects are even greater in red light.

High temperature dormancy has been shown to be overcome by the addition of thiourea (Thompson and Horn, 1944) and by ethrel and kinetin (Smith et al., 1968; Sharples, 1973 and Harsh et al., 1973).

An additional environmental effect on the germinability of lettuce seeds has been described by Girad and Monin (1977) who found that the lettuce cultivar Merveille des Guatre Saisons raised in short days produced seed which was more dormant at harvest than seeds from plants raised in long days. Conversely, a change in daylength during the last 12 d of seed ripening is apparently sufficient to affect the germinability of Grand Rapids seed. Similarly seeds developed and ripened under short day conditions (8 h) germinated faster than seeds from long days (20 h) (Gutterman, 1973), while the maturation of Grand Rapids seed under high temperatures or in continuous light (24 h) can be used to increase the high temperature tolerance of seed during germination both in continuous dark and after a short light-break (Koller, 1962).

6. Seed Production Practices

Production of high quality seed is possible only in a favourable environment with good growing conditions which will ensure that uniformity of the crop can be achieved before harvesting. There appears to be ample literature available on lettuce plant production but, until recently, information on the production of lettuce seed crops has been comparatively limited.

6.1 Climatic and Soil Requirements

There is little difference in growing lettuce for seed or for market. Up to the stage when the market crop is ready to harvest, the same general recommendations can be made. From then on, the seed grower is concerned with the growing and handling of the crop until the crop is mature. Lettuce seed production requires a long, warm growing season which is relatively free from rain at harvesting time (Hawthorn and Pollard, 1954). A cool period at the time of sowing, followed by a steady increase in temperature so that flowering occurs under warm conditions, is best for seeding of lettuce (Milthorpe and Horowitz, 1943).

Soils selected for growing lettuce for seed should be fertile and have a high organic matter content. Because of the lettuce plant's demand for a plentiful supply of moisture during the growing season, heavy silt and clay loam soils are preferred

(Thompson, 1951). The soil reaction should be nearly neutral between ph 6 and ph 7 (Whitaker et al., 1974).

6.2 Cultural Procedures

Lettuce plants are generally produced in the nursery bed prior to transplanting into the field. However, some types, especially the leaf types, may be sown directly in the field. The seed should be planted thinly at the rate of 1-1.5 kg/ha. Several weeks later, the seedlings are thinned in the row. Spacing is usually about 25-30 cm in the row with the large heading types and 15-20 cm apart in the leaf types depending on the variety (Hawthorn and Pollard, 1954 and Duncan, 1965). In Grand Rapids, Pokanan (1981) obtained the highest seed yield (318 kg/ha) from a 30 x 75 cm plant spacing. Maximum seed yields per plant (12.5 g) were obtained at a 50 x 75 cm plant spacing.

Difficulties are not normally encountered with seedstalk elongation in leaf, cos or most butterhead varieties. With the crisphead type however, partial head removal or treatment may be necessary to allow seed-stalk 'escape' and development. If this is not done, the seed-stalk tends to curl inside the head or be delayed in its maturity as well as resulting in a reduction in yield. If heads are split too early the plant will continue to head and if delayed too long, seed stalk injury will result. A common method which overcomes this problem is to peel back the leaves on each plant by hand so as to expose the growing point but this is labourious and costly (Harrington, 1960; Hawthorn and Pollard, 1954).

6.3 Harvesting

Lettuce seeds ripen unevenly. If seed is allowed to develop to full maturity, losses from shattering may be severe. There are definite flowering peaks for individual lettuce plants and approximately 12 d is necessary from anthesis to the maturity of an individual seed. It is apparently advisable to harvest when the plants are showing about 50% "feather" (showing white pappus) even though it has been observed that better yields are obtained when the crop is left until it reaches the "full-feather" stage. The longer the seeds are left on the plant the greater the chance of shattering by wind or rain (Jones, 1927).

For commerical seed production (Thompson, 1938) advised that two harvests of seed should be made although it was believed that the second harvest seed recovered was inferior to that harvested first. Soffer and Smith (1974a) showed that in lettuce, 90% of the seed yield comes from flowers which open during the first 35 d. Highest seed yields are obtained by hand harvesting methods where flower head were shaken into a bag. This process can be repeated two or three times during a season (Duncan, 1965). Seed harvested in this manner is much easier to clean since there is little chaff mixed with it (Hawthorn and Pollard, 1954).

Douglass (1939) and Shoemaker (1953) suggested that lettuce plants should be pulled out of the ground when the heads begin to swell and turn yellow or white and stacked on a canvas sheet. The shattering of the early seed will then fall on the canvas. At the same time, the seed heads are still able to draw on the moisture and nutrients available in the cut plant. This allows them to continue development until the seed reaches maturity.

Duncan (1965) recommended, for large lettuce seed production areas, that plants should be cut when the majority of the seeds are yellowish in colour. The seeds can be threshed as soon as heads and outer-most branches have dried sufficiently. Threshing without seed injury is best accomplished by putting the plants through a combine harvester which has some teeth removed from the peg drum.

In general, the yield of lettuce obviously depends on many factors, including locality, spacing, soil fertility etc. However, major yield differences have been recorded with different cultivars. The New York No. 12 cultivar for example, has been shown to produce 200 kg/ha (Claypool, 1933) compared with only 100 kg/ha in Great Lakes (Harrington, 1960). In Israel, average seed yields are 250 kg/ha in butterhead No. 615 and 70 kg/ha in crisphead No. 923 (Globerson and Ventura, 1973). In Thailand, Grand Rapids has been shown to be capable of producing about 300 kg/ha of seed (Pokanan, 1981).

6.4 Disease and Pests

Even though the production of lettuce seed is not troubled by a large number of diseases and insects, those which are important may become so serious that they may limit the production of seed.

Downy mildew (Bremia lactucae R) causes the flower parts and plants to slightly stunt (Dixon, 1981). Control of this disease is by using resistant cultivars such as Grand Rapids (Verhoeff, 1960) or Meikoningen butterhead lettuce (Schultz and Roder, 1938). Soft rot (Botrytis spp.) results in considerable damage to plants, particularly in head lettuce. It can be controlled by early removal of heads and keeping soil moisture uniform to prevent tipburn (Elia and Piglionica, 1964). Under cool, moist conditions or following over-irrigation of heavy soils, the lettuce plant may be affected by sclerotinia rot (Sclerotinia sclerotiorum Lib). Hawthorne (1974) also found that crisphead and butterhead lettuce plants which have the lower leaves lying flat on the ground are more liable to infection by sclerotinia than cos lettuce which have more upright lower leaves. If the weather is relatively warm and humid, the plants may be affected by powdery mildew (Erysiphe cichoracearum DC) either in the field or in the greenhouse (Schnathorst, 1960).

Several species of aphids spread lettuce mosaic virus, the ultimate effect on growth and yield being dependent upon time of infection; later infection causes less plant damage while plants infected early become yellow and stunted (Zink asnd Kimble, 1961). Infected plants that become reproductive show necrotic areas along the seedstalk and in the seed heads. Ryder and

Duffus (1966) showed that lettuce mosaic virus delayed flowering, reduced seed stalk height and reduced total seed yield but did not affect seed germination.

Aster yellows, spotted wilt and 'big vein' are the other important viral diseases of lettuce. They are not seed borne, but sometimes are difficult to control. Aster yellows is transmitted by leaf hoppers and causes the flower parts to form no seed (Jagger and Chandler, 1934; Ryder, 1979).

Aphids can be a most troublesome insect pest on lettuce. There are often times when they may cause a reduction in seed yield. The lettuce seed stem aphid is particularly damaging. The use of insecticide such as Parathion has been shown to increase seed yields compared to untreated aphid-infected plants (Hawthorn and Pollard, 1954).

6.5 Tipburn

Lettuce contains a substance called lactucin which is a sleep-inducing drug (Ryder, 1979). This latex-type of material occurs in a system of ducts called laticifers. Tipburn, a non-pathogenic disorder of lettuce, is manifested by necrosis of leaf margins on relatively immature leaves of maturing lettuce plants. Rupture of the laticifers near the leaf margins, releases latex causing collapse of parenchyma, occlusion of xylem elements, and most significantly, coagulation of latex within the entire laticifer system between the point of rupture and the leaf margin, resulting in dark brown spots (Tibbitts et al., 1965; Olsen et al., 1967).

In both glasshouse and growth chamber situations, tipburn may develop on young plants when enlarging leaves begin to bend inwards, partially enclosing the young leaves around the growing point. Under field conditions tipburn usually develops at or near plant maturity and is more likely to appear with overmaturity (Termohlen and Van de Hoeven, 1966). Tipburn development has been associated with environmental conditions that encourage rapid dry matter accumulation and a high demand for calcium in expanding leaf tissue. The symptoms develop quickly in young plants when they are exposed to high light intensities, extended photoperiods and high temperatures (Tibbitts and Roa, 1969., Tibbitts and Bottenberg, 1976; Tibbitts and Read, 1976; Cox et al., 1976.

Calcium nutrition is in some manner associated with the events leading to tipburn. However, much confusion is apparent in explanations of the role of environmental influence. Kruger (1966) first prevented tipburn by applying calcium salts directly to the sensitive tissue. Thibodeau and Minotti (1969) led the generally accepted theory that lettuce tipburn is a calcium related disorder. Likewise, Ashkar and Ries (1971) were able to control tipburn in head lettuce growing in nutrient solution in growth chambers by adding at least 5mM calcium to the solution. They also found higher tipburn incidence with higher nitrate additions.

Crisp et al. (1976) induced tipburn by withholding boron which in turn increased the endogenous auxin level. A common factor in nearly all relationships between growth and the incidence of tipburn is that this condition increases with an increase in growth rate (Cox et al., 1976).

The most effective procedure for tipburn control has been the use of cultivars tolerant to the injury (Cox and McKee, 1976) or by developing either chemical or physiological screening procedures for use on individual seedlings (Collier et al., 1977). At present, there are no recommended procedures the grower can use that will guarantee tipburn prevention in field-grown lettuce (Collier and Tibbitts, 1982).

7. Seed Development

Yield is an extremely important and common parameter for measuring genetic differences. To obtain differences in yield among varieties they are usually grown together under controlled conditions (Kramer, 1978). However, differences in yield may be associated with the location in which the seeds were originally produced and the variation in seed quality which can occur at any time during seed development.

Although the amount of literature on seed development in grasses and legumes is voluminous, relatively little information appears on lettuce seed development. Studies on other vegetables like carrot (Borthwick, 1931), cabbage (Thompson, 1933), sugar beet (Artschweager and Starett, 1933) and pepper (Cockran, 1937) seem to indicate that their purpose was to obtain a better morphological understanding of flower and seed development prior to the undertaking of a breeding or crop improvement programme.

Seed development is concerned with the various processes and stages occurring during the period from fertilization until the seed is fully formed and ready to harvest (Copeland, 1976). It is characterised by a complex of structural and nutritional interrelationships between the embryo and endosperm tissues. Central to these interrelationships is the development of the endosperm and its subsequent digestion by the developing embryo. Endosperm development is obligatory to seed development (Pollock and Roos, 1972).

During seed maturation, seeds pass through several anatomical and physiological stages until the mature dry seed is produced or until the seed reaches its maximum dry weight (Harrington, 1972). Any attempt to accelerate these changes may produce seeds which, when dry, appear normal but are physiologically imperfect and incapable of initiating rapid and coordinated growth.

Koller (1962) showed that warm temperatures during the maturation of Grand Rapids seed reduced seed dormancy. Harrington (1960) also found that deficiencies of potassium and calcium in lettuce decreased germination and reduced seed storage life. Such deficiencies also produce severe plant symptoms but do not prevent seed production.

Seed maturity is usually reflected in mean seed dry weight or size (Austin, 1972). The size of lettuce seeds has been found to affect both growth and yield (Scaife and Jones, 1970; Renard, 1978; Smith et al., 1973b; Soffer and Smith 1974a).

Seed development occurs in two distinct phases (Mullett, 1981). During the first phase, food materials are transported from the parent plant and accumulated in the seed. A rapid increase in the dry weight of the seed occurs at this stage. The second phase, known as the maturation phase, occurs after food transport from the parent plant has ceased. The transported sugars and other simple compounds are converted into starches, fats and storage proteins to become the endosperm and to provide protein for the development of the embryo. During this time a considerable loss of water occurs and the fresh weight of the seed declines sharply, while the dry weight is unchanged. In seeds which do not have endosperm, the embryo develops at this time. The seed utilises some transported food materials and stores any surplus to its immediate energy requirement in the cotyledons or seed leaves. In seeds with minimal embryo development, the storage material becomes a separate non-cellular endosperm, which is the food supply for further development of the embryo during germination.

Seed development and maturation are associated with an overall loss of moisture. Usually very young seed has the highest moisture content. Leininger and Urie (1964) and Kersting et al. (1961) found a steady decline in the percentage moisture of ripening seeds from an initial 80-90% to 10-20%. Austin et al. (1969) found with carrot seeds that after a period during which the moisture content declined to 50-60% there was no further growth in embryo size. Delouche(1980) reported that seeds attain physiological maturity at moisture contents ranging from 32-35% (e.g. corn, sorphum, rice) to 50-55% (e.g. soybeans, peanuts, beans).

Jones (1927) made a study on the pollination and life history of lettuce cv. Iceberg. He found that the bracts subtending the flower head start to open at the summit beause of the development of the individual flower buds. These buds elongate rapidly during the 24 h prior to anthesis. The style and stigma of the pistil are covered with small brush hairs. The anthers dehisc to the inside prior to the elongation of the pistils. As the pistils elongate, the hairs on the side of the pistil brush the pollen up out of the pollen sacs of the dehisced anthers. The lobes of the stigma separate, allowing pollen to fall on the stigmatic papillae located on the inside surface of the stigma. As soon as the lobes have expanded, they begin to curl backward. Pollination probably takes place when this has occurred.

The lettuce plant as a whole usually shows definite flowering peaks over a 70 day period. This is often followed by a cessation of flowering although in some plants there may be a continuation of flowering for several days and then another flowering peak of less magnitude a month later. The general flowering curve may contain minor irregularities which are due mainly to fluctuations in temperature (Jones, 1927) or light intensity (Soffer and Smith, 1974a).

The flowers usually open for an hour or two only, the ligulate corolla then folds tightly together and does not reopen. Within two or three days the corolla, dehisced stamens, withered sytles and stigma are shed in a cluster. The bracts then close tightly about the developing achenes. The beak of the young fruit elongates and carries the pappus along in its upward growth. The rate of elongation is very rapid. Within four or five days after anthesis, the pappus begins to appear through the bracts, the average time from anthesis to maturity of the achenes being about 12 d. A recent report on lettuce seed development by Globerson (1981) contains much useful information about the effect of the age of lettuce seed at different harvest times after anthesis on their subsequent germination and seedling development under Israeli conditions. He found that ripe seeds with 80-85% dry matter developed 17 d after anthesis in May (mean temperature 19.7°C) whereas in July, (mean temperature 25°C) development took 14 d. Germination was faster in seeds 14 d old harvested in May. In July, seeds were able to germinate 9-10 d after anthesis. The largest seedlings developed from seeds harvested at least 14 d after anthesis in May and 12 d after anthesis in July. The cultivars used in his study were of the cos type: Yellow, No. 854 and No. 942 for the May harvest and of the crisphead type: Avon Crisp, Vanmax and Vanguard for the July harvest.

It might be concluded that temperature and photoperiod are two main important factors controlling vegetative growth and reproductive development in lettuce. Photoperiodic response however has been often modified in one way or another by changing temperature. Achieving understanding in this field could have immense practical consequences for both crop production and seed production in leaf lettuce.

CHAPTER 2

PRELIMINARY STUDY

Leaf lettuce is the main commercial salad vegetable in Thailand. It is commonly grown throughout the year. The most popular variety is a black seeded cultivar, referred to in the present study as "Thai", but known in Thailand as Pak Kard Horm Bai Yig.

This black seeded cultivar has a strongly waved leaf margin, is yellowish-green in colour and does not form a head (Plate 2.1). It grows very successfully all the year round in Thailand but develops better if it is grown during the cooler months when the rainfall is moderate.

Although different types of lettuce are known, some cultivars have been improved through individual plant selection. This has led to the naming of a large number of cultivars, many of which are phenotypically similar or are distinguished by only minor differences (Thompson, 1944., Huyskes and Rodenburg, 1957). This situation can lead to difficulties and occasional misunderstandings among seed dealers and farmers. In Thailand agriculture, other cultivars which are similar to the Thai cultivar are not apparently available. This is perhaps because of a lack of information on the varieties which are agronomically suitable and also because of a high degree of resistance to 'new' or 'different' cultivars by the Thai customer.

The present experiment was designed to select lettuce cultivars from different sources which could grow successfully under the generally high temperature (20-30°C) and intermediate daylength (12-13 h) conditions likely to broadly represent the

Plate 2.1 Black seeded lettuce (Thai cv.)
a) in the field
b) as presented for the market

prevailing climate in Thailand (Appendix 1). It was hoped that such a screening trial would identify some cultivars which would closely meet the very precise Thai consumer acceptance requirements of: leaf type (loose leaf lettuce), yellowish-green colour, strongly waved leaf margin, wrinkled leaf surface and slow bolting. It was hoped that those varieties which most closely met these criterias could be used for further growth and seed production studies under controlled conditions.

MATERIALS AND METHODS

Seeds of eighteen cultivars (Table 2.1) were grown in a glasshouse (30/20 ± 5°C, day/night and 12-13 h daylength) at the Seed Technology Centre, Massey University.

Seeds were sown directly in 200 mm diam. black polythene bags filled with Smith's* soil containing peat, pumice and sand. This is a completely sterile mixture containing balanced proportions of fertilizer and slow release trace elements plus Terrazole soil fungicide. After two weeks the seedlings were thinned to one plant per container. There were 12 plants per cultivar. Hand watering was done every day until harvesting.

Measurements

The following visual criteria were recorded:

1. Seed colour (from the seed lot)
2. Leaf colour at harvest
3. Leaf margin at harvest
4. Leaf surface: wrinkled, smooth or hairy
5. Days to bolting from planting to first visual signs of floral development (average from 5 plants).

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* Smith Soil Industries Limited, New Lynn, Auckland, New Zealand.

Table 2.1 Varietal characteristics in a range of different leaf lettuce cultivars

Cultivars	Source *	Seed colour	Leaf colour	Leaf margin	Leaf surface	Days to bolting	Type
1. Thai	Kasetsart Univ	Black	Yellow green	Strongly waved	Wrinkled	73	Leaf
2. Grand Rapids	Yates	Black	Yellow green	Strongly waved	Wrinkled	60	Leaf
3. Grand Rapids	E.J. Ryder	Black	Yellow green	Strongly waved	Wrinkled	70	Leaf
4. Grand Rapids	Morran Seed	Black	Yellow green	Strongly waved	Wringled	70	Leaf
5. Slobolt	E.J. Ryder	White	Yellow green	Slightly waved	Wrinkled	80	Leaf
6. Salad Bowl	E.J. Ryder	Black	Yellow green	Lobed	Smooth	-	Leaf
7. Salad Bowl	Asgrow seed	Black	Yellow green	Lobed	Smooth	-	Leaf
8. Salad Bowl	Morran seed	Black	Yellow green	Lobed	Smooth	-	Leaf
9. Waldmann's Green	E.J.Ryder	Black	Dark green	Strongly waved	Wrinkled	65	Leaf
10. Waldmann's Green	Morran Seed	Black	Dark green	Strongly waved	Wrinkled	65	Leaf
11. Prize Head	E.J. Ryder	White	Reddish green	Slightly waved	Wrinkled	65	Leaf
12. Prize Head	Peto seed	White	Reddish green	Slightly waved	Wrinkled	65	Leaf
13. Deep Red	E.J.Ryder	White	Reddish green	Slightly waved	Wrinkled	75	Leaf
14. Sumnmer Queen	Asgrow seed	Black	Yellow green	Not wavy	Slightly wrinkled	-	Butterhead
15. Brazil 48	Asgrow seed	Black	Yellow green	Not wavy	Slightly wrinkled	-	Butterhead
16. Brazil 221	Asgrow seed	Black	Yellow green	Not wavy	Slightly wrinkled	-	Butterhead
17. Tania	Morran seed	White	Yellow green	Not wavy	Slightly wrinkled	-	Butterhead
18. Manoa	R.W.Hartman	Black	Yellow green	Not wavy	Slightly wrinkled	-	Butterhead

* Address: Kasetsart University, Horticulture Department, Bangkok, Thailand
E.J. Ryder, U.S. Agricultural Research Station, Salina, California, U.S.A.
R.W. Hartman, University of Hawaii, Manoa, U.S.A.
Peto Seed, P.O.Box 4206, Saticoy, California, U.S.A.
Morran, Seed, 1155 Harkins Road, Salina, California, U.S.A.
Asgro Seed, Kalamazoo, Michigan, U.S.A.
Yates, P O Box 16-147, Hornby, Christchurch, New Zealand

RESULTS AND DISCUSSION

In Thailand consumer is traditionally accustomed to the use of leaf lettuce rather than the 'heading' or 'bunch' type common in many other countries. In particular, the lettuce plant must traditionally show a number of fairly precise vegetative characteristics including a waved leaf margin and non-heading tendency. Cultivars which do not show these characteristics are strongly discriminated against by the customer. These vegetative characters are also important since one use of lettuce is in the garnishing of food to make dishes look more attractive. Visual characters therefore assume great importance (Plate 2.2).

There are a number of different lettuce cultivars of leaf type which can be grown. Many of these, although they might differ in one or two characteristics, still meet the general vegetative characteristics, previously stated. A number of these are described in Table 2.1 The cultivar which most nearly meets the comparative requirements to the Thai cultivar in terms of leaf colour, leaf margin, and leaf surface is Grand Rapids. Grand Rapids plants are grown from a black seeded cultivar and are yellow-green in leaf colour, with a very wavy leaf margin and a wrinkled leaf surface. However, there are differences in time to bolting between seed sources. Both of the Grand Rapids seed samples obtained from the U.S.A were slower in bolting than the New Zealand lot when grown under the same environmental conditions. The sample of Grand Rapids from the Morran Seed Company U.S.A. was chosen for further experiments due to the amount of seed available. The close similarity in the appearance of Grand Rapids to the Thai cultivar is shown in Plate 2.3. Grand Rapids itself originated from Black Seeded Simpson. Selections were made and tested for 15 years by Eugen Davies in 1890 (Wittwer et al.,1965). The Thai cultivar is also believed to be a Black Seeded Simpson type or possible a direct selection from this cultivar.

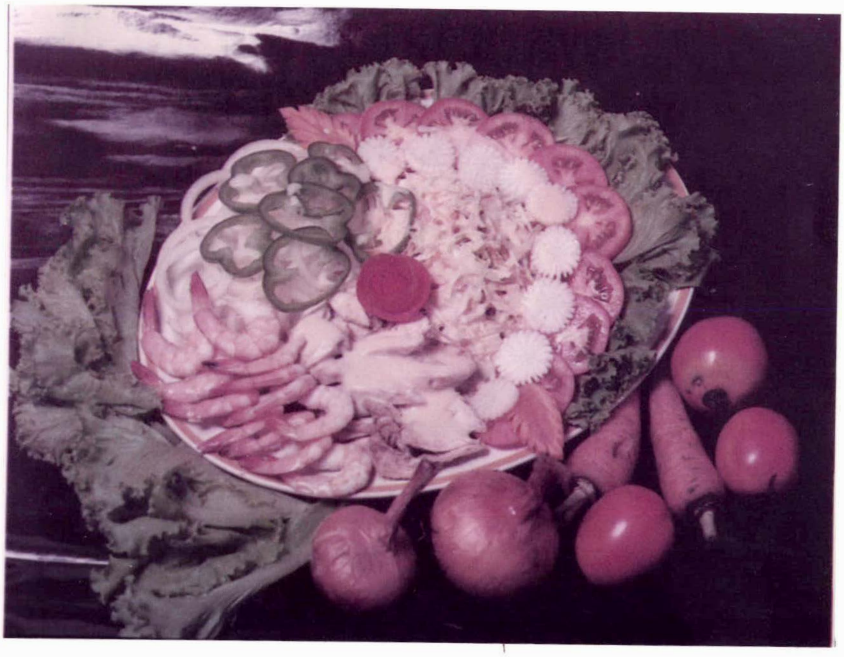


Plate 2.2 Typical Thai dishes prepared for the table

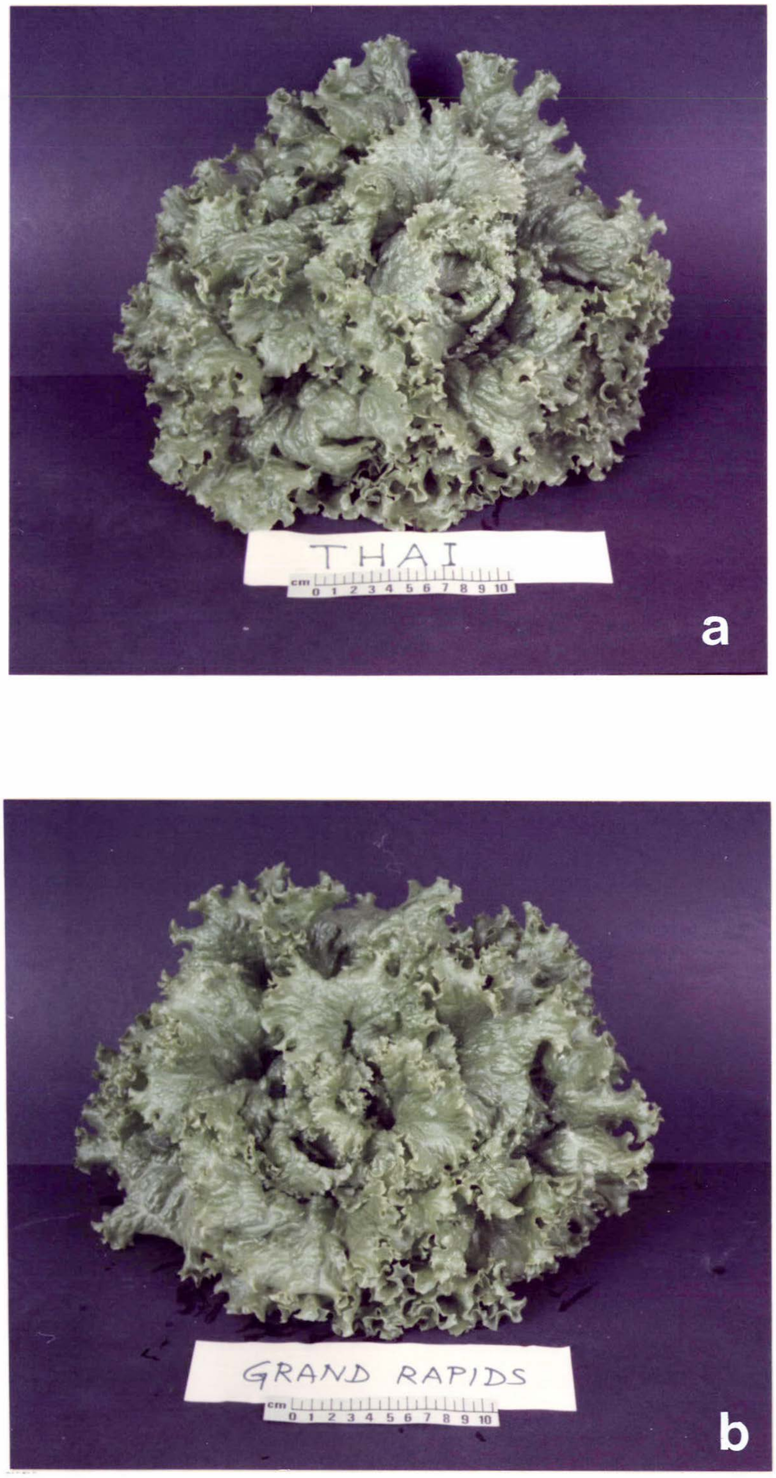


Plate 2.3 A plant of cultivar
a) Thai
b) Grand Rapids
at 60 d after sowing

Slobolt was another interesting cultivar which met most of the vegetative requirements. It is a white seeded cultivar, yellow green in leaf colour, with a slightly waved leaf margin and a wrinkled leaf surface (Plate 2.4a). Its main agronomic advantage is its slow and late bolting character (80 days from sowing). Thompson and Kosar (1948) reported that Slobolt was one of the slowest bolting of all lettuce varieties and was therefore difficult to handle in commercial seed production. However, this character was thought to offer commercial possibilities for the green vegetable market in Thailand.

Waldmann's Green is a further cultivar which is similar to both the Thai variety and Grand Rapids except that the plants are darker green in colour (Plate 2.4b). This is because Waldmann's Green is a strain of Grand Rapids (Wittwer et al., 1965). Although the Waldmann's Green cultivar meets some of the desired vegetative requirements it's very dark green leaf colour makes it unacceptable to the Thai consumer. Leaf colour is particularly important in the assessment of lettuce quality in Thailand because this is the first trait that registers to the eye and mind of the potential consumer.

Although the remaining cultivars tested showed no sign of bolting, they did not meet suffient of the requirements to be considered suitable for further study.

Deep Red and Prize head have finely fringed and ruffled leaves but were unacceptably reddish-green in leaf colour (Plate 2.5).

Brazil 48, Brazil 221, Summer Queen, Tania and Manoa, showed similarity in visual appearance (Plates 2.6 and 2.7). They form relatively small loose heads with broad, oily and slightly wrinkled soft textured leaves which although characteristic of a butterhead lettuce (Ryder, 1979) were not acceptable as leaf lettuce cultivars within the confines of the present study.

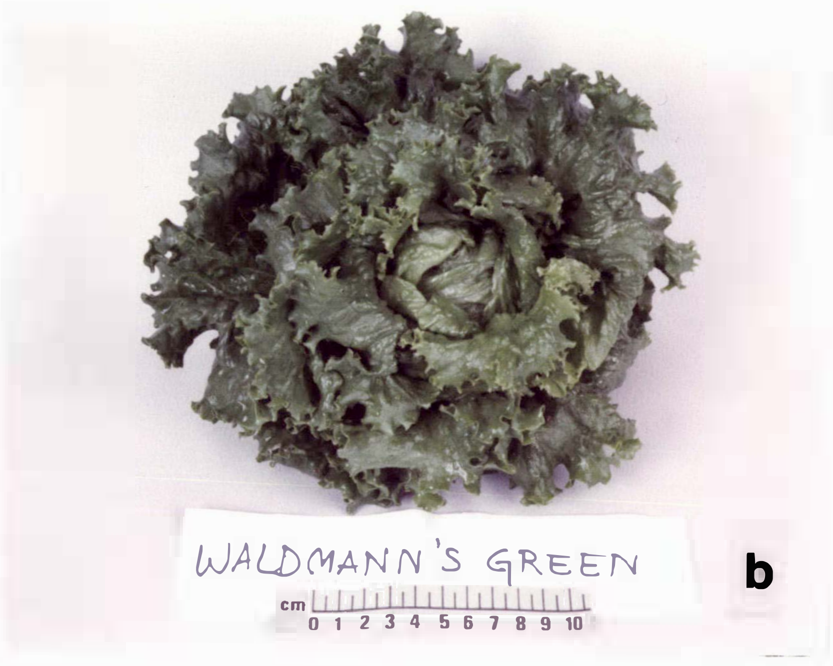
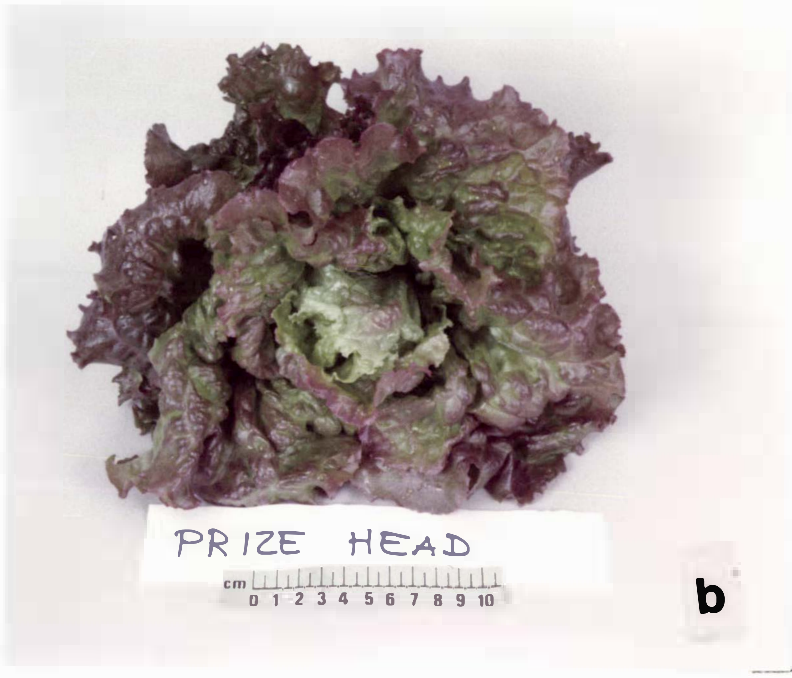
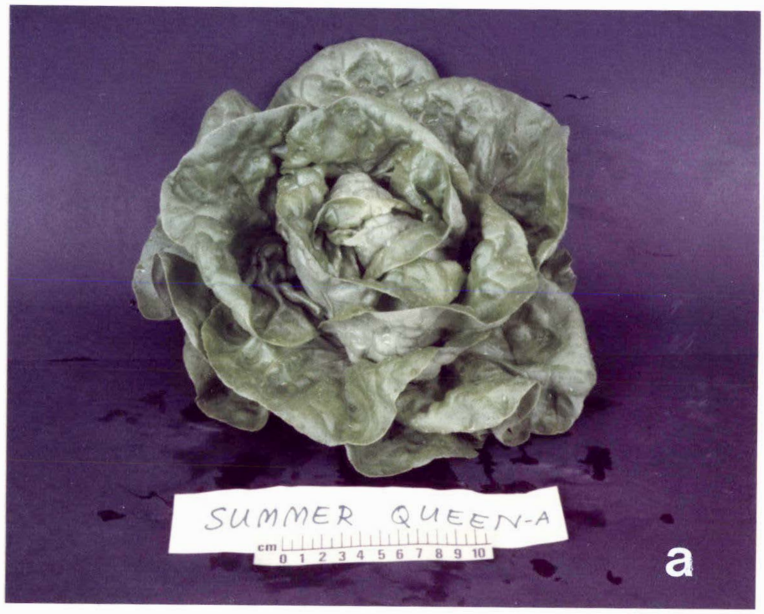


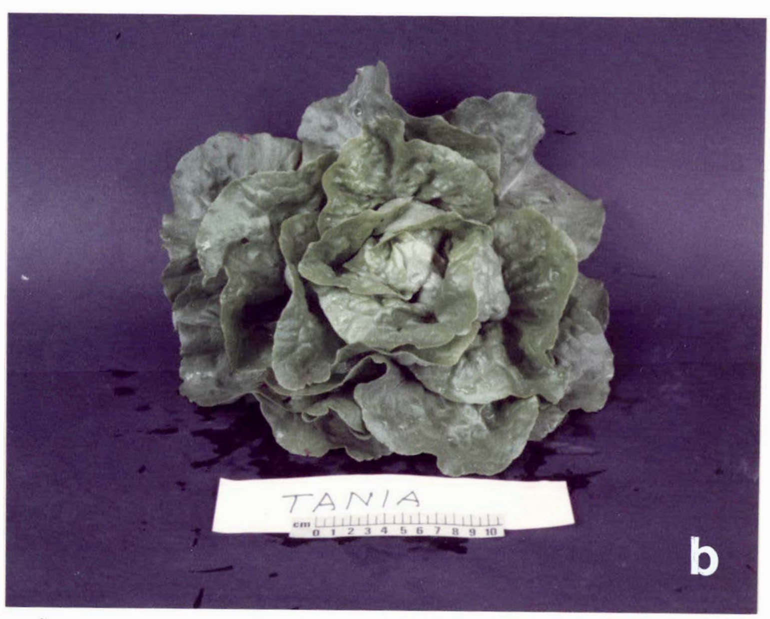
Plate 2.4 A plant of cultivar
a) Slobolt
b) Waldmann's Green
at 60 d after sowing



<u>Plate 2.5</u> A plant of cultivar
a) Deep Red
b) Prize head
at 60 d after sowing

Plate 2.6 A plant of cultivar
a) Brazil 48
b) Brazil 221
at 60 d after sowing





<u>Plate 2.7</u> A plant of cultivar
a) Summer Green
b) Tania
at 60 d after sowing

The cultivar Salad Bowl, although a leaf type lettuce, showed a different leaf shape and leaf margin, with the leaves typically (and unacceptably) lobed (Plate 2.8).

The three chosen cultivars: Thai, Grand Rapids and Slobolt were therefore selected from the 18 different cultivars studied because they most closely met the stated vegetative requirements. Although light and temperature often influence the ultimate size, shape and physiology of the plant (Thompson and Knott, 1933; Bensink, 1971; Soffe et al., 1977; Craker and Seibert, 1983), under the same environment, Grand Rapids and Slobolt cultivars behaved in their vegetative growth similarly to the Thai cultivar.

It is difficult to judge exactly which cultivars are most suitable for Thailand conditions since there are many variables to be considered including locality trials, marketing, etc. This preliminary screening experiment was therefore considered to be just a first step in determining suitable cultivars for further growth and seed production studies under controlled environment conditions. Certainly the Thai, Grand Rapids and Slobolt cultivars most closely met the required criteria.

Plate 2.8 A plant of cv. Salad Bowl at 60 d after sowing

CHAPTER 3

VEGETATIVE GROWTH

Variation in plant growth and development has been observed in many lettuce cultivars when grown under different temperature, photoperiod and irradiance conditions (Brouwer and Huyskes, 1968; Bensink, 1971; Dullforce, 1971; Dennis and Dullforce, 1974a,b; Holsteijn, 1980a,b; Grey and Steckel, 1981; Wurr et al., 1981). Generally the experiments have been conducted with the purpose of obtaining optimum growth, often under poor light conditions in winter (short days), and have been carried out with the butterhead lettuce.

In contrast, research on the leaf lettuce has been largely concerned with the better utilization of light in controlled environments (Hammer et al., 1978; Tibbitts and Kozlowski, 1980; Krizek and Ormrod, 1980; Tibbitts et al., 1983; Cracker and Seibert, 1983; Glenn, 1984) and satisfying human nutritional requirements during long term space habitation (Knight and Mitchell, 1983). Obviously then, general details of leaf lettuce growth and development for practical agricultural purposes are scarce.

Leaf lettuce grows successfully all year round but develops better during the cool months in Thailand and other tropical countries (Herklots, 1974; Carpio and Bantoc, 1968) than other lettuce types. It has less exacting growth requirements than butterhead or crisphead cultivars (Whitaker et al., 1974) but premature bolting and flowering in leaf lettuce is a common cause of marketing loss. This problem might be solved by following a research programme which would identify the environmental conditions best suited to either leaf production or to seed production. Such information would indicate which local conditions or areas are most favourable for the production of leaf or seed.

The climatic conditions in Thailand vary considerably within the country. Temperature during the cool dry season (November-February) is about 25/15°C day/night, while in the hot dry summer (March-May) and in the wet season (May to October), the average temperature is about 35/20°C day/night (Appendix 1). At high altitudes (approximately about 1000-1400 m above sea level), the temperature is lower and temperate vegetables may often be grown (Appendix 2). Daylength is generally about 11.5 h in the cool season and 13.5 in the wet season.

The present experiment was carried out as part of an investigation into temperature and photoperiodic effects on lettuce growth, as related to general climatic conditions in Thailand.

MATERIALS AND METHODS

The experiment was conducted in controlled environment rooms at the Plant Physiology Division, Department of Scientific and Industrial Research, Palmerston North, New Zealand.

Plant Material

Three cultivars of leaf lettuce (*Lactuca sativa* L.): Thai, Grand Rapids and Slobolt selected from the previous experiment were used.

Environment

The experiment was carried out at three successive times using the same two controlled environment rooms (3 x 3 x 3 m room). This was necessary to accommodate all the daylength x temperature combinations selected and to cope with the number of observations and harvests that were carried out.

1. Daylengths 10, 12 and 14 h
2. Temperatures:

   (a) 25/15±0.5°C (day/night)

   (b) 30/20±0.5°C (day/night)
3. Light

   The lighting system used comprised four 1000 W Sylvania "Metal-arc" high-pressure discharge lamps, together with four 1000 W Philips tungsten iodide lamps. The photosynthetic irradiance was constant over the photoperiod (there was no low light extension) and was measured at initial trolley height (2.3 m from the room thermal barrier) using a LI-COR 185 meter with LI-190SE flat response sensor (W/m^2). The photosynthetic photon flux density $\mu mol/(m^2 s)$ was also measured using an LI-190S quantum sensor (Appendix 3). When plants were about 0.75 m high (after 40 d), the pots were lowered by 0.3 m where they remained until the plants were harvested for seed. For the phase of flowering, the photosynthetically active radiation energy and photon flux densities at the top of the plants were about 220 W/m^2 and 1100 $\mu mol/(m^2 s)$. Fuller details of these light gradients and the lighting system are provided in Warrington et al. (1978).

4. Humidity

   The relative humidity was 60/90 ± 5% (day/night) for both temperature regimes. This resulted in vapour pressure deficits (VPD) of 1.25/0.17 kPa for the lower temperature regime and 1.66/0.2 kPa for the higher temperature regime.

5. Carbon dioxide

   Carbon dioxide was maintained in the range of 330 ±30 µl CO_2/l air during day conditions and 380 ± 40 µl CO_2/l air during the night.

Cultural Methods

Seeds of each cultivar were sown, five per pot, 1 cm deep into 4.5 dm^3 pots containing a 70:15:15 v/v coarse sand: peat: vermiculite growing medium. When the first true leaf was fully expanded (about 7 d), the plants were thinned for uniformity to three per pot, this being further reduced to one per pot after 10 d. The pots were placed in the controlled environment rooms immediately after sowing. Eight trolleys per room were used to avoid the risks of non-uniformity. There were 96 pots per room, i.e. 32 pots per cultivar. Twelve plants were used in the study of vegetative growth and development, the rest being used for the subsequent seed production experiment. The pots were hand watered until the seeds germinated (4 d) after which all containers received 200 ml applications of a modified half-strength Hoagland's nutrient solution (Appendix 4) four times daily through an automated micro-tube system through the experiment.

At 30 d after sowing, two trolleys were removed to avoid over-crowding. After day 40, the plants were thinned to 12 plants of each cultivar in each room, six pots per trolley and 36 plants/room. These plants were used for the following measurements:

1. Flowering pattern (3 plants/cultivar).

2. Seed development (4 plants/cultivar), being studied only at 12 h daylength at both temperatures.

3. Seed production (12 plants/cultivar). These plants were also used for flowering pattern studies. However, only eight plants were left in 12 h daylength conditions.

Plant Measurements

The growth of lettuce plants was recorded at 10, 20, 30 and 40 days after sowing. At each harvest, 3 plants of each cultivar from each temperature and daylength treatment were taken at random.

1. Fresh weight - the plants were cut at the hypocotyl and weighed immediately, to ensure only minimal loss of water and shoot wilting.

2. Dry weight - the dry weight of all plant parts (leaves and stems) was obtained by drying in a vacuum chamber at 40°C with 5 mm Hg pressure until the samples reached constant dry weight (normally 24 h). Samples were then weighed in a constant temperature and humidity controlled room (22°C and 50% RH).

3. Leaf number - the number of mature and developing leaves (longer than 1 cm) on the main stem were recorded.

4. Leaf area - determined using a leaf area meter LI-COR Model LI-3000 and LI-3100.

5. Stem length - after removal of the leaves, the stem was cut longitudinally and stem length measured from the cotyledonary node to the top leaf node. This measurement was not obtained at the first harvest (10 d from sowing) because the plants were too small.

6. Shoot numbers were counted at 40 d after sowing

7. General observations - tipburn injury levels and overall plant appearance were observed at intervals throughout the experiment.

Data Analysis

There was only one room used for each temperature x daylength treatment combination. The data for each harvest was analysed as a completely randomized design with a factorial arrangement involving three daylengths, two temperatures and three cultivars. The least significant difference (LSD) values for 5% confidence limits were calculated as part of each analysis of variance (Steel and Torrie, 1982).

The dry weight and leaf area data were analysed using regression techniques (Hunt and Parsons, 1974; Hunt, 1978) and the relative growth rates for dry weight (RGR) and leaf area (RLGR) of whole plants were calculated (Appendix 5).

RESULTS AND DISCUSSION

1. Plant Fresh Weight

Total plant fresh weight, as influenced by temperature, daylength and cultivar at different stages of growth is presented in Table 3.1 and Appendix 6. The fresh weight of plants increased throughout the duration of the experiment up to 40 d after sowing. However, differences between temperatures, daylengths and cultivars were small in the early stages of growth (10 d after sowing) and the greatest fresh weight increases occurred between days 20, 30 and 40.

The fresh weight of lettuce plants grown at 30/20°C (day/night) was significantly greater than of plants grown at 25/15°C at each harvest. Increasing the photoperiod from 10 to 14 h also increased plant fresh weight at all harvests. There was fourfold increase at 20 d and 30 d after sowing, but at day 40 this increase was only twofold.

Cultivar differences in plant fresh weight were most pronounced 40 d after sowing, Slobolt, despite its slower initial development, was significantly heavier than Grand Rapids which was significantly heavier than Thai.

Table.3.1 Effects of temperature, photoperiod and cultivar on fresh weight (g/plant) at each harvest

A MAIN EFFECTS

	Days after sowing			
Temperature °C	10	20	30	40
25/15	.083b	2.70b	39.8b	199.2b
30/20	.132a	6.38a	97.0a	349.0a
Daylength (h)				
10	.089b	2.31b	30.3c	184.8c
12	.063c	2.24b	52.0b	225.1b
14	.171a	9.08a	123.0a	412.5a
Cultivar				
Thai	.115a	5.11a	68.4a	248.0c
Grand Rapids	.122a	4.03c	67.6a	268.4b
Slobolt	.086b	4.48b	69.2a	306.0a

B INTERACTIONS

	Days after sowing			
	30		40	
Temperature x Daylength	25/15°C	30/20°C	25/15°C	30/20°C
10	18.9	41.8	126.8	242.8
12	28.1	75.9	146.4	303.8
14	72.5	173.4	324.5	500.6
L.S.D. .05	8.59		25.17	
Temperature x Cultivar				
Thai			162.4	333.5
Grand Rapids			212.4	324.4
Slobolt			222.8	389.2
L.S.D. .05			25.17	

Daylength x Cultivar	10	12	14
Thai	180.6	196.2	367.1
Grand Rapids	167.1	238.2	399.8
Slobolt	206.6	240.8	470.5
L.S.D. .05		30.20	

Values not followed by the same letter differ at P = 0.05

Although an increase in the photoperiod resulted in a progressive increase in plant fresh weight, an analysis of the interactions between temperature and daylength, and temperature and cultivar showed that the highest fresh weight was recorded at long days (14 h) and high temperatures (30/20°C). There were cultivar effects only at day 40. Slobolt had higher fresh weights than the others under longdays and high temperatures.

Reports examining the effects of photoperiod and temperature, and their interactions, on plant growth and development vary in their conclusions depending on light intensity. Increased vegetative growth in lettuce plants has been associated with relatively high irradiance levels and relatively long photoperiods (Tincker, 1933; Brouwer and Huyskes, 1968; Dullforce, 1971; Dennis and Dullforce, 1974a,b; Grey and Steckel, 1981; Cracker and Seibert, 1983) and high temperature (Bensink, 1971; Bierhuizen et al., 1973; Holsteijn, 1980a,b; Knight and Mitchell, 1983; Scaife, 1973; Wurr et al., 1981). Brouwer and Huyskes (1968) found that the fresh weight of cv. Rapide and its hybrid with cv. Hamadan produced higher yields under long day conditions (16 h) than short day conditions (8 h) when grown at 20°C at either high light intensity (120 W/m^2) or low light intensity (50 W/m^2), while Bierhuizen et al. (1973) demonstrated that a rapid linear increase in fresh weight occurred with an increase in temperature irrespective of light intensity or duration.

With cv. Cobham Green, Wurr et al. (1981) suggested that lettuce sown when the soil temperature was 20°C had heavier heads at maturity than those sown under cooler conditions (12-16°C). Gray and Steckel (1981) concluded that temperature does not appear to be the only factor of importance and it was considered likely that photoperiod and light quality were also contributing factors.

In this study, plants grown at both temperatures reached a marketable size between 30-40 d after sowing depending on other environmental conditions. Marketable plant size was reached at 30 d after sowing in plants grown at 12 or 14 h daylength at 30/20°C and 40 d after sowing in plants at 10 and 12 h daylength at 25/15°C. However, the commercial grower is not only interested in the yield of fresh weight but also in the quality of the marketable head (Krizek *et al*., 1974).

Generally plants grown under a lower temperature regime showed a better quality than plants grown under the higher temperature. Plants at low temperature (25/15°C) were light yellow-green in leaf colour and were of optimal size and freshness. The best visual quality was obtained in plants grown at 14 h daylength, under the alternating temperature of 25/15°C and which were harvested 30 d after sowing. At 30/20°C, the plants produced pale green leaves and showed excessive softness. Shoemaker (1953) also suggested that high temperature caused a bitter taste and poor quality in lettuce.

Visual assessment of lettuce plants grown in this study suggested that since Thai consumers prefer young and fresh lettuce, the optimum time to harvest plants grown under 12 h daylength should be about 30-40 d after sowing at 25/15°C and 30 d at 30/20°C. By comparison plants grown at 10 h daylength did not reach optimum visual quality until 40 d after sowing at either temperature (Plate 3.1).

Although long days and high temperatures have a promotive effect on vegetative growth in leaf lettuce such conditions also promote early bolting (Thompson and Knott, 1933; Tincker, 1933; Rappaport and Wittwer, 1956a,b; Glenn, 1984) and the development of tipburn (Knott *et al*., 1937; Tibbitts and Rao, 1969; Cox *et al*., 1976). In the present study, plants of Thai and Grand Rapids began to bolt 40 d after sowing when grown at 14 h and at 30/20°C while Slobolt, a bolting-resistant cultivar, (Thompson anbd Kosar, 1948) remained vegetative. Such plants, while remaining vegetative, were considered to be of reduced market

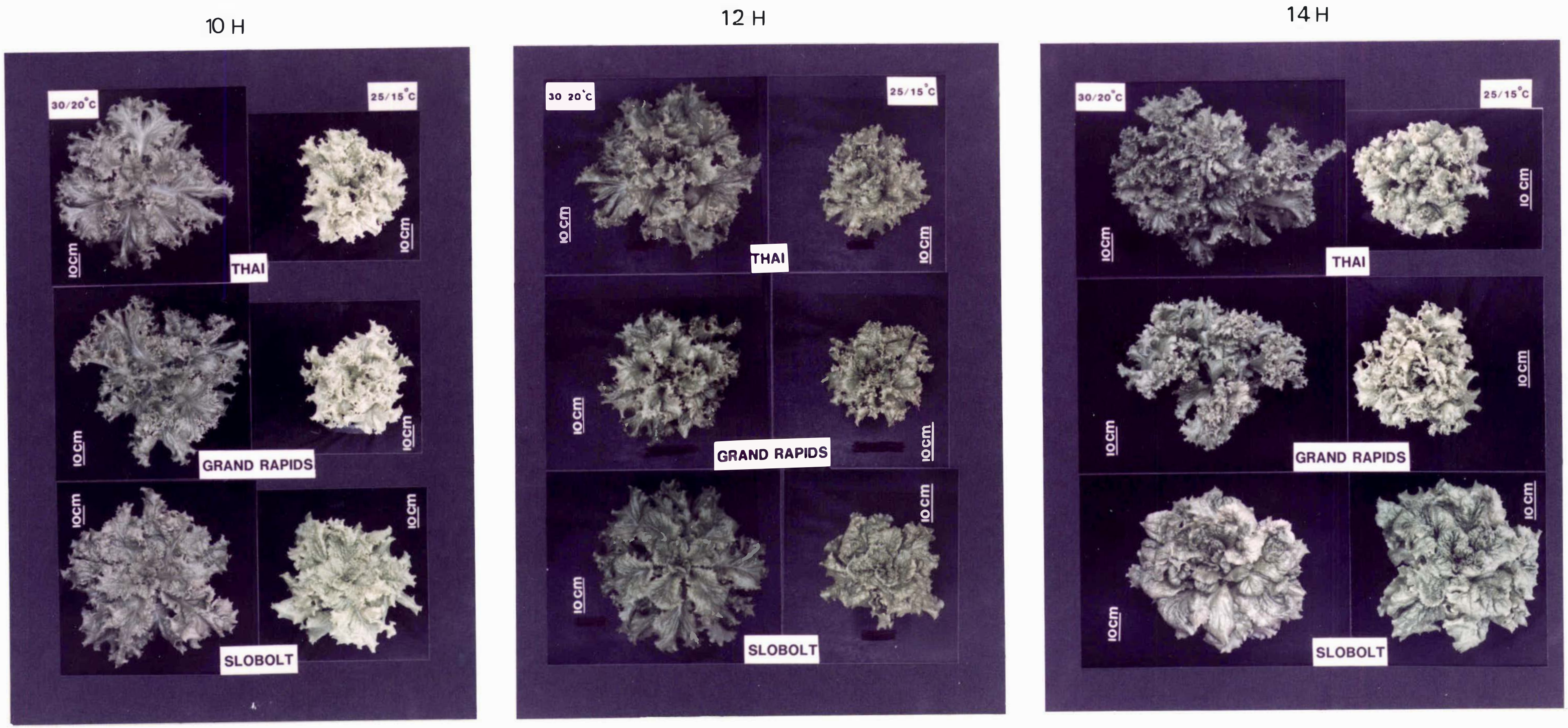


Plate 3.1 Visual appearance of lettuce plants at 40 d after sowing

value due to the production of oversized plants. Tipburn development was observed approximately 30 d after sowing in plants of both Thai and Grand Rapids grown under 12 or 14 h daylengths at 30/20°C. Slobolt, however, did not develop tipburn until about 40 d after sowing. Bolting was also delayed in all three cultivars grown at 25/15°C and 14 h daylength. However, the development of senescence and decay in the older leaves of plants grown under these condition substantially reduced the quality of the plants.

Thai and Grand Rapids developed similarly in terms of their vegetative characters. Slobolt generally had very wrinkled leaves compared to the more acceptable leaf characteristics of Thai and Grand Rapids. This difference was particularly evident in plants grown in 14 h daylength at both temperatures (Plate 3.1).

2. Plant Dry Weight

Plant dry weight generally followed the same trend as plant fresh weight in its reaction to temperature, daylength and cultivar (Table 3.2 and Appendix 7). In all cultivars, high temperature (30/20°C) and long photoperiod (14 h) both significantly increased plant dry weight at every harvest. A photoperiod of 12 h also produced plants with a higher dry weight than plants grown at 10 h daylength at all harvests beyond the first at 10 d from sowing.

At later stages of growth (40 d after sowing), cultivar differences were also observed. Slobolt had a higher dry weight than Thai and Grand Rapids.

As had been shown in previous results on fresh weight changes, Slobolt after an initially poor start during the first 20 d after sowing subsequently produced plants with a higher dry weight than the other two cultivars, 40 d after sowing.

Table 3.2 Effects of temperature, photoperiod and cultivar on dry weight (g /plant) at each harvest

A MAIN EFFECTS

	Days after sowing			
Temperature °C	10	20	30	40
25/15	.007b	.177b	2.45b	9.82b
30/20	.009a	.471a	5.15a	16.82a
Daylength (h)				
10	.005b	.163c	1.75c	8.90c
12	.005b	.197b	3.09b	10.94b
14	.014a	.611a	6.57a	20.12a
Cultivar				
Thai	.008a	.334a	3.73a	11.60b
Grand Rapids	.009a	.321a	3.74a	12.48b
Slobolt	.007b	.317a	3.94a	15.88a

B INTERACTIONS

	Days after sowing			
	30		40	
Temperature x Daylength	25/15°C	30/20°C	25/15°C	30/20°C
10	1.15	2.34	5.98	11.82
12	1.96	4.22	7.42	14.46
14	4.25	8.88	16.06	24.18
L.S.D. .05	.36		NS	
Temperature X Cultivar				
Thai	2.41	5.06	8.25	14.95
Grand Rapids	2.33	5.15	10.05	14.91
Slobolt	2.63	5.25	11.16	20.60
L.S.D. .05	.36		1.28	

	30			40		
Daylength X Cultivar	10	12	14	10	12	14
Thai	1.46	3.18	6.56	8.77	9.24	16.79
Grand Rapids	1.76	3.18	6.26	8.11	11.30	18.03
Slobolt	2.02	2.92	6.88	9.82	12.29	25.54
L.S.D. .05	.44			1.57		

Values not followed by the same letter differ at P = 0.05

The interaction between temperature and daylength showed that the increases in dry weight, caused by increasing photoperiod, were accentuated at the high temperature (30/20°C). This effect was most noticeable 30 d after sowing.

The main cultivar effect was modified when the temperature interacion was considered 40 d after sowing. The response to high temperature was greater for Slobolt than Thai and Grand Rapids.

The evaluation of the cultivar x daylength interaction 40 d after sowing, showed that Slobolt had the greater response of the cultivars to the 14 h daylength.

In the present experiment, the changes in temperature generally doubled the dry matter yields in favour of the higher temperature regime, 30/20°C. Other studies have also shown that increasing temperature results in a significant increase in dry-matter yield (Nichols, 1977; Lorenz and Wiebe, 1980).

Tibbitts and Kozlowski (1980) found that Grand Rapids plants produced higher yields under 25/15°C day/night than 15/20°C day/night even when they received a photosynthetic photon flux density in excess of 900 μmol/(m^2s) (181 W/m^2). Waldmann's Green and Salad Bowl also produced higher dry matter yields at 25/25°C day/night than under 25/20°C day/night temperatures (Knight and Mitchell, 1983). Larger plants are produced under longer photoperiods and higher irradiance levels (Brouwer and Huyskes, 1968; Holsteijn, 1981; Cracker and Seibert, 1983).

As stated earlier, dry matter yields of plants in the present study were approximately doubled when the daylength was increased from 12 to 14 h duration. This supports previous work by Cracker and Seibert (1983) which also showed that the total accumulation of vegetative dry weight in lettuce was mainly affected by photoperiod. They found that plants of Grand Rapids at market maturity produced three times more dry matter when grown under a 24 h photoperiod than under an 8 h photoperiod at 20/12°C day/night and 113 W/m^2. Differences of this magnitude have been directly ascribed to differences in light intensities and temperatures or to light duration by Whatley and Whatley (1980).

A linear relationship was observed between the logarithm of plant dry weight of each cultivar, at each temperature and daylength, with time. Mean differences in relative growth rate (RGR) for each cultivar during the exponential growth phase were not significantly different under different temperatures or photoperiods (Appendix 4). Similar results have been obtained by other workers who have shown that the RGR of Waldmann's Green and Salad Bowl were the same for plants grown at 25/20°C or 25/25°C day/night even though total plant dry weight was greater at higher temperatures (Knight and Mitchell, 1983). This lack of relationship was further shown by Scaife (1973) and Wurr et al, (1981), who demonstrated that the RGR of Cobham Green plants was not affected significantly over a wide temperature range from 10°C to 16.5°C. However at 22°C the RGR was higher than at 10°C, i.e. 0.35 gg^{-1} d^{-1} at 22°C and 0.11 gg^{-1} d^{-1} at 10°C (Scaife, 1973). A rise of about 10°C temperature has also been shown to cause a doubling of the respiration rate (Evans, 1972). This may play an important part in determining the overall net gain in dry weight with time.

3. Leaf Area

Leaf area results showed a similar trend to those obtained for fresh and dry weight (Table 3.3 and Appendix 8). The main effects of temperature, photoperiod and cultivar generally gave significant results. There was a consistent increase in leaf area with increasing temperature at every harvest. The greatest area was exhibited by plants grown under the longest daylength (14 h) at all harvests. A daylength of 10 h generally produced the smallest plants. Despite an initial slower leaf area accumulation, Slobolt plants ultimately produced a significantly

Table 3.3 Effects of temperature, photoperiod and cultivar on leaf area (cm^2/plant) at each harvest

A MAIN EFFECTS

	Days after sowing			
Temperature °C	10	20	30	40
25/15	3.65b	91.3b	991b	4036b
30/20	5.83a	209.5a	2009a	7056a
Daylength (h)				
10	4.26b	81.7c	833c	4365b
12	2.79c	101.4b	1154b	4605b
14	7.17a	268.0a	2649a	7669a
Cultivar				
Thai	4.98a	150.8a	1516b	4650b
Grand Rapids	5.21a	148.4a	1429b	4979b
Slobolt	4.04b	151.9a	1690a	7011a

B INTERACTIONS

	Days after sowing			
	30		40	
Temperature x Daylength	25/15°C	30/20°C	25/15°C	30/20°C
10	586	1080	3257	5474
12	656	1653	3015	6196
14	1732	3565	5836	9503
L.S.D. .05	156.3		396.5	
Temperature x Cultivar				
Thai	941	2092	3138	6162
Grand Rapids	930	1928	3939	6019
Slobolt	1104	2277	5031	8991
L.S.D. .05	NS		396.5	

Daylength x Cultivar	10	12	14	10	12	14
Thai	692	1193	2665	3914	3950	6086
Grand Rapids	809	1183	2295	3778	4488	6671
Slobolt	997	1088	2986	5404	5378	10251
L.S.D. .05		191.4			687.6	

Values not followed by the same letter differ at P = 0.05

higher leaf area than the other two cultivars at both 30 and 40 d after sowing. No differences were observed between Thai and Grand Rapids.

The interaction between daylength and temperature showed that at all daylengths, high temperature (30/20°C) doubled leaf area. This response was greatest at the 14 h daylength and high temperature.

When the interactions between temperature and cultivars were investigated, the only significant result appeared at 40 d after sowing. Grand Rapids produced a significantly higher leaf area than Thai at the low temperature (25/15°C) whereas, no difference between Thai and Grand Rapids was observed at the higher temperature (30/20°C). A comparison of the daylength x cultivar interaction showed that Slobolt generally produced greater leaf area than Thai and Grand Rapids; this effect being most pronounced at the final harvest and at the longer photoperiod (14 h). Slobolt's ultimate superiority, despite an apparently slower start, was attributed to its capacity to remain vegetative and to increase leaf area for a longer duration prior to bolting. This was most evident in the 30/20°C temperature and 14 h daylength treatment. However, the mean relative leaf growth rate (RLGR) for the 40 d period showed no significant differences between cultivars at either temperature or at any daylength (Appendix 4).

Other investigators have measured increased leaf area of lettuce under high temperature (22°C) (Lorenz and Wiebe, 1980) and under higher temperature (25.5°C) combined with low light intensity (90W/m^2) (Nichols, 1977) or long photoperiod (24 h) under a low light level of 14.1 W/m^2 (Cracker and Seibert, 1983). In contrast, Verkerk and Spitter (1973) found no differences in leaf areas of plants grown at 25/17°C or at 21/13°C if radiant energy was maintained at a low level of 12.8 W/m^2.

The above studies only cover the growth of lettuce under low light conditions. Such conditions are generally only relevant to greenhouse lettuce production in the winter or to the utilizaation of light in some controlled environment agriculture facilities.

The results of the present study, support observations by previous workers of the promotive effect of long photoperiods and high temperature on leaf area development in lettuce.

4. Leaf Number

It was evident that from 10 - 40 d after sowing, the number of green leaves (>1 cm long) increased with increasing temperature and daylength (Table 3.4). The increase was most pronounced in Slobolt grown under high temperature and in long days (14 h). Although there were significant differences between plants grown at 10 or 12 h photoperiods at 20 and 30 d after sowing, these differences were relatively small; plants grown under 12 h generally only developed one or two more leaves than plants developing under a 10 h daylength.

The interaction between temperature and daylength showed that the high temperature (30/20°C) resulted in a marked increase in leaf number for plants at 14 h daylength.

Generally, leaf number was similar for each cultivar within any one temperature or daylength (Fig 3.1) but overall Slobolt had the highest leaf number (Table 3.4). Presumably the longer vegetative growth period of Slobolt caused by its genetic late bolting character resulted not only in increased leaf area but also greater leaf numbers. This effect was particularly apparent at late harvests (30 and 40 d after sowing).

Data in this study indicated that high temperature and long days increased lettuce leaf numbers. Other workers have reported that butterhead lettuce plants produce leaves in an essentially

Table 3.4 Effects of temperature, photoperiod and cultivar on leaf number/plant at each harvest

A MAIN EFFECTS

	Days after sowing			
Temperature °C	10	20	30	40
25/15	3.33a	7.44b	15.26b	25.74b
30/20	3.89a	9.96a	22.15a	37.70a
Daylength (h)				
10	3.50a	7.50c	15.00c	26.94b
12	3.33a	8.11b	17.11b	27.28b
14	4.00a	10.50a	24.00a	40.94a
Cultivar				
Thai	3.67a	8.44b	17.94b	29.50b
Grand Rapids	3.67a	8.61b	18.17b	31.17b
Slobolt	3.50a	9.06a	20.00a	34.50a

B INTERACTIONS

	Days after sowing			
	30		40	
Temperature x Daylength	25/15°C	30/20°C	25/15°C	30/20°C
10	12.56	17.44	21.89	32.00
12	14.78	19.44	23.11	31.44
14	18.44	29.56	32.22	49.67
L.S.D. .05	1.04		2.48	

Values not followed by the same letter differ at P = 0.05

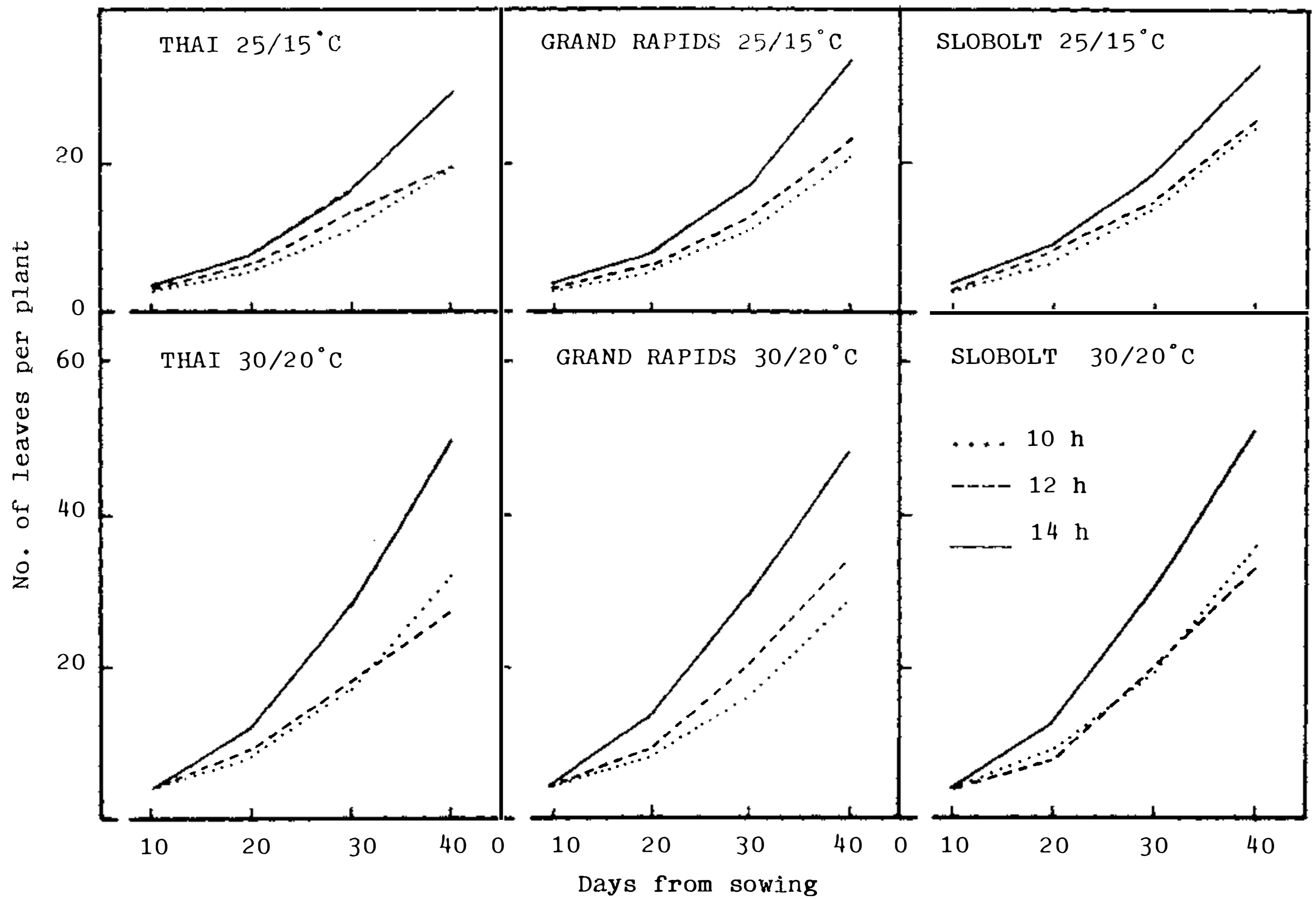


Fig. 3.1 Number of green lettuce leaves (> 1 cm) for each cultivar at different temperatures and photoperiods.

linear fashion. The rate of production was shown to increase with increasing temperature at a constant light intensity (Bensink, 1971; Lorenz and Wiebe, 1980). A similar result was observed when increasing photoperiods and high irradiance levels were used with Grand Rapids (Cracker and Seibert, 1983).

It is clear from these experiments that large increases in the economic yield of lettuce can be obtained through the use of high temperatures and long daylengths. However, this experiment showed that while dry weight and leaf area of leaf lettuce plants was significantly increased by high temperatures and long daylengths there was also an increase in leaf number.

5. Stem Length

There was a consistently significant increase in stem length with increasing temperature and extending daylength at each harvest. Generally the Thai cultivar produced greater stem lengths than Grand Rapids, and Slobolt plants produced shorter stems than either of the other two (Table 3.5 and Fig. 3.2).

The temperature x daylength interaction showed that stem length was consistently greater under the 14 h photoperiod particularly under the high temperature environment (30/20°C).

The cultivars also showed a differential response under both temperatures. Under the low temperature (25/15°C) there were only small differences between all three cultivars whereas larger differences were observed between the Thai cultivar and the other two cultivars under the high temperature (30/20°C).

With increasing daylength there is an increase in the magnitude of stem length differences between cultivars. Thai had a greater increase in stem length than the other cultivars particularly under the 14 h daylength. It was also noticed that longer stems produced longer internodes (Plate 3.2).

Table 3.5 Effects of temperature, photoperiod and cultivar on stem length/plant (mm) at each harvest

A MAIN EFFECTS

	Days after sowing		
Temperature °C	20	30	40
25/15	3.15b	12.15b	34.3b
30/20	6.59a	31.56a	121.8a
Daylength (h)			
10	3.50c	12.44c	41.1c
12	4.11b	20.00b	59.2b
14	7.00a	33.11a	128.9a
Cultivar			
Thai	5.72a	24.44a	98.4a
Grand Rapids	5.06b	24.00a	84.4b
Slobolt	3.83c	17.11b	51.4c

B INTERACTIONS

	Days after sowing: 30		Days after sowing: 40	
Temperature x Daylength	25/15°C	30/20°C	25/15°C	30/20°C
10	8.44	16.44	22.9	69.2
12	10.33	29.67	25.6	92.9
14	17.67	48.56	54.6	203.3
L.S.D .05	2.58		6.90	
Temperature x Cultivar				
Thai	13.22	35.67	33.9	163.0
Grand Rapids	12.67	35.33	39.2	129.6
Slobolt	10.56	23.67	29.9	72.9
L.S.D. .05	2.58		6.90	

	30			40		
Daylength x Cultivar	10	12	14	10	12	14
Thai	11.83	21.50	40.00	52.3	61.8	181.2
Grand Rapids	13.83	23.00	35.17	47.2	70.3	135.7
Slobolt	11.67	15.50	24.17	38.7	45.5	70.0
L.S.D. .05	3.16			9.7		

Values not followed by the same letter differ at P = 0.05

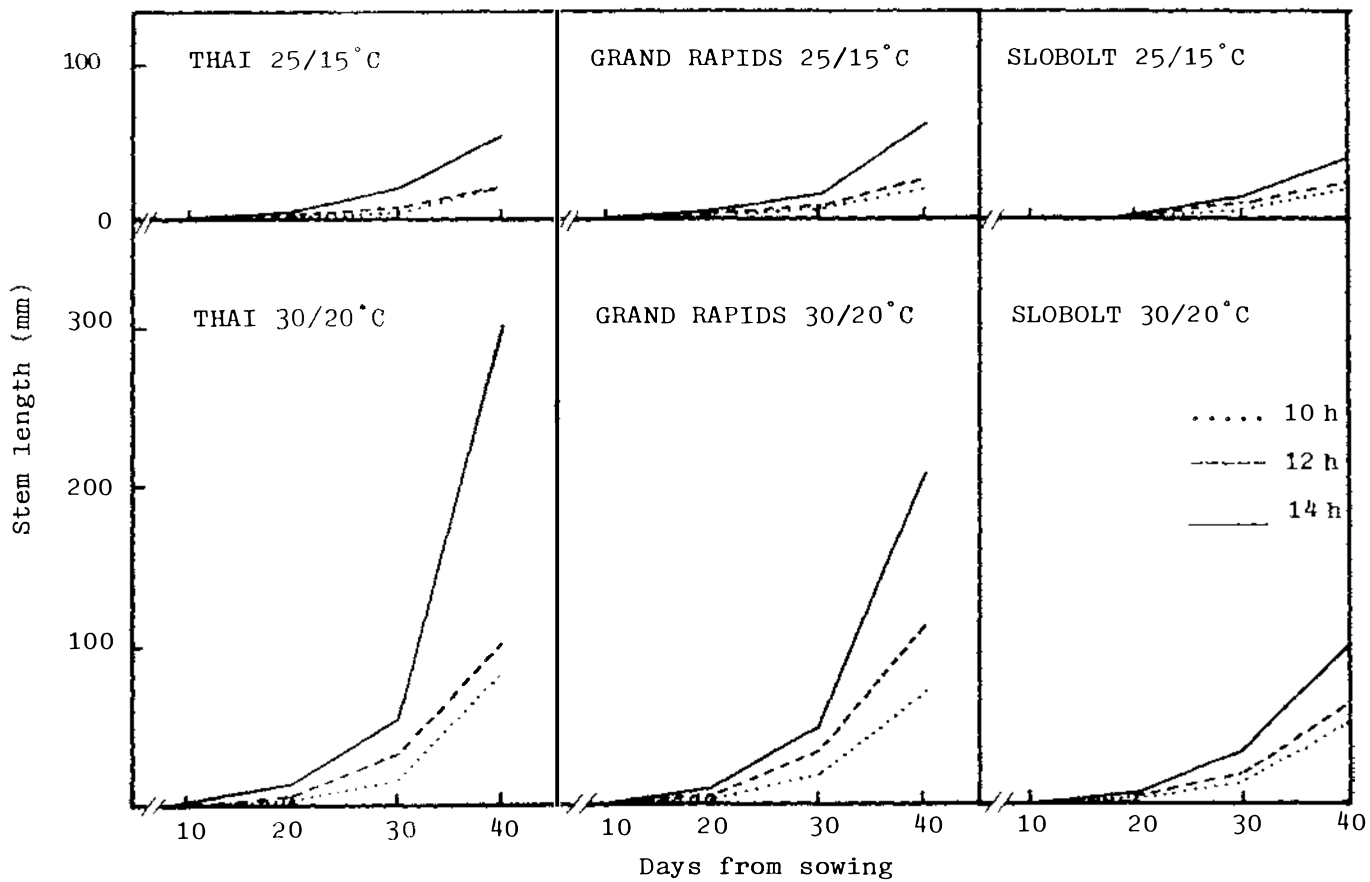
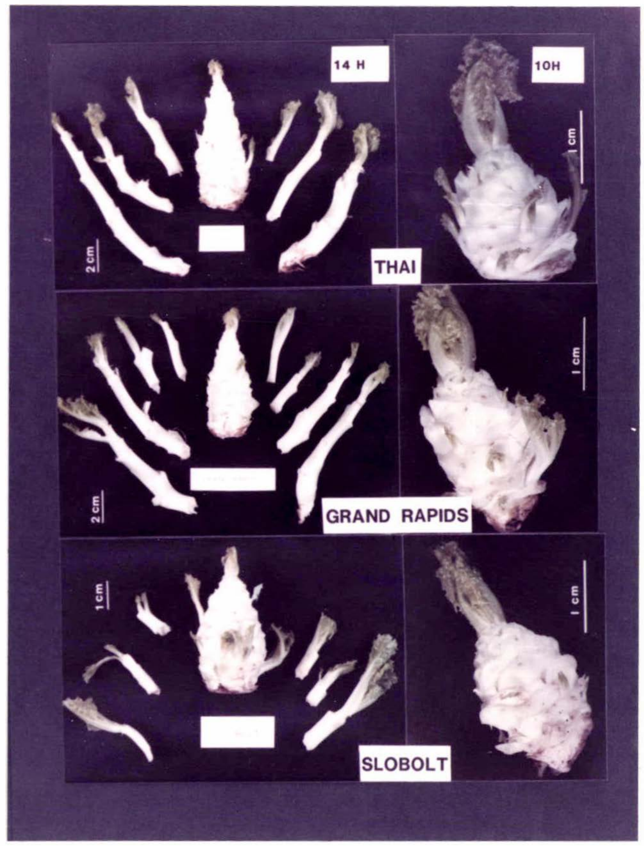
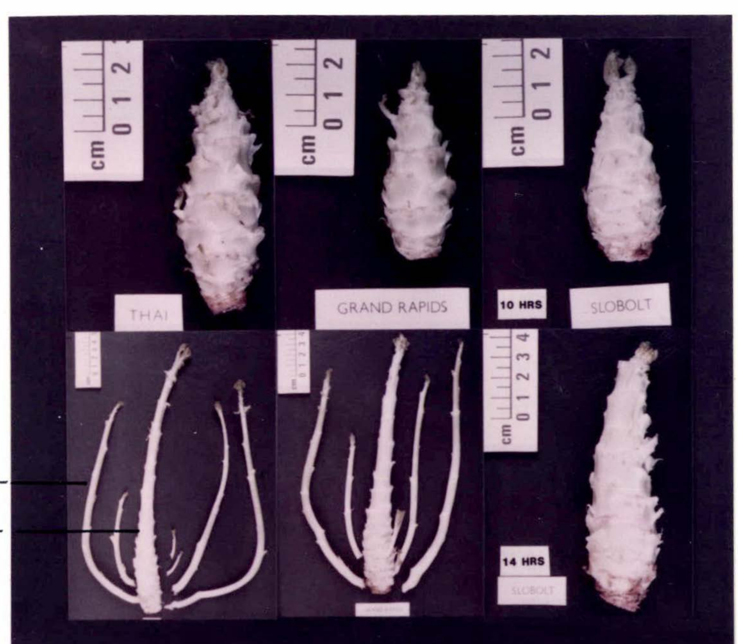


Fig. 3.2 Stem length (mm) of lettuce for each cultivar at different temperatures and photoperiods.



25/15 C



30/20 C

Shoot

Stem

Plate 3.2 Stem and shoot development characters in three leaf lettuce cultivars under 10 and 14 h daylengths at 25/15°C and 30/20°C

In most lettuce cultivars, stem elongation normally accompanies floral initiation and often destroys green vegetable market acceptability. High temperatures have been identified as a main cause of this development (Thompson and Knott, 1933; Andrew, 1953; Raleigh, 1959; Rappaport and Wittwer, 1956a; Ito *et al.*, 1963; Rappaport and Wittwer, 1956b; Yamazaki, 1962; Cytovic, 1967a; Hiraoka, 1967).

The importance of temperature in combination with photoperiod in influencing stem elongation has been reported by Rappaport and Wittwer (1956b) in Grand Rapids. They demonstrated that stem elongation could be induced by either high night temperatures (21°C) or long photoperiods (16 h). Some cultivar variation in response was observed. For example, cv. Tender Green only required a long photoperiods (16 h) while cv. Bibb responded better when, in addition to long days, plants were given warm night temperatures. Krickl (1954) also observed in cv. Maikonig that a short day treatment (9 h) a few days after emergence delayed bolting even under normally promotive high temperature conditions.

It is interesting that nearly all previous work described in the literature between 1933 and 1969 evaluated head lettuce using a wide range of temperatures (10 to 30°C) and photoperiods (8 to 24 h).

In the present experiment leaf lettuce was investigated under two temperature regimes which differed in their alternating temperatures by only 5°C (30/20°C, 25/15°C), and a range of photoperiods which differed by only 4 h (10 to 14 h). This suggests that the transition of lettuce from the vegetative to the reproductive stage is markedly sensitive to even relatively small differences in temperature and photoperiod.

For successful production of leaf lettuce for the vegetable market, lower temperature is recommended. Plants grown at low temperatures and in short days (10-12 h) remain vegetative for a longer time, allowing a more extended harvest period. Observations also suggest that under these conditions leaf quality and therefore consumer acceptability is higher.

However, under high temperature, lettuce plants could be harvested earlier than those at low temperature conditions. Delays in harvest however result in the plant bolting and in the production of poor quality plants.

6. Number of Shoots

The leaf lettuce cultivars used in this study showed a variable capacity to produce side shoots during a transition of vegetative to reproductive stage. This capacity differed between cultivars and was modified by environmental conditons.

Plants grown at 25/15°C generally developed more shoots than those at 30/20°C. Long day conditions (14 h) also produced plants exhibiting higher shoot numbers than plants grown at 10 or 12 h daylength. Plants of Thai and Grand Rapids produced more shoots than Slobolt under each of these conditions. Slobolt however only produced shoots in the low temperature and long day environment. High temperature severely suppressed shoot development in Slobolt and also in the other two cultivars unless they were grown in long days (Table 3.6 and Plate 3.2).

These results suggest that the onset and extent of shoot development is under photoperiodic control. However, this development also differs between cultivars at higher temperatures (30/20°C). Shooting in lettuce often destroys the marketable value of the crop. However, those shoots produced under short days were small and did not initially cause a lettuce plant to loose its vegetative quality.

Table 3.6: Number of shoots (< 1 cm long) 40 d after sowing

Temperature °C	Cultivar	Photoperiods (h) 10	12	14
25/15	Thai	3	2	7
30/20		0	0	7
25/15	Grand	2	2	9
30/20	Rapids	0	0	6
25/15	Slobolt	0	0	7
30/20		0	0	0

The results show that in Thai and Grand Rapids there is a production conflict between optimum vegetative and reproductive development. In these two cultivars high temperatures and long days were important in promoting vegetative growth. However, they were also positively related with premature seeding (bolting). Consequently the conditions favouring rapid production of a saleable green vegetable were also instrumental in reducing the length of time such vegetative plants retained their market acceptability.

A similar problem has been described by other workers in relation to lettuce growth (Thompson and Knott, 1933) and stem elongation (Rappaport and Wittwer, 1956b). In Slobolt however, the cultivar's delayed bolting characteristic ensures a longer period of market acceptability. In this situation the apparent conflict between vegetative and reproductive development is not so important.

CHAPTER 4

REPRODUCTIVE GROWTH, FLORAL INITIATION, FLOWERING PATTERN AND SEED PRODUCTION

A knowledge of those conditions which predetermine flowering and seed formation is useful in planning for the successful production of lettuce seed. Many workers have shown that most lettuce cultivars require high temperatures (21-26° C) and long days (16 h) for the stimulation of seed stalk formation (Garner and Allard, 1920; Thompson and Knott, 1933; Tincker, 1933; Krickl, 1954; Rappaport and Wittwer, 1956a, Raleigh, 1959; Ito et al., 1963; Cytovic, 1967a; Hiraoka, 1967a, 1969). Such work has also shown that flowering in lettuce is seriously delayed by short days. Leaf lettuce cultivars are particularly responsive to photoperiod and temperature changes (Rappaport and Wittwer, 1956b; Cytovic, 1967a) and flowering rate has been shown to be particularly influenced by fluctuations in temperature (Jones, 1927) or light intensity (Soffer and Smith, 1974a). However, in Grand Rapids good seed set has been observed only at night temperatures between 17 and 23°C under short day (8 h) conditions (Koller, 1962).

Most investigations have involved the study of lettuce plants growing under natural seasonal changes or under artificial conditions with either very short or very long photoperiods. There has apparently been little if any work on the mechanism by which the environment controls flowering pattern and seed fertility, particularly in leaf lettuce cultivars.

This study attempted to determine the effects of various temperature and daylength combinations on time to flowering, flowering pattern and seed production to provide a better understanding of the effect of these variables on the components of seed yield and quality.

MATERIALS AND METHODS

Three cultivars of leaf lettuce: Thai, Grand Rapids and Slobolt were grown under the same temperature and daylength combinations as described earlier in the vegetative growth section (Chapter 3). Details of the treatments and cultivation methods are also given in the previous section.

Plant Measurements

1 Floral Initiation (bolting) and Flowering Pattern

1.1 Days to bolting - days from sowing until flower bud formation was first observed (plate 4.1).

1.2 Days to anthesis - days from sowing until the first opened flower appeared.

1.3 Days to peak flowering (PF) - the number of days from sowing until the highest number of flowers open daily was counted throughout the experiment (3 plants/treatment) and the days to the first peak (PF1) and second peak (PF2) of flowering was recorded.

A photographic record was made of the various stages of flower head development (plate 4.2).

During the floral bud initiation stage, each plant was staked to avoid subsequent lodging of the stems and branches.

2. Seed Production

2.1 Number of florets/flower head - the number of florets (plate 4.3) present on 25 heads/plant was recorded at each peak flowering.

2.2 Number of seeds (fertile florets) per seed head - the number included only seeds which were fully formed (plate 4.4).

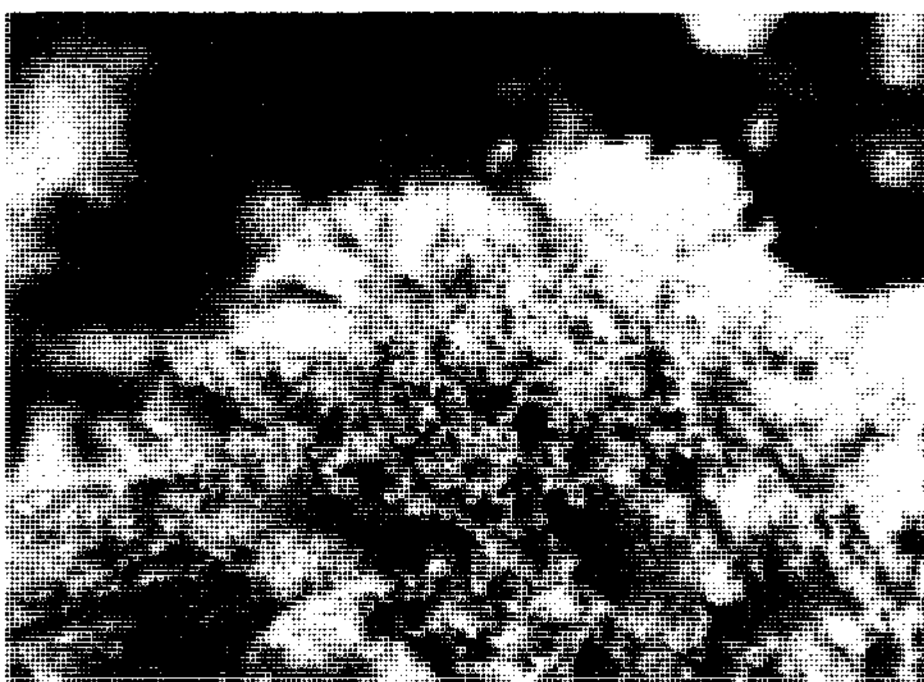


Plate 4.1 Floral initiation

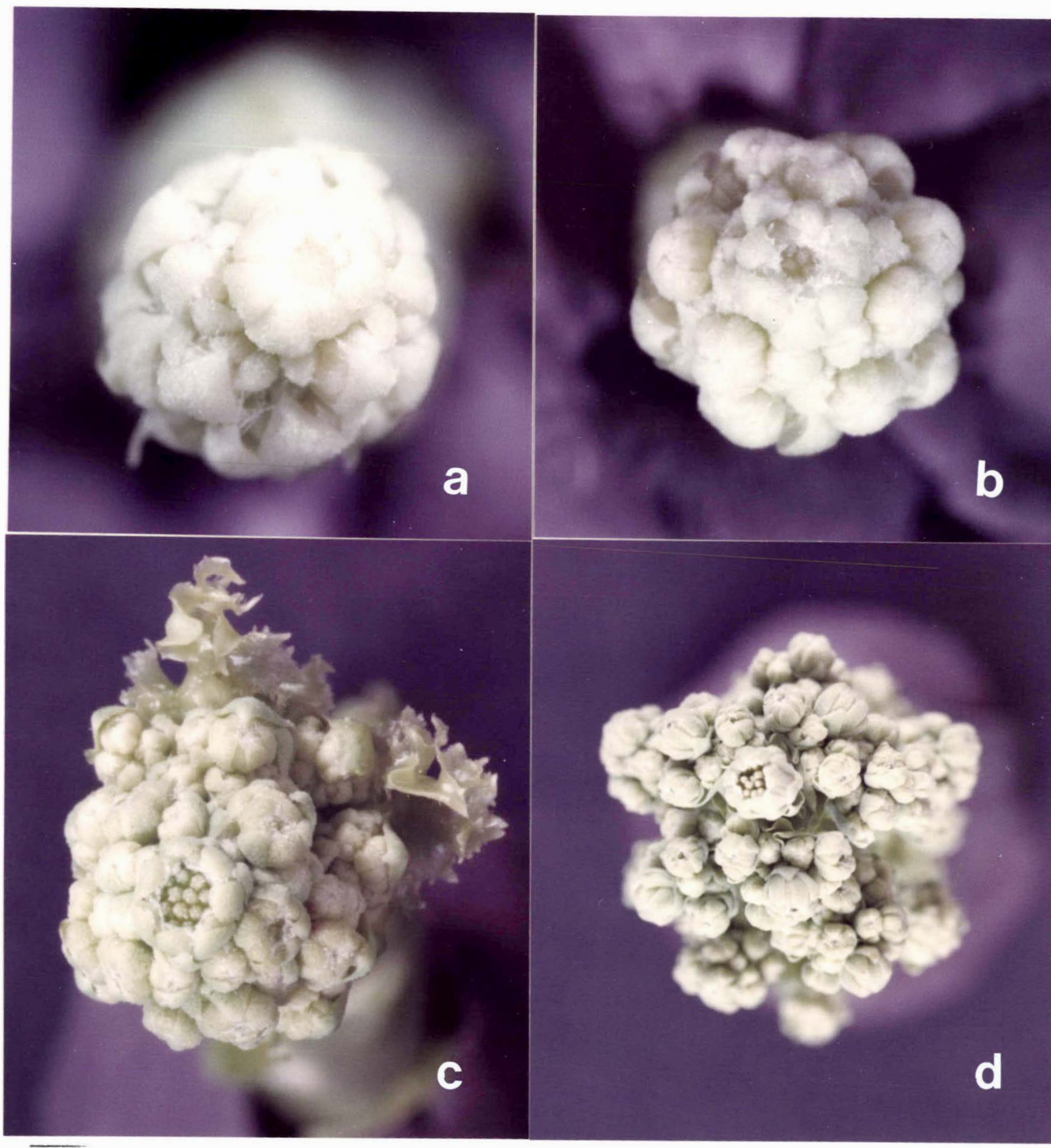


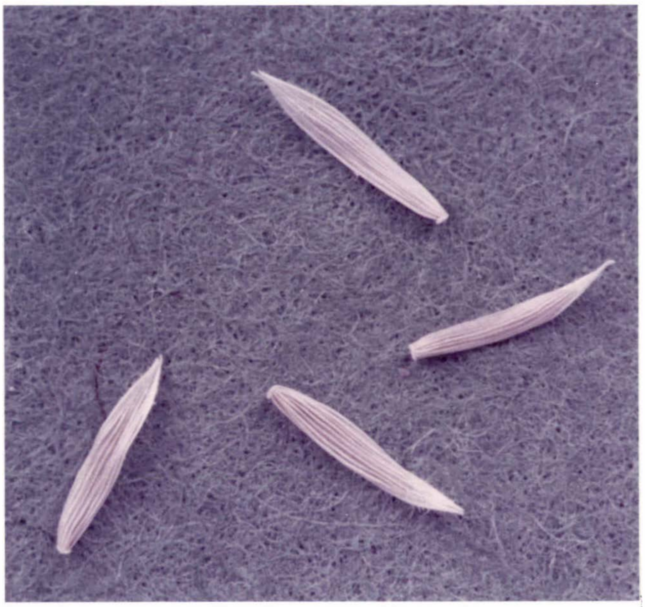
Plate 4.2 Flower development
a - b, terminal and lateral flower bud development
c - d, the first flower head showing the appearance of the corolla

a) Flower head at anthesis

b) Longitudinal section of flower head
showing individual florets

Plate 4.3 Lettuce flower head

Fully developed seed



Empty seed

Plate 4.4 Lettuce Seed

2.3 Number of empty seeds/seed head - seeds which showed no obvious contents either as result of seed abortion or due to lack of effective fertilisation (Plate 4.4).

2.4 Seed set (%) - the number of full seeds per 100 florets calculated from 2.2 and 2.3 above.

Data Analysis

A completely randomised design was used with a factorial arrangement of temperatures x daylengths x cultivars for the flowering study. For the seed set data, components were analysed using an analysis of variance at each flowering peak.

Definitions

The following definitions have been adopted in the reproductive study:

Floral initiation (bolting)	-	when flower buds were first observed (plates 4.1, 4.2).
Flower head	-	composed of many separate florets closely grouped to form a head (plate 4.3)
Floret	-	a small individual true flower (plate 4.3)
Inflorescence	-	seed stem with number of branches forming a cluster of flower heads or seed heads (plate 4.5)
Seed Head	-	pollinated flower head (plate 4.6)
Secondary branch	-	branch which developed from the main stem or lateral branch (Fig 4.1)
Tertiary branch	-	branch which developed from the secondary branch (Fig.4.1)
Lateral branch	-	branch which developed from axillary buds (Fig. 4.1)

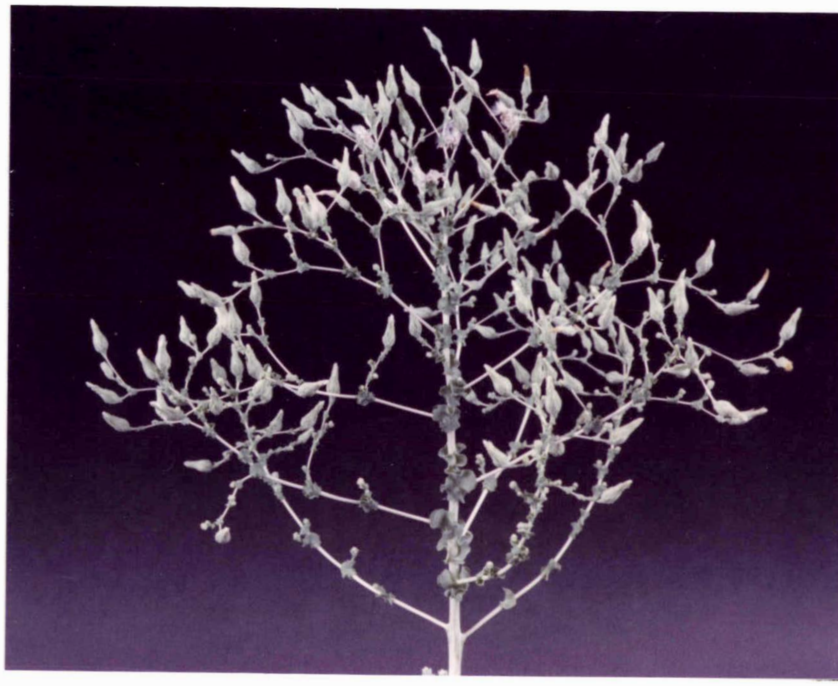


Plate 4.5 An individual lettuce plant inflorescene with a cluster of seed heads in various stages of development

Plate 4.6 Individual seed heads

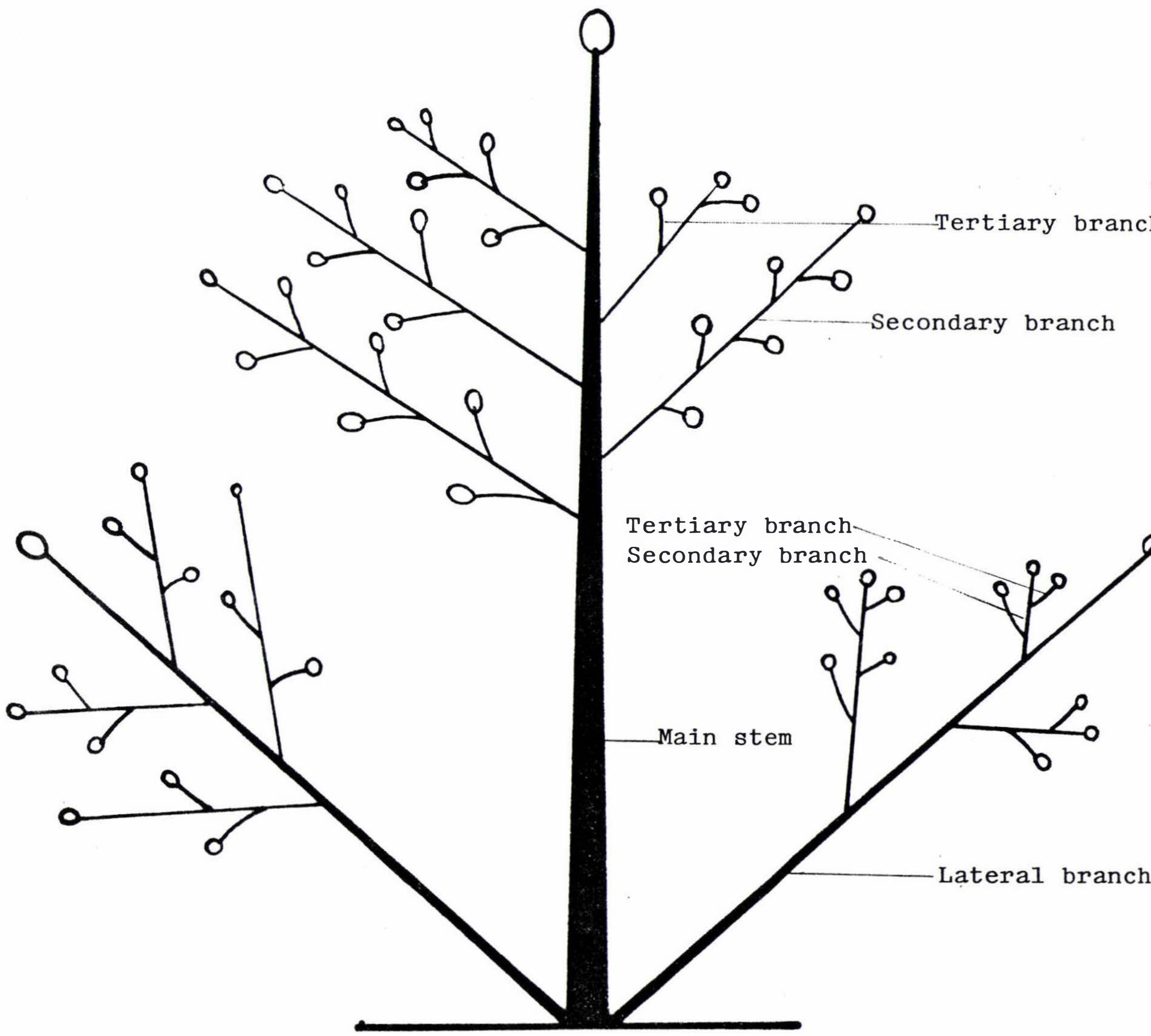


Fig 4.1 Diagrammatic representation of the inflorescences and branching of leaf lettuce

o = flower head

RESULTS AND DISCUSSION

1. Flowering Pattern

The number of days from sowing to floral initiation (bolting), anthesis (first flower appearance) and peak flowerings, consistently decreased with increasing temperature and extending daylength. This occurred in all three cultivars. However, the floral development of Slobolt was significantly delayed compared to Thai and Grand Rapids. Grand Rapids bolted and reached its first peak flowering before the other cultivars. Although Grand Rapids preceded Thai in this respect, the differences between them were small (Table 4.1, Fig 4.2).

An evaluation of the interactions showed that progressive increases in daylength from 10 to 14 h resulted in a proportionate decrease in the number of days to bolting, to anthesis, and to first peak flowering at the low temperature (25/15°C). However, at the high temperature (30/20°C) only the long daylengths of 14 h markedly reduced the times to these developmental stages. The 10 and 12 h daylengths showed only minor differences. Slobolt consistently took longer to bolt, flower and reached its first peak flowering than either Thai or Grand Rapids, particularly with increasing temperature. At the high temperature (30/20°C) there were only small differences between Thai and Grand Rapids in the number of days to reach their respective peaks of flowering. However, at the low temperature (25/15°C) the Thai cultivar took slightly longer than Grand Rapids to bolt, flower and reach its first peak flowering.

Interactive effects between the daylength treatment and the cultivars were similar for the times to bolting, anthesis and first peak flowering. Slobolt was significantly delayed in its flowering pattern when compared to Thai and Grand Rapids particularly under the 10 h daylength., There were few differences between Thai and Grand Rapids and these cultivars

Table 4.1 Effects of temperature, photoperiod and cultivar on lettuce flowering

A MAIN EFFECTS

	Days to Bolting	Days to Anthesis	Days to PF1
Temperature °C			
25/15°	68.19a	87.74a	107.11a
30/20°	50.74b	67.78b	86.04b
Daylength (h)			
10	65.10a	83.44a	104.72a
12	60.50b	82.33b	98.33b
14	52.28c	67.50c	86.67c
Cultivar			
Thai	53.56b	72.56b	90.72b
Grand Rapids	52.22c	71.72b	87.39c
Slobolt	72.61a	89.00a	111.61a

B INTERACTIONS

	Days to Bolting		Days to Anthesis		Days to PF1	
Temperature x Daylength	25/15°C	30/20°C	25/15°C	30/20°C	25/15°C	30/20°C
10	76.00	55.22	95.22	71.67	120.44	89.00
12	68.89	52.11	93.67	71.00	106.33	90.33
14	59.67	44.89	74.33	60.67	94.56	78.78
L.S.D. .05	1.24		1.26		1.76	
Temperature x Cultivar						
Thai	64.00	43.11	83.67	61.44	99.11	82.33
Grand Rapids	61.89	42.56	81.33	62.11	95.33	79.44
Slobolt	78.67	66.56	98.22	79.78	126.89	96.33
L.S.D. .05	1.24		1.26		1.76	

	Days to Bolting			Days to Anthesis			Days to PF1		
Daylength x Cultivar	10	12	14	10	12	14	10	12	14
Thai	57.67	55.50	47.50	77.17	78.00	62.50	93.83	94.33	84.00
Grand Rapids	57.17	53.50	46.00	76.50	77.17	61.60	91.83	89.33	81.00
Slobolt	82.00	72.50	63.33	96.67	91.83	78.50	128.50	111.33	95.00
L.S.D. .05	1.53			1.64			2.15		

Values not followed by the same letter differ at P = 0.05

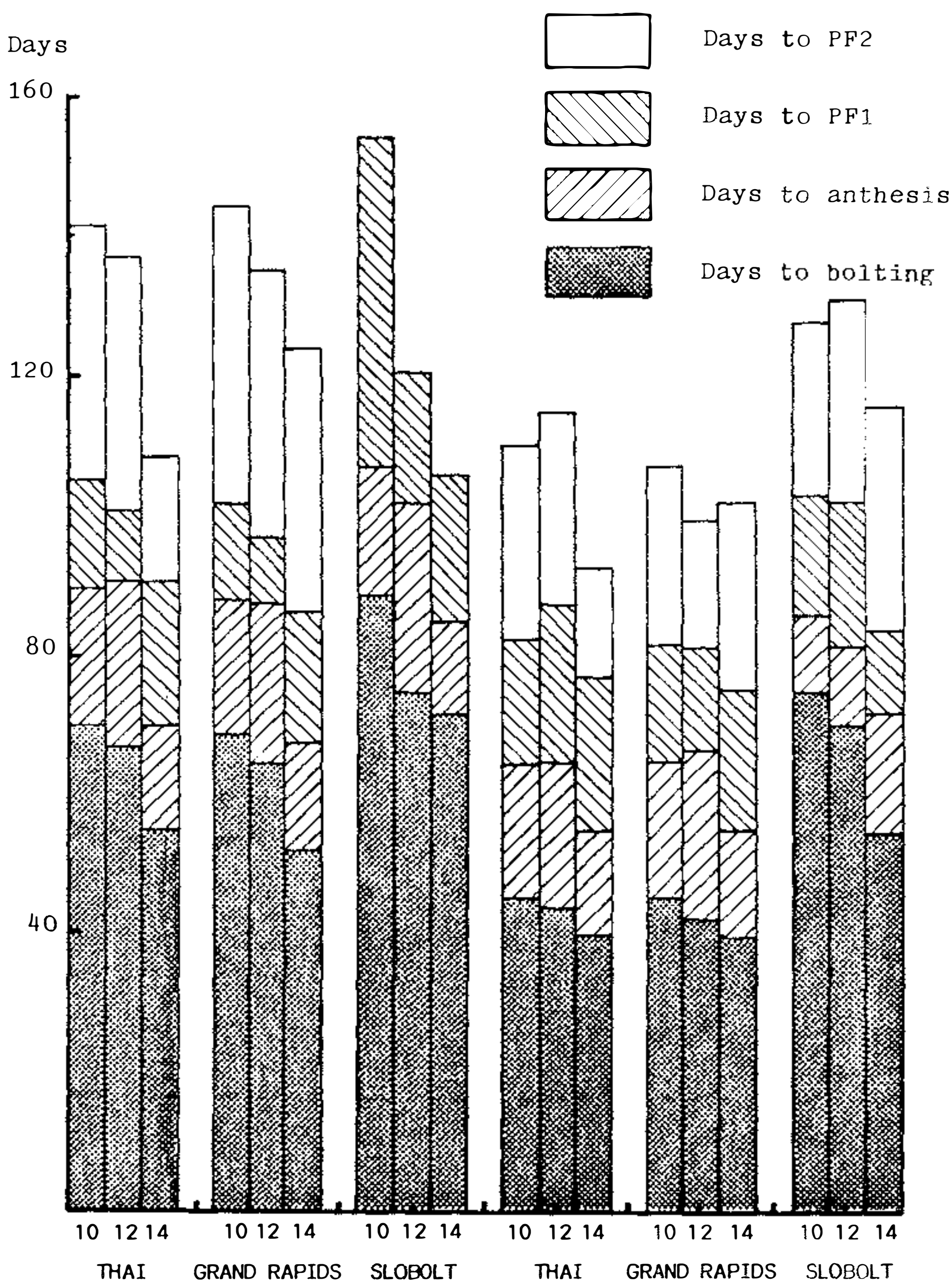


Fig. 4.2 Days to bolting, anthesis and peak flowering

really only responded to the long daylength of 14 h duration (Fig. 4.2).

The flowering responses of lettuce cultivars to temperature and photoperiod support the view that high temperatures (Thompson and Knott, 1933; Roberts and Struckmeyer, 1938; Ito et al., 1963; Hiraoka, 1969) or long days (Garner and Allard, 1920; Tincker, 1933; Krickl, 1954; Rappaport and Wittwer, 1956a,b; Yamazaki, 1962, Hiraoka, 1967; Cytovic, 1967a) are essential for floral induction.

In the Thai and Grand Rapids cultivars, flowering pattern was influenced primarily by high temperatures and photoperiod had a smaller effect. However, for Slobolt long days and high temperatures both accelerated bolting (Fig. 4.2). Other research has shown that Grand Rapids will flower under either warm nights or long photoperiod conditions (Rappaport and Wittwer, 1956b). Slobolt has also been shown previously to be very slow in bolting even after vernalization (Thompson and Kosar, 1948).

The increases in daylength from 10-12 h did not hasten bolting or flowering in Thai and Grand Rapids by any significant amount at either temperature (Fig. 4.2). These results are contrary to those of other workers. For example, Cytovic (1967a) reported that 8-12 h daylength sharply retarded flowering in leaf lettuce cultivars Moskovskij Parnikovyj, Boul and Bibb. However, some head lettuce cultivars are reported to be less sensitive to daylength (Hiraoka, 1967a; Cytovic, 1967a).

In this study, it was confirmed that Thai, Grand Rapids and Slobolt were quantitative long day plants at both temperatures. This result was particularly surprising considering the fact that lettuce is normally considered to be a quantitative long day at high temperatures and day neutral at low temperatures (Vince - Prue, 1975). Such differences are possibly due to:-

i) the range of temperatures that were used in this study;

25/15 and 30/20°C are considered to be high or optimum for floral initiation in lettuce (Thompson and Knott, 1933; Rappaport and Wittwer, 1956b).

ii) cultivar differences, and

iii) the daylengths that were used in this study were more typical of those which occur naturally in contrast to those used by many other workers where photoperiods are often very short or very long (e.g. 7 to 24 h).

In general it was shown that flowering occurred in all of the lettuce cultivars under daylengths ranging from 10 to 14 h and under the day/night temperatures of 25/15°C and 30/20°C.

In this study plants of all cultivars each showed the potential to produce two definite flowering peaks (Fig. 4.3 and 4.4 within an approximate 50 d flowering period. All three cultivars had two peaks at 30/20°C and at 25/15°C except Slobolt, which only had one peak of flowering, when plants were grown at 25/15°C, due to the delay in bolting. Slobolt only began to flower after the other cultivars had already reached their second flowering peak (Fig. 4.2). This delay resulted in the inability of Slobolt to produce a second peak of flowering within the 160 d experimental period. It is likely, however, that if the trial had been extended, Slobolt would have eventually produced a second flowering peak when grown in the 25/15°C environment.

The number of days taken to reach the first and second peak flowering are presented in Fig. 4.2. The second peak flowering pattern for each treatment followed the same trend as the first peak flowering pattern and generally followed the first peak by between 20 and 30 d.

There were differences in the flowering intensities of each cultivar (Figs. 4.3-4.4). The combination of 25/15°C temperature

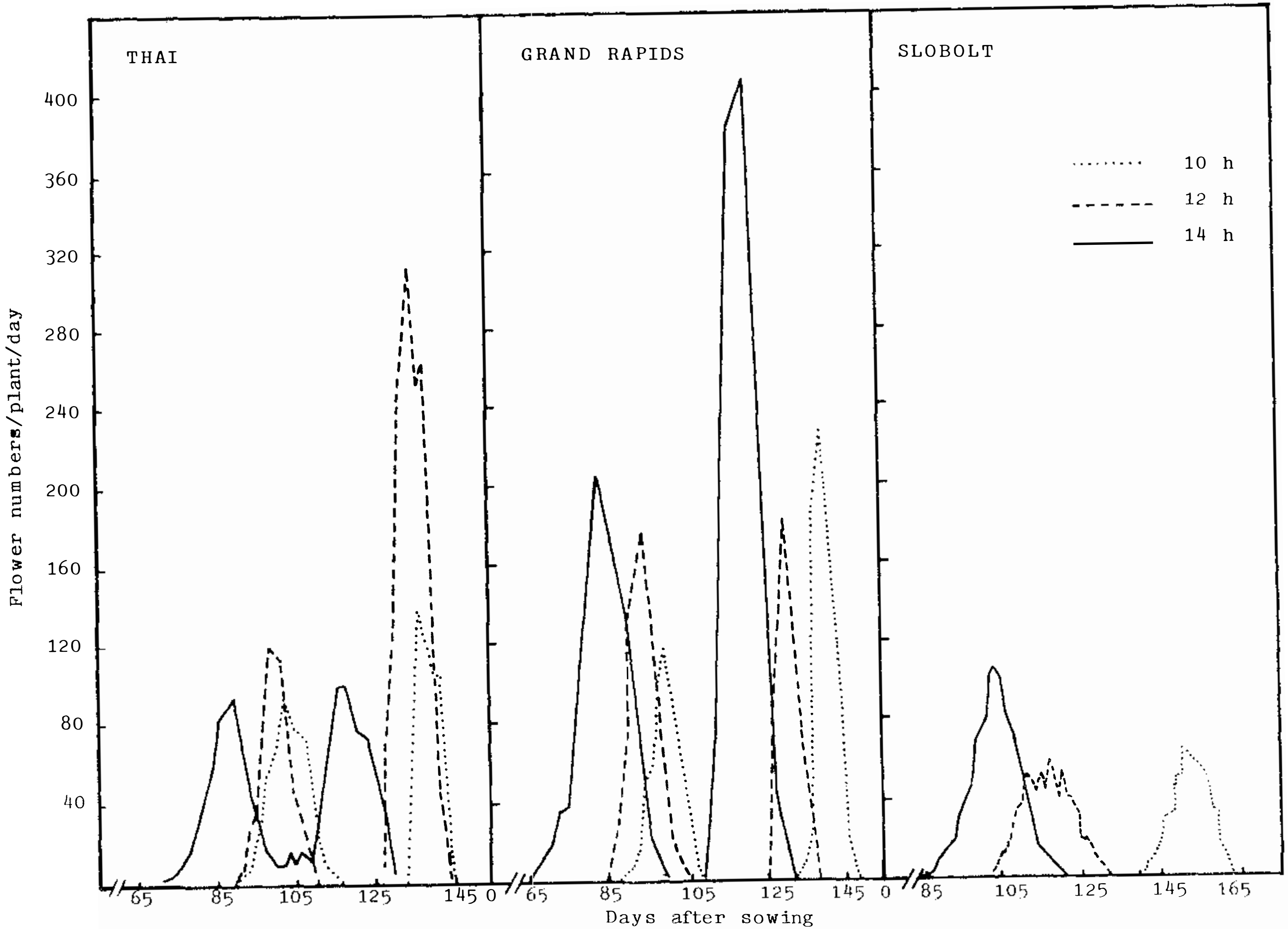


Fig. 4.3 Flowering pattern of three lettuce cultivars under different daylengths at 25/15°C

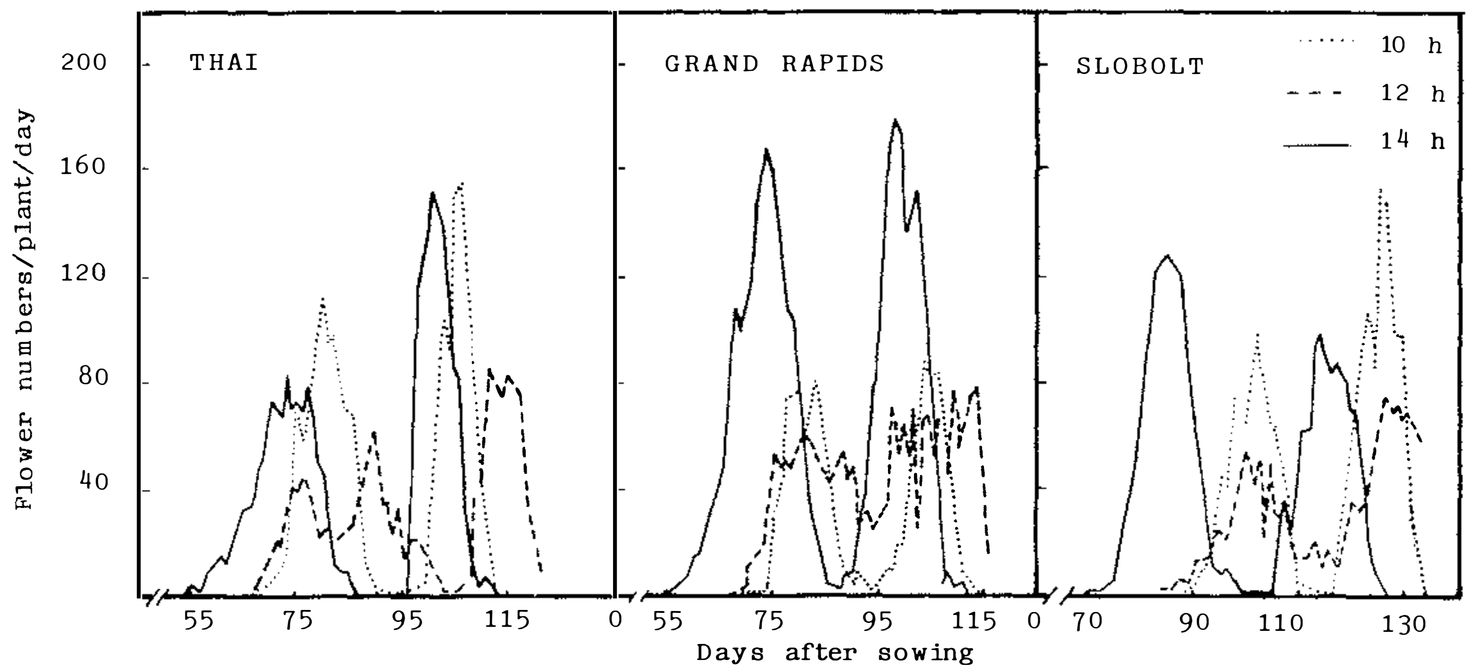


Fig. 4.4 Flowering pattern of three lettuce cultivars under different daylengths at 30/20°C

and 12 h daylength, resulted in a maximum number of flowers at both peak flowering times for the Thai cultivar. In contrast, maximum flower numbers in Grand Rapids grown at this temperature were produced at the 14 h daylength. At 30/20°C, Grand Rapids produced more intense flowering peaks than Thai under all daylengths (Fig. 4.4). Slobolt produced only one peak of flowering at 25/15°C, and in general produced flower number intensities which were considerably lower than the other two cultivars. However, although Slobolt produced a lower number of flowers on any single day it did have a very concentrated flowering pattern. At 30/20°C, although the peaks were delayed, the flowering characteristics were similar to those for the Thai cultivar.

In all instances, although the second peak flowering produced far greater flower numbers, it has been previously observed that seed developing from the first peak may suppress the potential yield (Soffer and Smith, 1974a). In all cases the 25/15°C temperature produced significantly higher flowering peaks than the 30/20°C temperature. Under 25/15°C conditions, the most intense flowering patterns were observed at 10 and 14 h with Thai and Slobolt and 14 h with Grands Rapids. This suggests that these temperature, daylength and cultivar combinations have the potential to produce maximum seed yields.

Plants grown at the 12 h daylength under the 30/20°C temperature did not produce two distinct flowering peaks. The reasons for this are unclear. Jones (1927) observed that flowering pattern was influenced by fluctuations in temperature. Soffer and Smith (1974a) have also suggested that light intensity might influence flowering pattern and found more than two peaks over a 70 day flowering period under greenhouse conditions in head lettuce cv. Calmar.

In this experiment, plants were grown in controlled environment rooms with a single constant light intensity and under a constant day/night temperature. So this effect may have been specifically related in some way to the 30/20°C temperature at 12 h daylength conditions.

2. Seed Production

The effects of temperature, daylength and cultivar on floret number per flower head, seed number per seed head and proportion of seed set per head at each peak flowering are presented in Table 4.2 and Appendix 9.

One lettuce flower contains 10 to 22 florets (Jones, 1927; Whitaker et al., 1974). This variation was shown in the present experiment to be temperature or cultivar dependent since plants grown at 30/20°C produced significantly more florets per flower head than plants grown at 25/15°C. This effect occurred at both peak flowerings. Slobolt however, produced more florets per flower head than either Thai or Grand Rapids.

It was also noticed that floret numbers per flower head at the time of first peak flowering was higher than at second peak flowering. This was due to flower head size differences. Also, flower heads produced during the first peak flowering were larger than those produced during the second peak flowering. This difference may have been caused by the onset of senescence involving an imbalance in the relative levels of growth hormones (Wareing and Phillips, 1978). In addition to being less vigorous by the second peak flowering as a result of senescence, plants were also more substantially affected by bacterial disease. Competition for growth assimilates caused by the 'draw' on nutrients caused by seed production following the first peak flowering and that produced during the second peak flowering may also have influenced flower head size and floret numbers per flower head.

Table 4.2 Effects of temperature, daylength and cultivar on floret numbers seed numbers per head and percentage of seed set at each peak flowering

A MAIN EFFECTS

	Floret No.		Seed No.		Seed Set (%)	
	PF1	PF2	PF1	PF2	PF1	PF2
Temperature °C						
25/15	18.37b	15.89b	15.88a	13.39a	86.15a	84.3a
30/20	20.90a	17.51a	16.55a	13.46a	78.85b	76.2b
Daylength (h)						
10	19.42a	16.18a	14.79b	12.07b	72.28b	75.2b
14	19.84a	17.22a	17.64a	14.77a	88.72a	85.3a
Cultivar						
Thai	19.32b	16.92a	15.74b	13.79a	81.63b	81.7a
Grand Rapids	19.23b	16.49a	14.47c	13.05a	75.34c	78.8a
Slobolt	20.34a	-	18.43a	-	90.52a	-

B INTERACTIONS

Floret No. (PF1)

Temperature x Daylength	25/15°C	30/20°C
10	18.52	20.32
14	18.21	21.47
L.S.D. .05	1.04	

Table 4.2 (continued)

Temperature x Cultivar	Floret No. (PF1) 25/15°C	30/20°C
Thai	17.39	21.25
Grand Rapids	17.94	20.52
Slobolt	19.76	20.92
L.S.D. .05	1.28	

Temperature x Daylength	Seed No. PF1 25/15°C	PF1 30/20°C	PF2 25/15°C	PF2 30/20°C
10	15.66	13.91	12.90	11.25
14	16.10	19.18	13.88	15.67
L.S.D. .05	1.38		2.17	

Temperature x Daylength	Seed Set (%) PF1 25/15°C	PF1 30/20°C	PF2 25/15°C	PF2 30/20°C
10	84.15	68.41	84.0	66.4
14	88.15	89.29	84.5	86.0
L.S.D. .05	5.08		7.19	

Values not followed by the same letter differ at P = 0.05

Significant interactions did occur between temperature and daylength and between temperature and cultivar at first peak flowering with respect to floret numbers. At 30/20°C, the 14 h daylength resulted in the production of flowers bearing higher floret numbers than at the 10 h daylength. Conversely, at 25/15°C, daylength was relatively ineffective. Slobolt however, produced more florets than either Thai or Grand Rapids, but only at 25/15°C.

Although plants grown at 30/20°C, produced more florets per flower head than at 25/15°C, no differences in seed numbers per head were observed at either peak flowering. This compensatory effect resulted from as higher percentage of seed set at 25/15°C. Long days (14 h) also increased both seed numbers and percentage of seed set. Again, Slobolt produced higher seed numbers and greater seed set than Thai or Grand Rapids respectively. Although Thai had higher seed numbers and greater seed set in the first peak flowering than Grand Rapids, the differences were quite small.

Generally the first peak flowering produced more seeds than occurred at the second peak flowering (16.20 and 13.42, respectively). Jones (1927) reported an average of 16.20 seeds per head in head lettuce grown in the field.

A temperature x daylength interaction was observed at both peak flowerings for seed number and seed set; at 30/20°C, there were always lower seed numbers and less seed set under 10 h compared with 14 h daylength conditions whereas differences were negligible at 25/15°C. Similar results by Koller (1962) showed that good seed set was obtained when Grand Rapids plants were grown at a night temperature between 17 and 23°C under short day (8 h) conditions.

Soffer and Smith (1974a) found no relationship between average seed weight and the number of mature seeds in a single seed head. This indicates that there is little competition among seeds on the same seed head. It also suggests that plants which are capable of producing high seed numbers per head should also produce higher seed yields, provided the plant also has a high number of flowers at peak flowering, uniformity of seed maturity and is able to be harvested before seed shattering begins.

The results clearly show that the 14 h photoperiod was most favourable for seed set in leaf lettuce at either of the two alternative temperatures used in this study., They also suggest that if plants are grown at 10 h daylength then the lower alternating temperature appeared to be the more favourable for seed production.

In terms of practical seed production, factors such as total flower numbers per plant, flowering uniformity and pattern, seed size and seed fertility must be considered to be of importance in affecting lettuce seed yield and quality.

CHAPTER 5

SEED MATURATION AND VIABILITY

Considerable attention has been given to the vegetative development and flowering of leaf lettuce cultivars under a range of environments in the previous chapters. One other important objective of the present study was to describe the sequence of seed development. In addition, it was considered important to be able to determine the effects of environment, particularly in relation to temperature and daylength on the components of seed yield and quality.

Seed yield is often used as an important parameter for measuring genetic, enviromental and cultural differences. Seed quality, on the other hand, is normally determined during seed development (Austin, 1972; Jones, 1977; Delouche, 1980). The stage of seed maturation is also a major factor responsible for variation in the viability and size of seed. Moreover, seed size has been found to be one factor likely to affect subsequent plant growth and yield (Scaife and Jones, 1970; Smith et al., 1973b; Soffer and Smith, 1974a; Renard, 1978).

In lettuce, it is very difficult to determine the optimum seed harvesting time because flowering tends to continue for a long time (Soffer and Smith, 1974a). In addition, the duration of flowering can also fluctuate with changes in temperature (Jones, 1927; Soffer and Smith, 1974a). Correct harvest timing is particularly important, since delayed harvesting can result in much of the seed being lost because of shattering (Hawthorn and Pollard, 1954), while early harvesting, especially if it takes place before seed physiological maturity is reached, can reduce seed yields and quality particularly in relation to seed storage life (Harrington, 1972).

The correct assessment of the best time for harvesting will vary from area to area, and from year to year due to differences in weather conditions (Jones, 1927; Globerson, 1981).

In this chapter, seed development is discussed in relation to changes in weight, seed colour and germination capacity.

MATERIALS AND METHODS

In this experiment, plants from both the 25/15°C and 30/20°C temperature under a 12 h photoperiod environment were used to study the sequence and duration of seed development. Four plants of each cultivar were examined at each temperature.

At the time of flowering, newly opened individual flowers were tagged with coloured wool (Plate 5.1). This procedure was followed on alternate days for about 30 days. Approximately one hundred flower heads per cultivar within each temperature regime were tagged at each time. When the first tagged flower heads had begun to shatter further tagging was discontinued.

Seeds of each cultivar were collected from 1 to 21 d after anthesis at 25/15°C and 1 to 17 d after anthesis at 30/20°C due to the earlier seed shattering problem.

At each sampling the following measurements were made:

1. Fresh weight - 200 seed from each seed age category were weighed immediately after harvest.

2. Dry weight - seeds from each age category were dried at 130°C for one hour (ISTA, 1976), then placed in a desiccator to cool for 30-45 min and reweighed.

Plate 5.1 Tagged flower of leaf lettuce cv. Grand Rapids a few hours after anthesis

3. Moisture content (%) - the moisture content as a percentage by fresh weight was calculated using the method prescribed in the ISTA Rules (1976).

4. Shattering and seed colour changes were observed in different seed ages by reference to colour photographs. (Plates 5.2 - 5.3)

5. Germination (%) - seeds from each age group were germinated on top of paper at 20°C with light. Only one count at 7 d was made (ISTA, 1976). Normal seedlings, abnormal seedlings, fresh ungerminated seeds and dead seeds were counted.

6. Seed viability (%) - seeds which showed evidence of life (normal and abnormal seedlings and fresh ungerminated seeds) were counted as viable seeds.

RESULTS AND DISCUSSION

1. Changes in Seed Weight

Weight per 100 seeds was the measurement used to estimate the changes in fresh and dry matter from immediately after anthesis until seeds reached full maturity and completed the process of seed ripening. Physiological maturity (PM) was normally defined as the point at which the seed first reached its maximum dry weight (Harrington, 1972). The general trend was for a rapid increase in both seed fresh and dry weight at 25/15°C (Fig. 5.1) and 30/20°C (Fig. 5.2). This sequence followed the same pattern in all three cultivars. Dry weight continued to increase until approximately 13 d after anthesis at 25/15°C and 11 d after anthesis at 30/20°C. Fresh weight followed a similar trend but began to decline markedly due to the loss of water from the seed a few days before the seed reached physiological maturity.

In general, at physiological maturity, dry weight per 100 seeds was higher in Slobolt than in Grand Rapids and Thai cultivars although Slobolt and Grand Rapids showed similar seed dry weight at 30/20°C. Thai and Grand Rapids however, showed approximately similar results (Appendices 10 and 11).

The results, show that the length of time from anthesis to physiological maturity (PM) of lettuce seed was influenced by temperature but not by cultivar when photoperiod and light intensity were constant. Lettuce seed reached PM approximately 2 d earlier at 30/20°C than at 25/15°C. A similar result has been observed with other lettuce cultivars (Globerson, 1981) under Israeli conditions. He found that the ripe seed of cos lettuce cultivars reached 80-85% of total dry matter 17 d after anthesis in May (19.7°C) and 14 d after anthesis in July (25.4°C) with crisphead lettuce. With Ice-Berg lettuce, it took about 12 d from anthesis to seed maturity if the temperature was high. If the average temperature was low, the time from anthesis to seed maturity was extended (Jones, 1927). Regrettably, Jones (1927) only described the general morphology of lettuce seed but gave no details about changes in seed weight. However, his work does support and confirm the findings of the present experiment which have shown that high temperature hastens the development of seed maturity in leaf lettuce.

2. <u>Moisture Contents</u>

Seed development and maturation are associated with an overall loss of moisture (Adams and Rinne, 1980). During the early stages of lettuce seed development, the young seed has a moisture content between 70-80%.

The results shown in Figs. 5.1 and 5.2, while supporting this general trend, show that the moisture content of seed harvested one day after anthesis was often lower than at 3 d after anthesis particularly at 30/20°C. This effect was

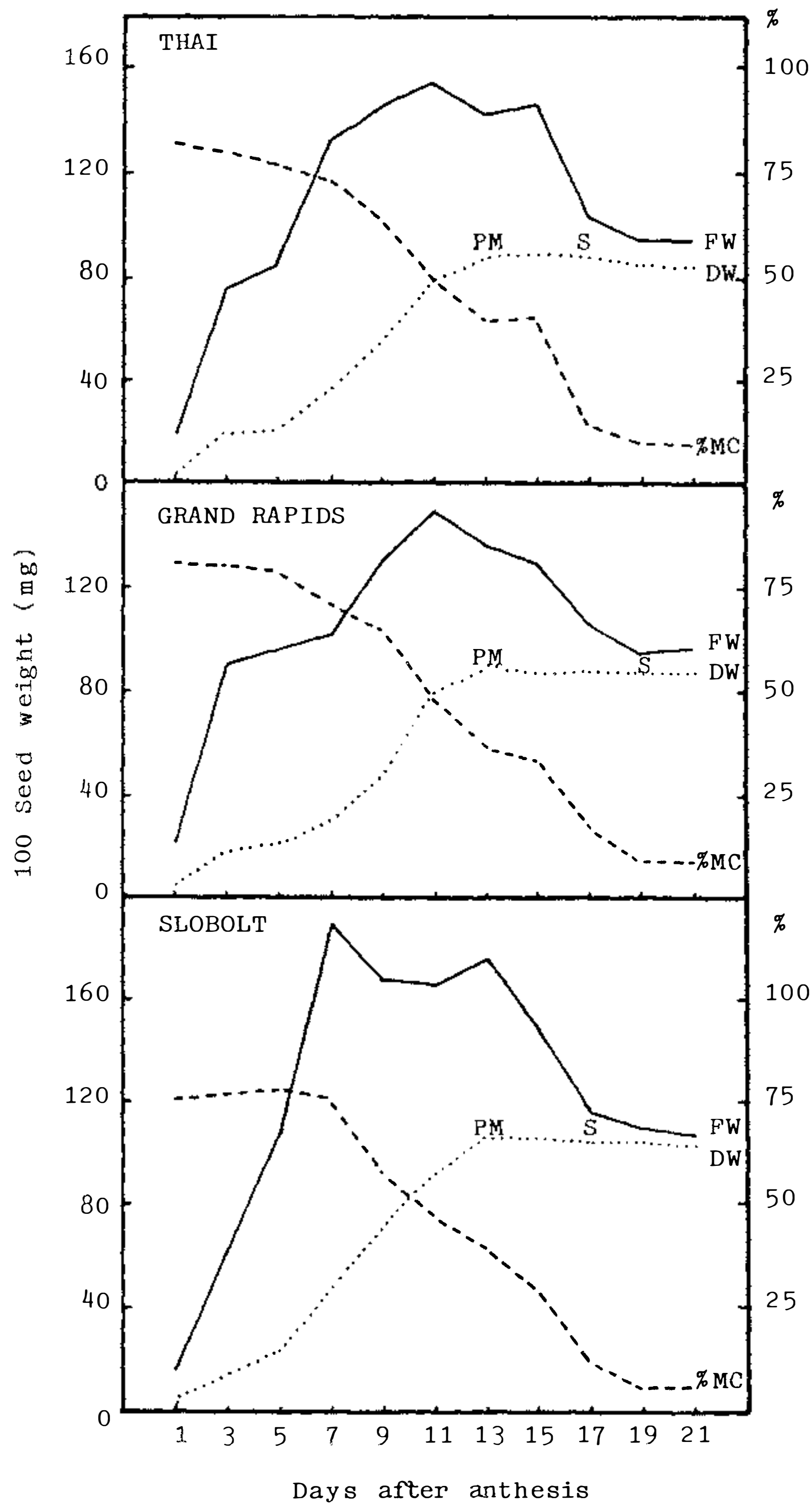


Fig. 5.1 Changes in physiological components during seed development at 25/15°C

S = shattering
PM = physiological maturity

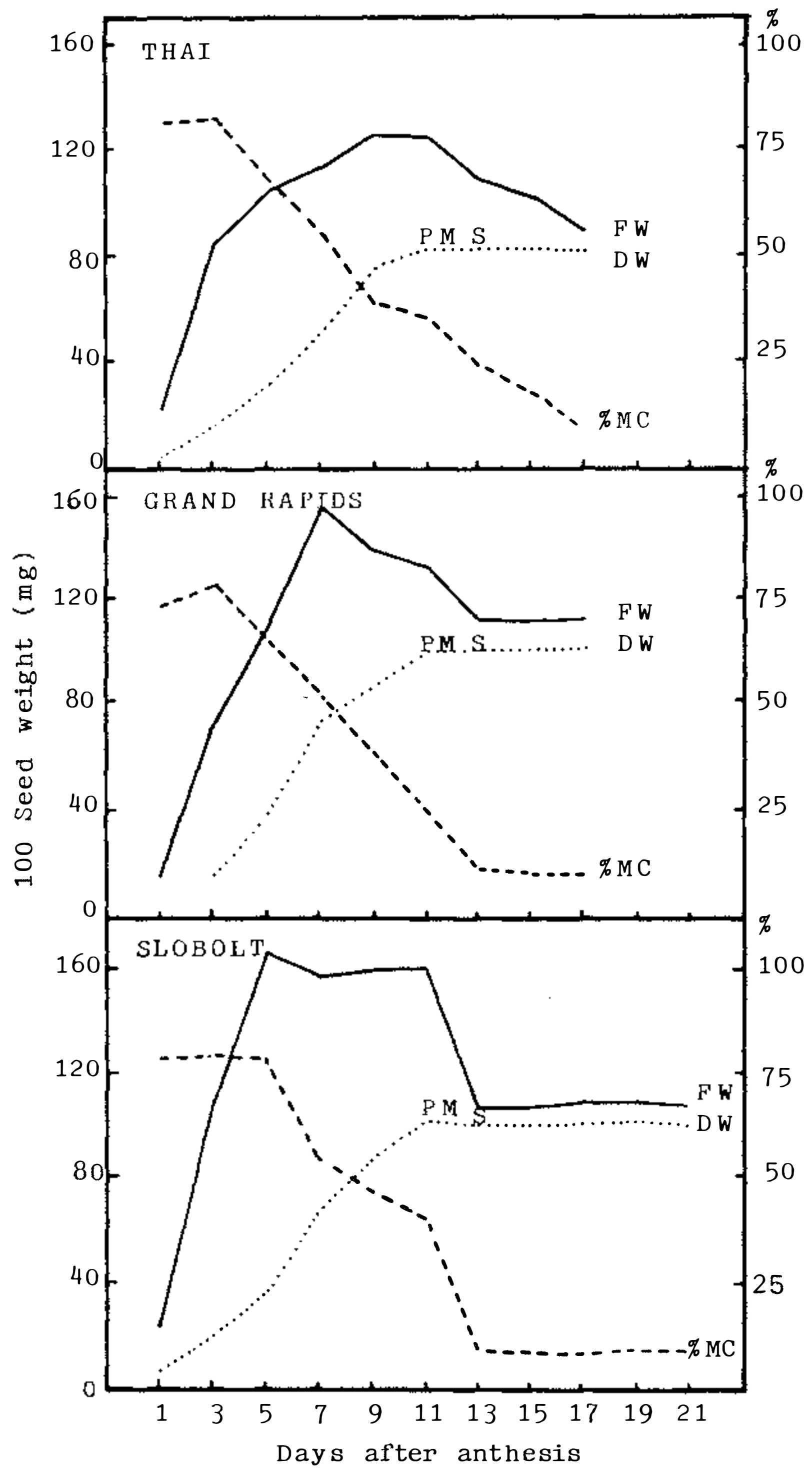


Fig. 5.2 Changes in physiological components during seed development at 30/20°C

S = shattering
PM = physiological maturity

considered to be due to loss of moisture during the collection, extraction and weighing of young, small seeds from the flower head.

Subsequently, moisture content continued to decrease as dry weight accumulation increased. Seeds at physiological maturity grown at 25/15°C (13 d after anthesis), had a moisture content of 35% in Grand Rapids, 39% in Thai and 40% in Slobolt (Fig. 5.1) while at PM under 30/20°C (11 d after anthesis), the moisture content had fallen to 24% in Grand Rapids, 35% in Thai and 37% in Slobolt (Fig. 5.2 and Appendix 12).

The moisture content of seed continued to decline markedly after food transport from the parent plant had ceased, and seed had reached its maximum dry weight (physiological maturity). Subsequently, however, the rate of dehydration increase - as much as 25-30% reduction in moisture content occurring in as little as 2-3 d. It was also noticed that the onset of shattering (S) occurred when the moisture content reached approximately 20% in all cases (Figs. 5.1 and 5.2). This indicated that the seed had become committed to a senescence programme as suggested by Adams and Rinne (1980). In the final stages of seed ripening, seed moisture content was almost constant, having reached equilibrium moisture content with the minimum level of relative humidity prevailing in the controlled environment room (60-90%).

3. Seed Shattering

Seed shattering seemed to be related to the rate of attainment of physiological maturity of seed. Generally the quicker physiological maturity was reached the sooner seed shattering started. As shown in plates 5.2-5.3, high temperature (30/20°C) hastened the onset of shattering in all three lettuce cultivars. Seed shattering started about 2 d after PM which was earlier than occurred in seed developed under the 25/15°C

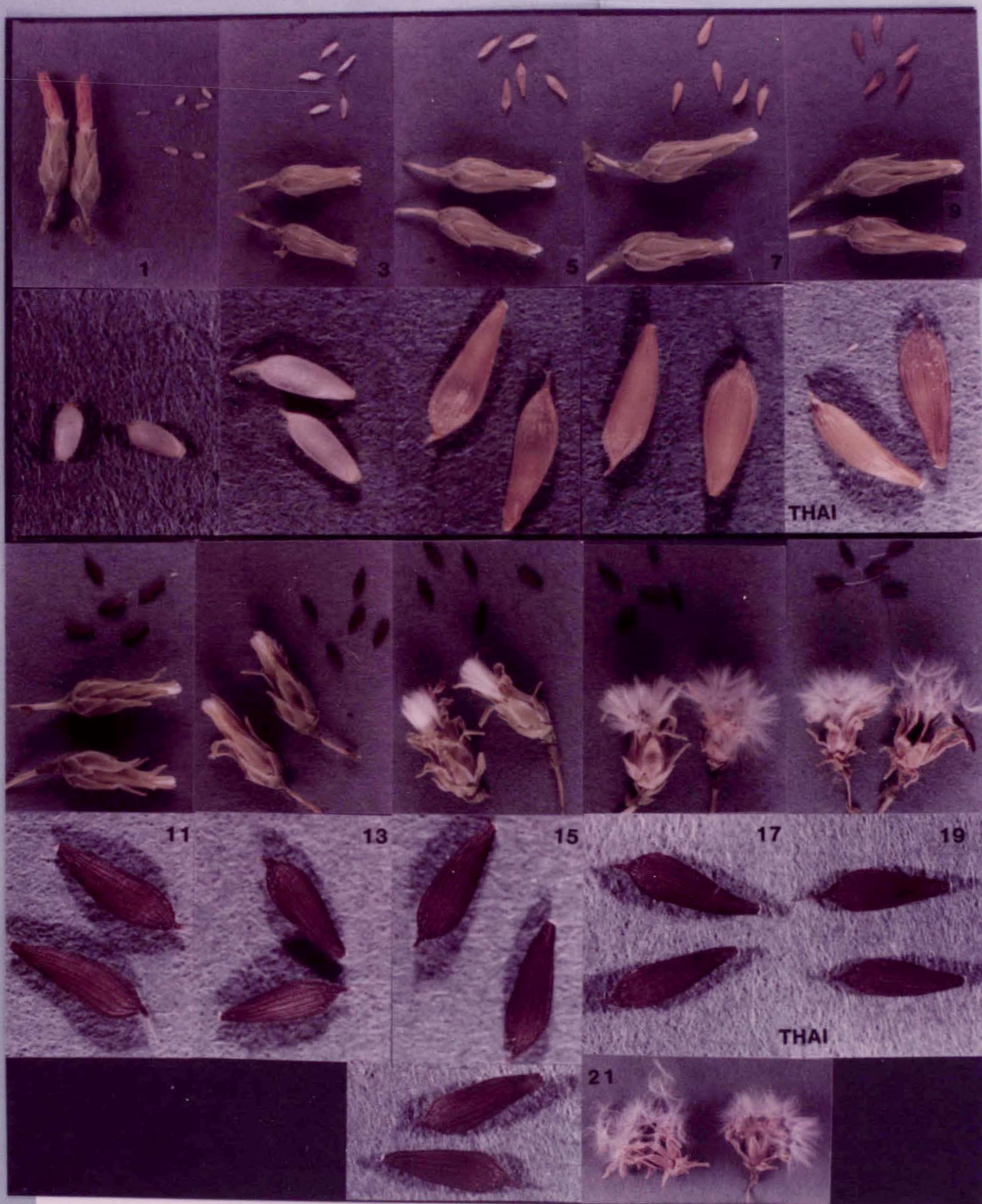


Plate 5.2a Changes in seed head and seed colour in Thai at 25/15°C

1.....21 days after anthesis

Plate 5.2b Changes in seed head and seed colour in Grand Rapids at 25/15°C

1.....21 days after anthesis

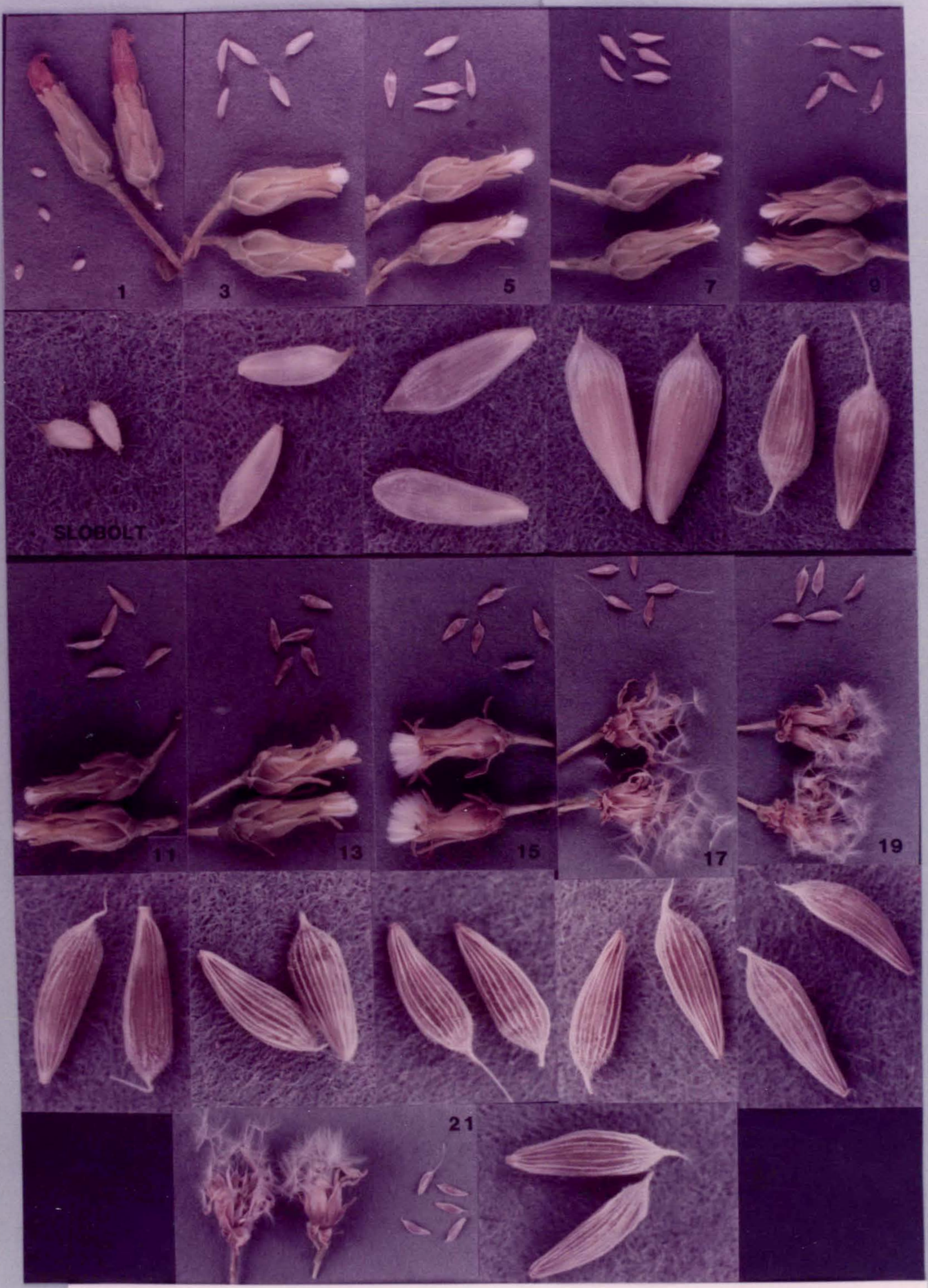


Plate 5.2c Changes in seed head and seed colour in Slobolt at 25/15°C

1.....21 days after anthesis

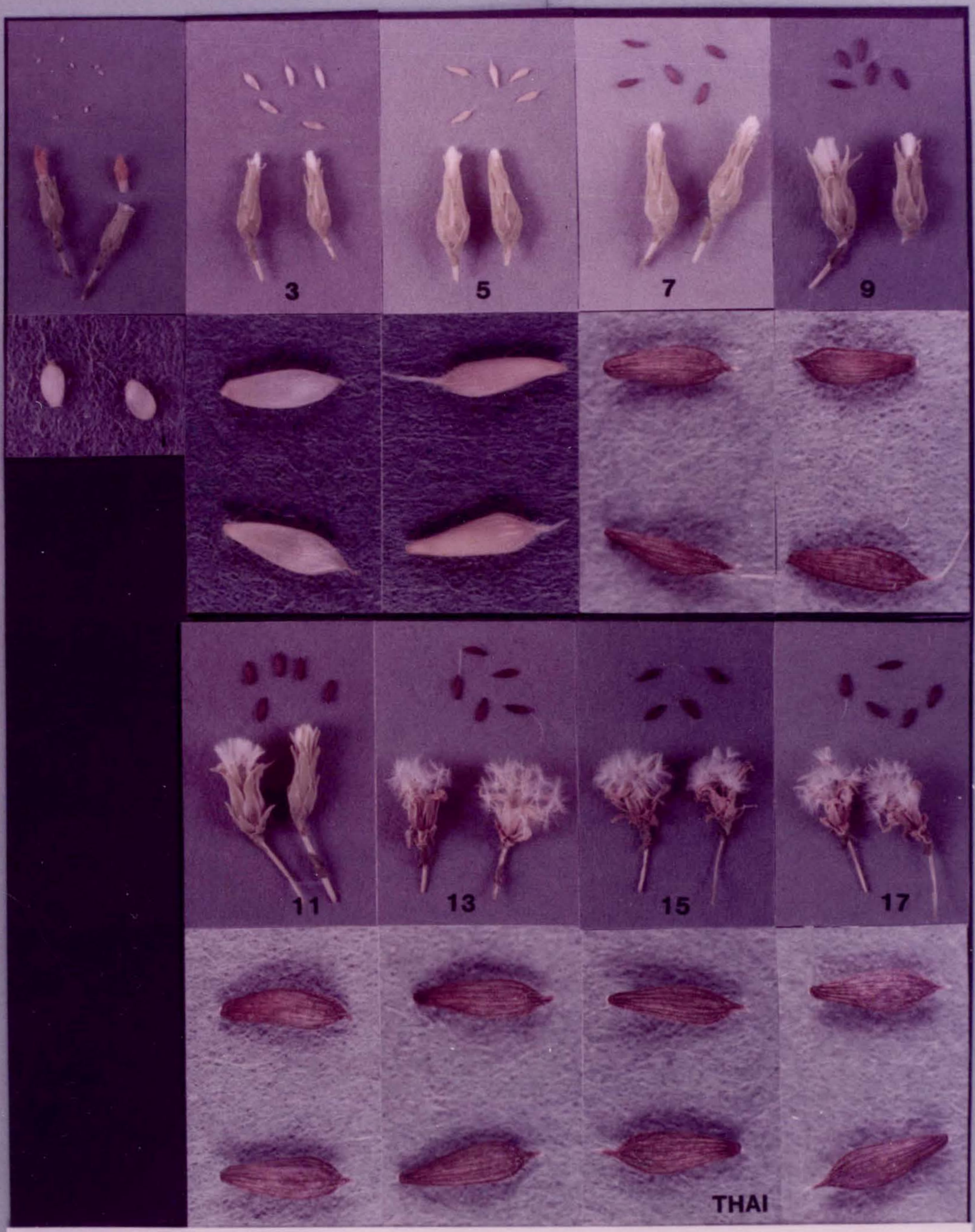


Plate 5.3 a Changes in seed head and seed colour in Thai at 30/20°C

1.....17 days after anthesis

Plate 5.3b Changes in seed head and seed colour in Grand Rapids at 30/20°C

1.....17 days after anthesis

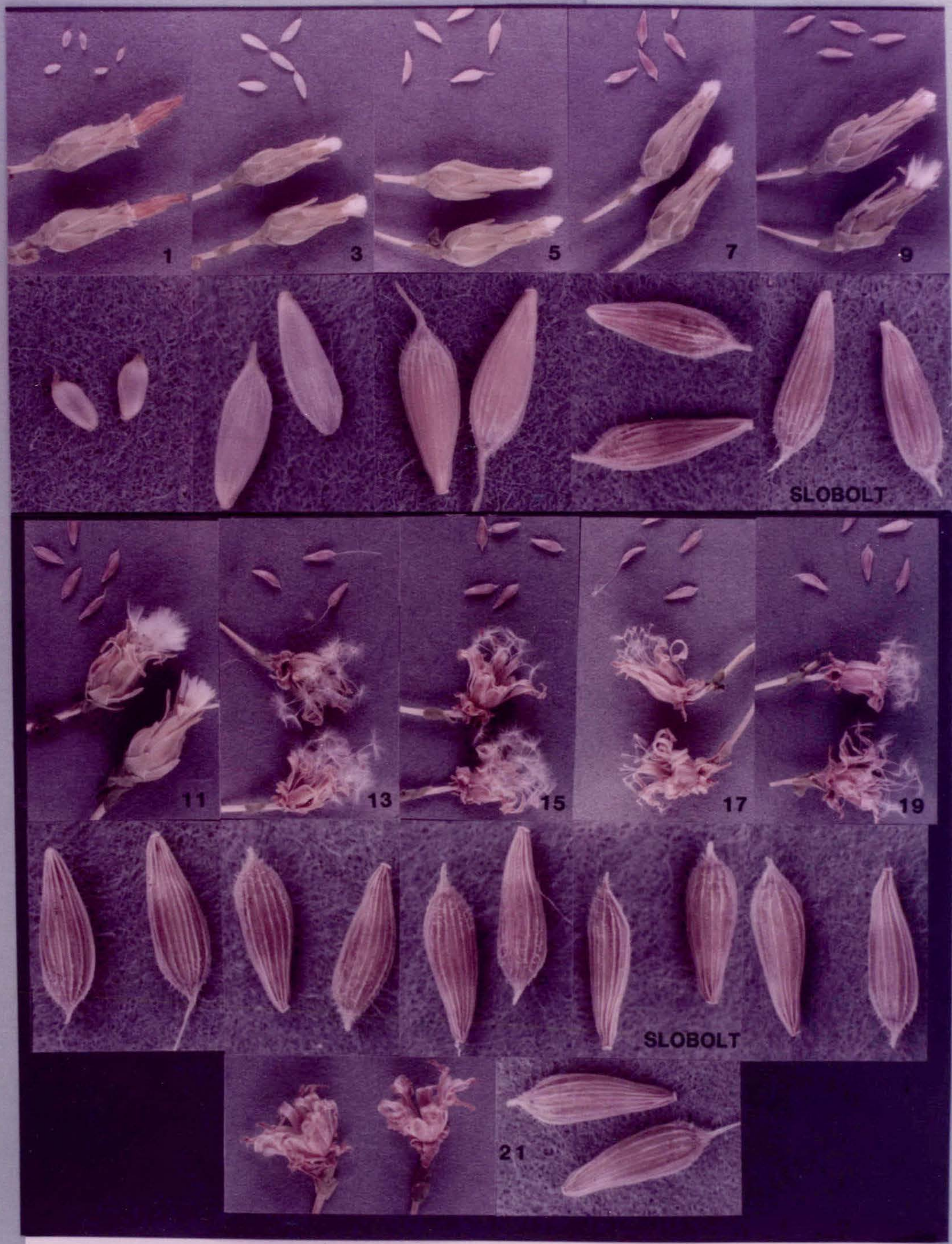


Plate 5.3c Changes in seed head and seed colour in Slobolt at 30/20°C

1.....21 days after anthesis

temperature. Under cooler seed development conditions (25/15°C) seed shattering was not observed to occur until 4 d after physiological maturity in Thai and Slobolt and 6 d after physiological maturity in Grand Rapids (Figs 5.1 and 5.2). However, the results suggest that if the temperature is high (30/20°C) during seed maturation, then harvesting should be carried out not more than 2 d after seed reaches physiological maturity. Visually, at this point, the seed head colour has turned brown and about 50% of pappus has appeared through the separated bracts (Plates 5.2-5.3). At lower temperature, (25/15°C) even though the seed has reached physiological maturity, harvesting can be delayed for 4-6 d before seed shattering is likely to become important.

The results shown in Plates 5.2 and 5.3 were obtained under controlled enviornment conditions. Such conditions take no account of the effects of wind or rain. It is likely that controlled environments allow seed to remain on the head longer than it normally would in the field. However, the degree of shattering may be difficult to predict in the field even though it has been shown to relate to stage of seed maturity since it is so strongly influenced by environmental conditions (Jones, 1927).

4. Seed Colour Changes

Lettuce seed is actually one-seeded fruit or achene which has developed from a one-celled ovary (Jones, 1927). Various studies have described the general morphology of lettuce seed including details of embryo development (Jones, 1927) and the development of the pericarp and other coats surrounding the embryo (Borthwick and Robbins, 1928). However, these studies generally lack details of the changes in seed colour and morphology occurring during seed maturation. When fully formed the seed is characteristically longitudinally ribbed with a tuft of hair attached (Poole, 1941 and Isely, 1947).

As the seed becomes dehydrated during the ripening phase, there is enlargement of the seed which has been shown to involve an increase in the thickness of the integuments and an enlargement of the embryo (Jones, 1927; Borthwick and Robbins, 1928). From 1-3 d after anthesis, the seed is still translucent at both 30/20°C and 25/15°C. By day 5, at 30/20°C, the longitudinal ribs with the tuft of hairs attached become evident and embryo is clearly outlined inside the seed and the seed has darkened in colour (Plate 5.3). In contrast, at 25/15°C although the seed colour has just started to change after day 5 the embryo is not fully developed until day 7 (Plate 5.2). At this stage, although the seed has not yet reached physiological maturity, seed colour changes are complete (black or dark brown in the Thai and Grand Rapids cultivars and white or light brown in Slobolt). This change occurs approximately 4 d before the seed reaches physiological maturity. At this stage serration of the longitudinal ribs becomes increasingly evident particularly in the black seeded cultivars (Thai and Grand Rapids).

In general, seed is considered to be 'harvest ripe' when seed colour changes are complete. The results of this experiment suggest such a criterion cannot be used as a reliable measure of full development in lettuce since it normally precedes seed physiological maturity. The assessment of harvest ripeness in lettuce seed would be better based on more closely related characters such as the attainment of maximum seed dry weight, the moisture content and the onset of seed shattering.

5. Germination and Viability

Seed which shows evidence of life is considered as viable seed; and seed which is able to germinate and produce normal seedling is classed as germinable seed (ISTA, 1976).

Seeds first attained the ability to germinate 5 d after anthesis at 30/20°C and 7 d after anthesis at 25/15°C. In both

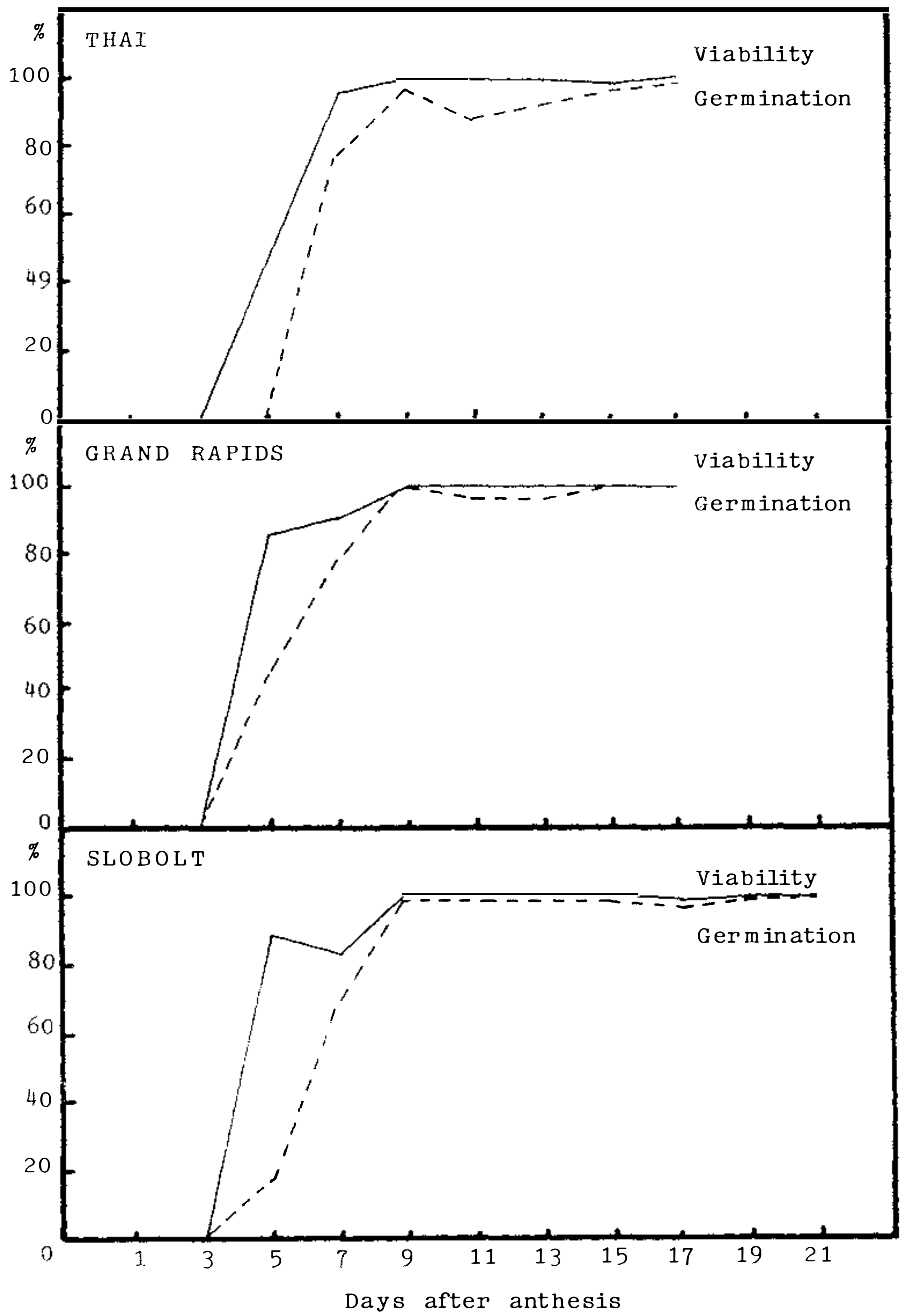


Fig. 5.3 Percentage of germination (normal seedlings) and seed viability at 30/20°C.

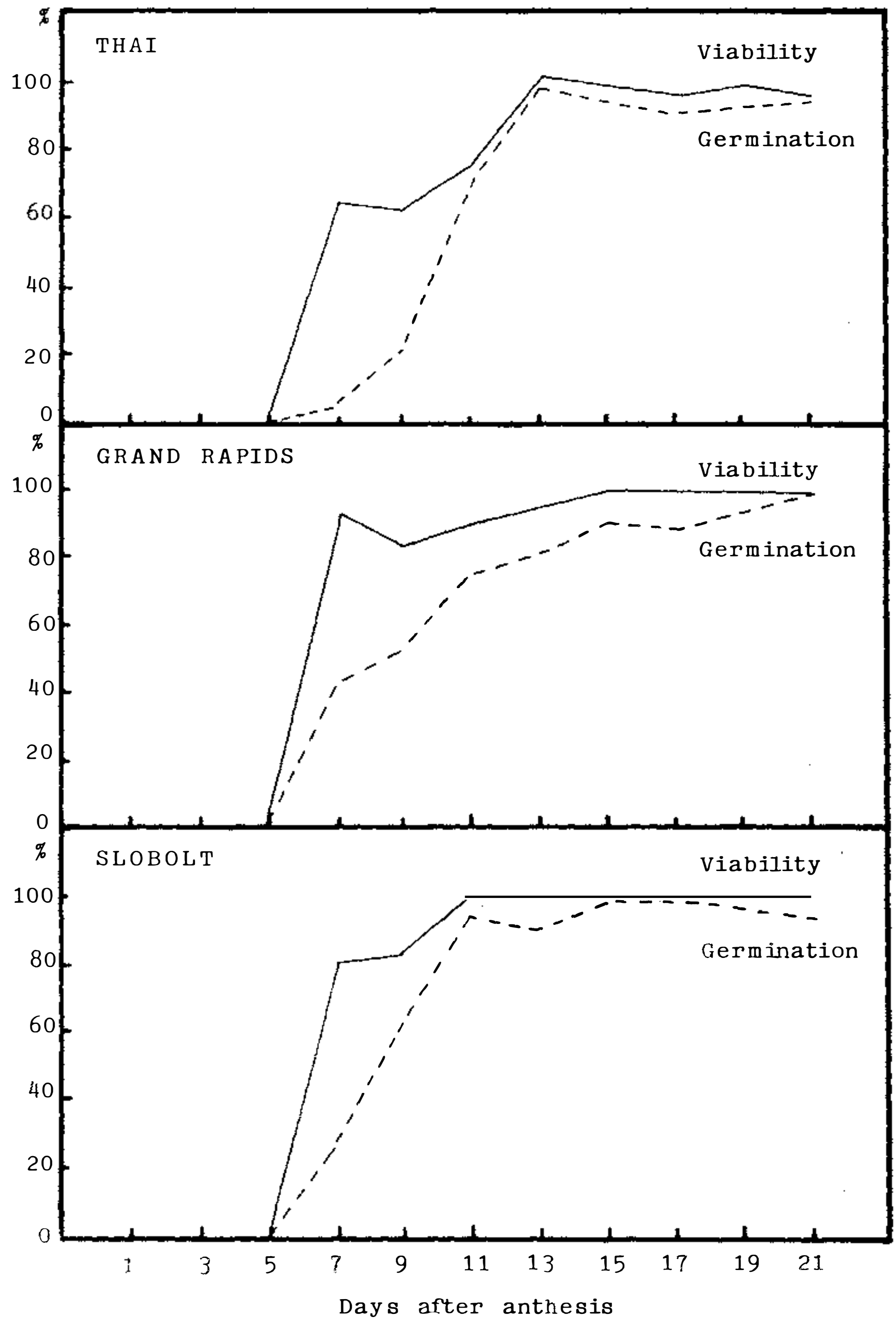


Fig. 5.4 Percentage of germination (normal seedlings) and seed viability at 25/15°C

situations seed moisture content was still high and seed colour was not well developed. As seed continued to develop, the level of total viability and germinability increased as well (Figs. 5.3, 5.4 and Appendices 13-15).

At 30/20°C, higher viability was associated with a higher percentage of normal seedlings and reached its maximum 9 d after anthesis. This was two days before seed physiological maturity was reached at this temperature while the seeds contained about 37-45% moisture content (Figs. 5.1, 5.2). At 25/15°C, seed viability and germination percentage reached their maximum 11 d after anthesis in Slobolt, and 13 d after anthesis in the Thai cultivar. This represents a point which was two days before physiological maturity in Slobolt but which coincided with physiological maturity in the Thai cultivar. In Grand Rapids the attainment of maximum seed viability was delayed to 15 d after anthesis but did not reach maximum germination percentage until about 21 d after anthesis when the seed moisture was very low, about 9.6% (Figs 5.2, 5.4). This delay in the attainment of full germination capacity in Grand Rapids seed grown at 25/15°C might have been due to the lower temperature during seed maturation increasing seed dormancy (Koller, 1962). The fact that viability percentage reached its maximum 15 d after anthesis and remained constant up to 21 d after anthesis. At this stage some seedlings produced were abnormal in their development. The main types of abnormal seedlings found (Plate 5.8) were seedlings exhibiting a spiral hypocotyl, short and thickened pocotyl, necrotic cotyledons or deformity. Such abnormal seedling types have been previously described in lettuce by Bekendam and Grob (1979).

During the early stages of seed development, (5 d after anthesis at 30/20°C and 7 d after anthesis at 25/15°C, those few seeds which were capable of germination also produced abnormal seedlings. In these cases, however, abnormality was particularly characterised by unbalanced development or lack of essential structures, i.e. small or weak development, no root, no shoot or decayed seedlings (Plate 5.4). These effects were a feature of seeds which were immature and have been noted as an important factor contributing to both dormancy and poor storage longevity by Thompson (1936).

The present study showed that lettuce seeds do not exhibit dormancy provided they have been allowed to develop to maturity in order to produce high vigour seeds. Although immature seed itself is able to germinate, the seedlings formed are generally weak, resulting in poor growth and low yield (Renard, 1978; Smith et al., 1973b; Soffer and Smith, 1974b). Conversely, seeds which have been germinated under optimum conditions (20°C with fluorescence light) as prescribed by ISTA (1976) do not generally exhibit seed dormancy. Similarly a day-light germinator maintained at a temperature of 15° to 18°C provides excellent conditions for the germination of lettuce seed of a wide range of cultivars (Shuck, 1934).

Plate 5.4 Examples of the types of abnormal seedlings found in seeds removed from lettuce plants during the stage of seed development

1. Normal seedling
2. Primary root short and with lesion on hypocotyl
3. Primary root short and weak with short and thick hypocotyl
4. Short and weak seedling
5. Short and thick hypocotyl
6. Weak and watery seedling
7. Decayed seedling

8 and 9. Hypocotyl with constriction and grainy lesions

10. Hypocotyl twisted.

CHAPTER 6

SEED YIELD AND QUALITY

The increasing demand for lettuce seed in Thailand continues to greatly exceed the domestic supply. This has resulted in a situation where much of the seed sown in Thailand is imported. Thai growers traditionally prefer to grow lettuce for the fresh vegetable market rather than for seed. The main motivation for this decision involves rapid turnover and high profits in a short time. Research on lettuce seed production in Thailand has shown that Grand Rapids is capable of producing a seed yield of only 1.29 g/plant in the northern highland (Tonguthaisri et al., 1978) compared with the yield up to 10 g/plant in the northeast, Pakchong (Pokanan, 1981). This variation in seed yield suggests that management factors such as sowing date and harvest timing may be major contributors to such large differences in seed yield. However, such yield differences also suggest that climatic conditions, particularly temperature and daylength may have a contributing role in influencing seed yield.

Although the results of extensive experiments and reports on Lactuca sativa L. are available, the process of seed production is still not fully understood. Most of the reported work has been done with particular emphasis on flower induction in head lettuce. While this work is of interest, much of it has only limited relevance to the Thailand situation. For this reason it was thought to be important to more critically assess the physiological and climatic requirements of leaf lettuce. Hopefully such an assessment would allow more meaningful interpretation of the conditions likely to be most suitable for leaf lettuce seed production in Thailand.

The objective of this study was to determine the effects of variations in photoperiod and temperature on seed yield and quality in relation to harvest time in three leaf lettuce cultivars.

MATERIALS AND METHODS

Three cultivars of leaf lettuce; Thai, Grand Rapids and Slobolt were grown under the same temperature and daylength combinations described earlier in the vegetative growth section (Chapter 3) where details of treatments and cultural practices are also given.

Twelve plants were used in each cultivar/temperature/daylength combination.

Plant Measurements

Six seed harvests were made for each cultivar and daylength in each temperature treatment:
10, 15 and 20 d after PF1 and PF2 respectively at 30/20°C and
15, 20 and 25 d after PF1 and PF2 respectively at 25/15°C.

The actual harvest times were chosen with particular reference to the time from anthesis to the onset of seed shattering which has been previously described in the seed development study, i.e. 13 d after peak flowering for plants grown at 30/20°C and 17 d after peak flowering for plants grown at 25/15°C (see Chapter 5).

As number of Slobolt plants grown in a 12 h daylength and particularly at 25/15°C died following the first flowering peak. This resulted in insufficient plants being available to obtain information on seed yield and quality of Slobolt following the second peak flowering. This situation meant that data was only obtained at harvests after the second flowering peak from 10 h and 14 h daylength treatments, from Thai and Grand Rapids plants at both temperatures and only from Slobolt plants grown at the high temperature (30/20°C).

At each time of harvest, two plants from each treatment were harvested and measured for the following parameters:

1) Height (m) - measured as the distance from the cotyledonary node to the top of the plant at peak flowering.
2) Number of secondary branches - those branches which appeared on the main stem and on the lateral branches.
3) Number of tertiary branches - those branches which developed from secondary branches.

Seed heads were removed from two plants, were put in an open cardboard box and air dried at 30°C for 2 - 3 d until the seed heads had dried and the majority of seeds had shattered. The heads were then threshed by hand and the inert material and dust (pappus, bracts, etc.) separated from the seed using a Dakota seed blower (Burrows Seed Co.). A hand purity examination was used to ensure the seperation of any light seeds from the inert material fraction.

The pure seeds from each treatment were studied as follows:

1) Seed yield/plant (g) seeds were weighed and moisture content (%) determined by the air-oven method at 130°C for one hour (ISTA, 1976). The seed moisture content varied from 5 to 7%. Seed weight values were adjusted at each harvest to a constant 6% mc.

2) Germination (%) - Seeds from each treatment were germinated at 20°C with light in a plastic box on top of blotting paper with Kimpack* underneath to maintain

* A cellulose material with high water holding capacity

a suitable level of moisture. Fifty seeds were tested per box and there were four replicates for each treatment. Normal seedlings, abnormal seedlings, 'fresh ungerminated' seeds and dead seeds were recorded after 7 d (ISTA, 1976).

The 'fresh' ungerminated' seeds found in any treatment at the end of the normal test period were transferred onto filter paper which had been soaked in 0.2% KNO_3 solution and kept at 20°C with light for a further 7 d before final evaluation.

3) Seed weight - 1000 seed dry weight (mg) was obtained by the air-oven method, at 130°C for one hour (ISTA, 1976).

Data Analysis

A completely randomised design was used with a factorial arrangement of daylength x cultivar harvest time in each temperature at each flowering peak. An analysis of variance comparison was also completed within each flowering peak to determine differences between temperatures.

RESULTS AND DISCUSSION

1. Height

As shown in Table 6.1, plants were generally taller at the 30/20°C temperature. However, plants in the 14 h daylength were taller if grown at 25/15°C. Plants grown in daylengths of 10 and 12 h were generally of similar height at each temperature. Cultivars only showed significant height differences at 30/20°C. Slobolt was taller than Thai and Grand Rapids. It was also noticed that time of harvest had little effect on plant height since maximum plant height was generally reached before seeds had developed to harvest ripeness.

Table 6.1 Effects of temperature, daylength and cultivar on plant height (cm) at each peak flowering.

	PEAK FLOWERING			
Temperature °C	PF1		PF2	
25/15	153b		155b	
30/20	167a		165a	
	25/15°C		30/20°C	
Daylength (h)	PF1	PF2	PF1	PF2
10	152b	148b	171a	168a
12	150b	-	172a	-
14	158a	159a	149b	150b
Cultivar				
Thai	154a	156a	161a	158b
Grand Rapids	152a	152a	158a	155b
Slobolt	155a	-	162a	167a

Values not followed by the same letter differ at P=0.05

Plant height had some influence on the suitability of lettuce plants for seed production simply because it affected seed stalk strength. In leaf lettuce plants the stems were long and brittle. This was particularly true of plants grown at 10 or 12 h daylengths and particularly at 30/20°C where plants were taller, produced softer stems and needed more staking than plants at 14 h. Staking to prevent stem-break is expensive and is generally not practical in a field situation. The 25/15°C temperature however, produced shorter stemmed and more 'sturdy' plants which did not require staking.

It has been demonstrated in many plant species that stem growth is faster in the dark (Salisbury and Ross, 1978) and that plants produce spindly and weak stems at warmer temperatures due to their accelerated growth (Black and Edelman, 1970). Perhaps this explains the generally poor stem strength observed in plants grown under short days and high temperature in the present study.

2. Branch number

Branches which appeared on main stem and lateral branches (secondary branches) and on secondary branches (tertiary branches) were counted.

There was no effect of temperature on the number of secondary and tertiary branches formed up to the time of first peak flowering. However, plants grown at 30/20°C did produce significantly more tertiary branches than plants grown at 25/15°C by the time of second peak flowering (Table 6.2).

Maximum secondary branches were produced under a 14 h daylength but there were no differences between the number of tertiary branches on plants grown in 10 or 14 h daylength. However, plants grown under a 10 h daylength produced more secondary branches than plants grown at 12 h daylength. These extra branches were rather small. By the time plants had reached their second peak flowering more secondary and tertiary branches had often been produced, although the increases in branch numbers at this stage was generally small. In some cases, reduction in branching was recorded as a result of rotting in the case of secondary branches and breakage and senescense in the case of tertiary branches.

The differences in branching pattern described in this study suggest a change in dry matter distribution within the plant. This has been observed in other plants grown under different daylengths (Vince - Prue, 1975). The mechanism for these changes in the distribution of growth has not been examined in detail but it is possible that effects on hormone production are involved (Seth and Wareing, 1967).

Table 6.2 Effects of temperature, daylength, cultivar and harvest time on branch numbers

SECONDARY BRANCHES

Temperature °C	PEAK FLOWERING PF1	PF2
25/15	35.1a	36.0a
30/20	37.0a	37.7a

	25/15°C PF1	25/15°C PF2	30/20°C PF1	30/20°C PF2
Daylength (h)				
10	38.7b	38.4b	44.8b	47.3a
12	33.1c	-	30.5c	-
14	44.7a	58.0a	56.6a	51.2a
Cultivar				
Thai	34.0b	38.9b	43.4a	51.9a
Grand Rapids	51.5a	57.5a	46.1a	50.8a
Slobolt	31.1b	-	42.5a	45.1a
Days after PF				
10	-	-	47.3a	54.5a
15	36.1b	49.6a	44.8a	44.1a
20	41.8a	46.8a	39.8a	-
25	38.6b	-	-	-

TERTIARY BRANCHES

Temperature °C	PEAK FLOWERING PF1	PF2
25/15	317a	328b
30/20	349a	368a

	25/15°C PF1	25/15°C PF2	30/20°C PF1	30/20°C PF2
Daylength (h)				
10	301a	335a	354a	380a
12	-	-	-	-
14	329a	245a	368a	366a
Cultivar				
Thai	284b	314b	333a	402a
Grand Rapids	402a	366a	398a	383ab
Slobolt	259b	-	351a	336b
Days after PF				
10	-	-	384a	383a
15	323a	352a	343a	364a
20	310a	328a	355a	-
25	312a	-	-	-

Values not followed by the same letter differ at P=0.05

Cultivar differences were observed at both temperatures and at both peak flowering times. Generally, Grand Rapids produces a higher number of branches (secondary and tertiary) than either Thai or Slobolt, although this was not generally significant at 30/20°C. The Thai cultivar produced only higher branches than Slobolt at 30/20°C during the second peak flowering. Slobolt's comparatively lower branch number was a response to its lateness in bolting and to the tendency for plants to lose branches through stem rotting before the second peak of flowering eventuated.

The production of a stronger and more extensive branching frame work certainly suggests a greater potential for high seed yields than is likely to occur on plants bearing fewer secondary and tertiary branches.

3. Seed Yield

The total seed yield/plant, as influenced by temperature, daylength and cultivar, at different harvest times after the two respective peaks of flowering is presented in Table 6.3 and Fig. 6.1 (raw data in Appendix 16).

The 25/15°C temperature produced significantly higher seed yields at both flowering peaks. However, the second peak flowering generally produced higher seed yields than the earlier peak flowering. High seed yields were consistently obtained in all cultivars grown in 14 h daylength irrespective of the temperature treatment. Similarly, plants harvested 20 d after either first peak or second peak flowering produced most seed, except at 30/20°C where the removal of seeds from the plant 15 d after second peak flowering resulted in highest seed yield.

Highest seed yields were obtained in Grand Rapids plants irrespective of the environmental treatment (except at 30/20°C, first peak flowering) Slobolt produced a higher seed yield than

Table 6.3 Effects of temperature, daylength, cultivar and harvest time on seed yield (g/plant)

A MAIN EFFECT

Temperature °C	PEAK FLOWERING PF1	PF2
25/15	24.36a	36.40a
30/20	20.52b	33.60b

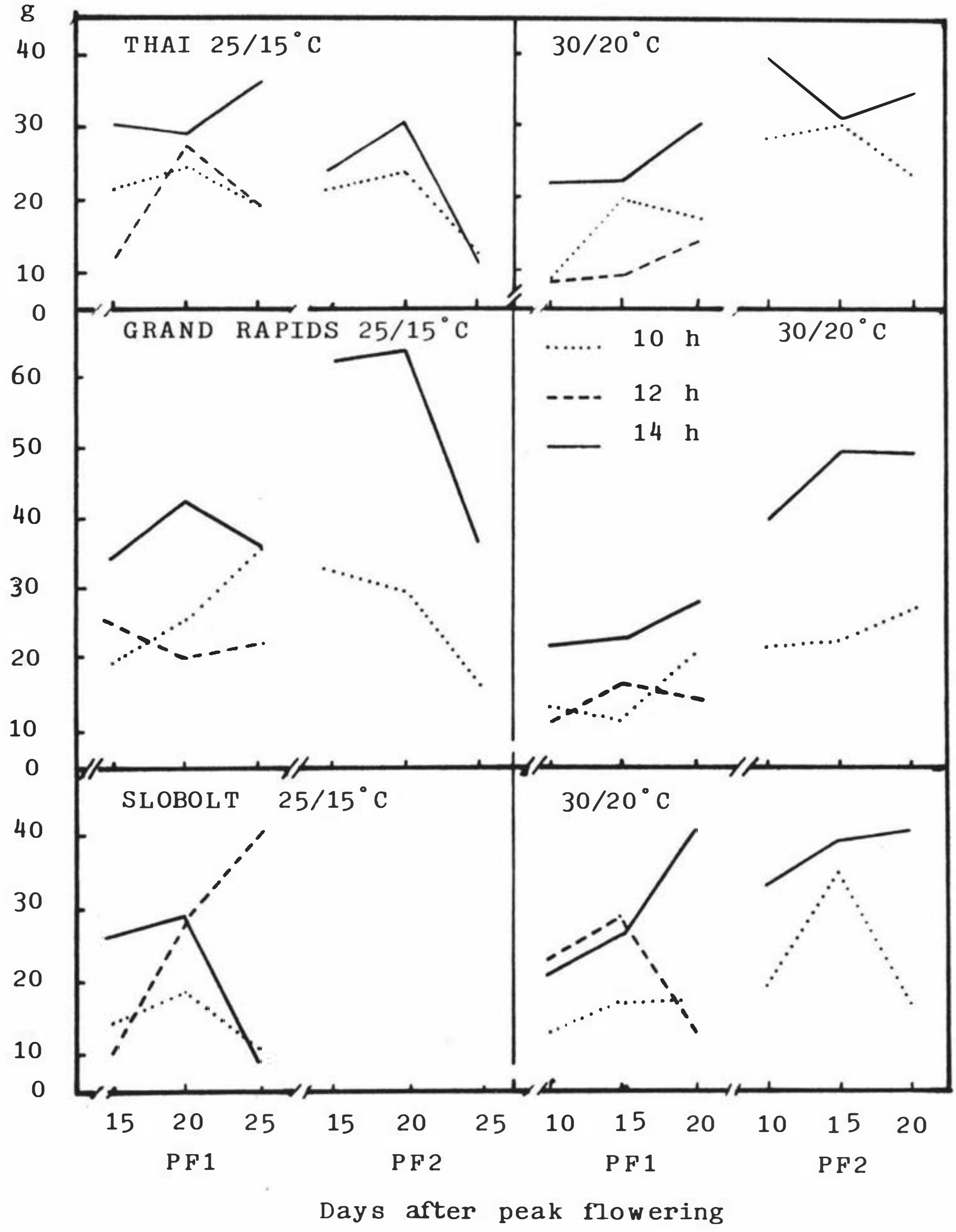
	25/15°C		30/20°C	
Daylength (h)	PF1	PF2	PF1	PF2
10	20.95b	22.96b	15.29b	25.02b
12	22.88b	-	15.26b	-
14	30.43a	38.68a	26.11a	39.68a
Cultivar				
Thai	24.07b	20.69b	16.76b	31.07b
Grand Rapids	29.40a	40.95a	17.82b	35.42a
Slobolt	20.80c	-	22.08a	30.56b
Days after PF				
10	-	-	15.63c	30.23b
15	21.53b	35.50a	19.20b	34.85a
20	27.14a	37.31a	21.84a	31.97b
25	25.59a	19.65b	-	-

B INTERACTIONS

25/15°C	PF1			PF2	
Daylength x Cultivar	10	12	14	10	14
Thai	21.20	19.44	31.56	19.14	22.24
Grand Rapids	27.26	22.79	38.13	26.78	55.13
Slobolt	14.38	26.41	21.61	-	-
LSD. .05		3.63			6.06

Daylength x Cultivar (30/20°C)					
Thai	15.12	15.28	15.46	27.22	34.93
Grand Rapids	10.59	13.75	21.45	24.49	46.34
Slobolt	24.55	24.43	29.34	23.35	37.76
LSD. .05		1.93			4.62

Values not followed by the same letter differ at P = 0.05



<u>Fig. 6.1</u> Seed yield (g/plant) at each daylength, temperature and time of harvest in three lettuce cultivars.

both Thai and Grand Rapids in the warmer environment following the first peak flowering.

Despite the general effect of temperature on seed yield, the quantity of seed produced from the first peak flowering was relatively insensitive to changes in daylength from 10 to 12 h in different cultivars.

Significant interactions between daylength and cultivar were obtained. At first peak flowering, 25/15°C temperature, increasing photoperiod from 10 to 12 h decreased seed yield in Grand Rapids and increased yield in Slobolt. Slobolt, however, only produced higher seed yield than Thai and Grand Rapids at the 12 h daylength. At 30/20°C, (PF1) increassing photoperiod from 10 to 14 h had no effect on seed yield in Thai. Grand Rapids however produced higher seed yield than Thai only in the 14 h daylength.

Following the second peak flowering, the interactions showed that Grand Rapids produced markedly higher seed yield than the other cultivars under a 14 h daylength at both temperatures.

Grand Rapids plants grown at 25/15°C and under a 14 h daylength produced a maximum seed yield of up to 65 g/plant at 15-20 d after second peak flowering (Fig. 6.1).

The results support earlier work on seed development. In particular they show that optimum seed harvest time (a compromise between delaying harvest to ensure the attainment of maximum seed weight and harvesting early enough to prevent loss of seed numbers due to shattering) varies depending on whether seed has been produced following the first or second peak flowering.

The differences in optimum harvest time recorded in this growth room study might be considered to be somewhat 'artificial' compared with the situation likely to prevail in the field. In particular, the effects of wind and rain are both likely to influence the onset and extent of seed shattering. Certainly, many workers have shown that delaying the harvesting of field grown lettuce can cause big losses in seed yield due to shattering (Jones, 1927; Duncan, 1965; Pokanan, 1981).

The results suggest that in the Thai cultivar, highest seed yields (the sum of yields obtained from both flowering peaks) were obtained under a 14 h daylength irrespective of temperature. Grand Rapids also produced maximum yields at 14 h daylength, but particularly at the lower temperature regime (25/15°C). Slobolt seed yield was also likely to be higher under a 14 h daylength. Regrettably, lack of plants, as previously described, prevented an evaluation of the contribution to total seed yield following the second peak of flowering at 25/15°C in Slobolt. This was disappointing since this cultivar seemed to be well suited to the 12 h daylength conditions found in Thailand, particularly at 25/15°C. It is possible however, that Slobolt may not attract commercial seed production by Thai farmers due to its slowness in bolting, as has happened in the U.S.A. (Thompson and Kosar, 1948). Grand Rapids and the Thai cultivar might be more favoured by Thai farmers as a cash seed crop under climatic temperatures around 25/15°C if the cost of production is lower than importing. Under a 30/20°C temperature combination, seed yield, although it took a shorter time to reach a maximum, was considerably less than at 25/15°C. If seed production has to be carried out in a climate involving 30/20°C and a 12 h daylength, Thai or Grand Rapids would be preferred. This is because Grand Rapids produces similar seed yields to the Thai cultivar despite the fact that they are both similar in vegetative growth and appearance.

It was regrettable that insufficient plants were available to allow seed yield assessments at the second peak flowering in plants grown under the 12 h daylength. Nevertheless substantial yields of seed were obtained in many cases. Certainly, a cumulative seed yield total (sum of maximum seed yield from each peak flowering of each cultivar of over 100 g/plant in Grand Rapids plants grown at 25/15°C compared with comparable values of approximately 60 g/plant in Thai at either 25/15°C or 30/20°C and approximately 80 g/plant in Slobolt at 30/20°C suggest that Grand Rapids has a dramatically higher seed yield potential than the other two cultivars (Fig. 6.1).

The results suggest however, that this potential is only expressed under relatively cooler conditions (25/15°C) and under longer daylengths (14 h). This is also due almost entirely to a stimulation of second peak flowering.

4. Germination

Lettuce seed germination has been shown to be influenced by genetic and environmental factors (Bothwick and Robbins, 1928; Thornton, 1936; Thompson, 1936, 1938; Harrington and Thompson, 1952; Koller, 1962; Gutterman, 1973; Girad and Monin, 1977).

Higher levels of germination were obtained from seeds grown on plants at 30/20°C at both flowering peaks (Table 6.4). These results support previous work by Koller (1962) who showed that warm temperatures (26/17°C) during the maturation of Grand Rapids lettuce seed increased germination capacity. In the present study differences between the treatments were small and sometimes significant. Fresh ungerminated seeds were also found in small numbers scattered randomly throughout different treatments. They were evaluated following extension of the normal 7 d germination period for a further 7 d. All normal seedlings and seedlings from fresh ungerminated seeds were combined in the final normal germination percentage. An indication of the levels of fresh ungerminated seed occurrence can be found in Appendix 17.

Table 6.4 Effects of temperature, daylength, cultivar and harvest time on germination percentage

	PEAK FLOWERING			
Temperature °C	PF1		PF2	
25/15	96.76b		97.25b	
30/20	98.51a		99.34a	
	25/15°C		30/20°C	
Daylength (h)	PF1	PF2	PF1	PF2
10	98.14a	98.79a	98.68a	99.06a
12	97.56ab	-	98.11ab	-
14	95.75b	94.88b	97.53b	99.19a
Cultivar				
Thai	98.03a	96.50a	98.04b	99.25a
Grand Rapids	98.00a	97.17a	98.92a	99.33a
Slobolt	95.42b	-	97.36b	98.79a
Days after PF				
10	-	-	97.29b	99.12a
15	96.17a	96.75a	98.39a	99.04a
20	97.25a	97.75a	98.64a	99.21a
25	98.03a	96.00a	-	-

Values not followed by the same letter differ at P=0.05

In most cases seed germination percentage was more than 95% although differences were found to be statistically significant. In practice these differences are of little agronomic consequence. However, generally, long days (14 h), low temperatures (25/15°C) and earlier harvests produced seeds with a slightly lower germination percentage than seeds from other treatments. Similar results have shown that Grand Rapids seed grown under short days (8 h) has a higher germination when compared to seed produced under a long daylength of 20 h (Gutterman, 1973).

The results of this study suggest that temperature and daylength have a minimal effect on seed germination, provided the seeds are physiologically mature. Similar results were found by Thompson (1936).

The small amount of seed dormancy found in this study was probably due to the inclusion of some immature seeds taken from flower heads after their respective flowering peaks. No dormancy problems were observed in seed which had reached physiological maturity (maximum dry weight) in any of the cultivars used in this study (Chapter 3). However, other workers have found dormancy problems with lettuce seeds of other cultivars (Borthwick and Robbins, 1928). Such dormancy can apparently be easily overcome by treating seeds with thiourea (Thompson and Horn, 1944), kinetin (Smith *et al*., 1968) or ethephon (Harsh *et al*., 1973). Under field conditions, where seedlings are raised in nurseries or greenhouses prior to transplanting into the field (Ryder, 1979), the problem of dormancy is easily avoided.

The types of abnormal seedlings found included seedlings with short and thick hypocotyls or deformed seedlings. Abnormal classification was based on work published by ISTA (Benkendam and Grob, 1979).

5. Seed Weight

Intensive studies on lettuce seed quality have indicated that seed from a single plant has a wide range of seed size and weight. Seed weight in lettuce has been found to be related to seed vigour and subsequent plant yield. The larger or heavier the seed, the greater the germination percentage and the percentage of marketable heads (Scaife and Jones, 1970; Smith *et* al., 1973a,b; Renard, 1978).

In this study, there was a wide range of seed weight and size within each treatment (Table 6.5, Appendix 18). Temperature only increased the weight of seed formed from the second peak flowering in plants grown at 25/15°C. Increasing photoperiod from 10 to 14 h progressively increased seed weight at 25/15°C and decreased it at 30/20°C. However, cultivar and time of harvest differences only affected the weight of seed formed from flowering at 30/20°C but the differences were small.

Table 6.5 Effects of temperature, daylength, cultivar and harvest time on seed weight (1000 seed dry weight: mg)

	PEAK FLOWERING			
Temperature °C	PF1		PF2	
25/15	927a		993a	
30/20	898a		889b	
	25/15°C		30/20°C	
Daylength (h)	PF1	PF2	PF1	PF2
10	833c	904b	920a	935a
12	926b	-	899a	-
14	1029a	1039a	821b	854b
Cultivar				
Thai	913a	950a	834b	868a
Grand Rapid	929a	994a	897a	911a
Slobolt	946a	-	908a	906a
Days after PF				
10	-	-	842b	889a
15	931a	1004a	886a	901a
20	916a	982a	910a	895a
25	940a	929a	-	-

Values not followed by the same letter differ at P=0.05

The quite large differences in 1000 seed dry weight exhibited by seeds from different treatments - particularly daylengths at 25/15°C were inversely related to seed germination percentage. Surprisingly, treatments which produced the heaviest seeds (Table 6.5) also exhibited the lowest germination capacity (Table 6.4). These differences however, were small and are probably of little biological importance.

Seed weight may also be less important in leaf lettuce production since the crop is harvested successively, especially under field conditions. Previous work by Soffer and Smith (1974b) with Calmar head lettuce has shown that seed weight could be used to predict the uniformity of lettuce during its early growth stages. They found that plants grown from small light seeds were small initially but later, at the heading stage, they reached yield equality with plants produced from large heavy seed.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSION

Light and temperature are two of the main ecological factors long known to affect plant growth and development (Garner and Allard, 1920, 1923; Roberts and Struckmeyer, 1938). Although it has been suggested that temperature during the vegetative period is generally regarded as having a greater influence than daylength in determining the time that vegetable crops will flower (Milthorpe and Horowitz, 1943), photoperiodic responses have often been found to be modified in one way or another by changes in temperature (Vince - Prue, 1975).

A considerable amount of work has been done on the effect of temperature and/or photoperiod and/or light intensity on the growth of butterhead lettuce and floral initiation and stem elongation in head lettuce. Comparative data relating to leaf lettuce cultivars, however, is generally lacking.

The present study contains information on the effects of temperature and photoperiod on vegetative growth and development, reproductive development and flowering, seed development, seed yield and quality in three leaf lettuce cultivars: Thai, Grand Rapids and Slobolt under controlled environment conditions.

These three cultivars were chosen because they most closely met the Thai consumer acceptance requirements relating to leaf type, leaf colour, leaf margin characteristics and slow bolting.

It has been observed that both temperature and photoperiod influence the growth and development of leaf lettuce plants. Fresh weight, dry weight, leaf area and leaf number were increased by higher temperatures and longer photoperiods in both the immature (10 -20 d after sowing) and mature (30 - 40 d after sowing) stages of vegetative growth. The magnitude of these increases differed between cultivars. Slobolt was generally more productive at these times than Thai or Grand Rapids, the latter two cultivars responding similarly in most cases. These results agree with those obtained by other investigators which have associated increasing vegetative growth in lettuce plants with relatively high irradiances and long days (Brouwer and Huyskes, 1968; Dennis and Dullforce, 1974a,b; Soffe et al., 1968; Grey and Steckel, 1981; Cracker and Seibert, 1983) and high temperatures (Bensink, 1971; Scaife, 1973; Nichols, 1977; Lorenz and Wiebe, 1980; Holsteijn, 1980a,b; Wurr et al., 1981; Knight and Mitchell, 1983; Glenn, 1984).

In leaf lettuce, Cracker and Seibert (1983) reported that the total accumulation of dry weight, number of leaves and leaf area in the cultivar Grand Rapids was mainly affected by photoperiod and that plants produced three times more dry matter yield when grown in a 24 h photoperiod than when exposed to an 8 h photoperiod at 20/12°C and 113 W/m^2. At a constant 25°C and 20 h photoperiod with a photosynthetic irradiance of 183 W/m^2, higher leaf dry weight was obtained in plants of Salad Bowl and Waldmann's Green than at 25/20°C (Knight and Mitchell, 1983). Tibbitts and Kozlowski (1980) reported that Grand Rapids also yielded better under 25/20°C, day/night than under 15/20°C, day/night. In the present investigation, plants were grown at a constant high irradiance level (150 W/m^2). Plants of all three cultivars produced about twice the dry matter yield at 30/20°C than at 25/15°C. However, dry matter yield increases of up to three times were obtained under a 14 h daylength compared with a 10 h daylength. Vegetative yield differences between plants grown at 10 and 12 h daylengths were small at both temperatures. However, a marked increase was obtained when daylength was extended to 14 h. These differences, were associated with higher leaf areas and leaf numbers causing increased plant dry weight.

It is suggested these differences are probably due to an increasing rate of photosynthetic activity in lettuce grown under long photoperiods and high irradiance levels as previously observed by Brouwer and Huyskes, 1968; Holsteijn, 1981; Cracker and Seibert, 1983. Similarly, high temperatures have been shown to increase cell extension (Bensink, 1971) and leaf expansion (Bierhuizen et al., 1973). In contrast, lettuce growth, as measured by changes in leaf number and leaf area, has been shown to be the same under temperature combinations of 25/17°C and 21/13°C when plants were grown at low levels of radiant energy (12.8 W/m^2) (Verkerk and Spitters, 1973). It is likely that light serves not only as an energy source through photosynthesis but also as a development regulator through the activation of photochrome and other photoreceptors. This latter activity has been shown to greatly influence the ultimate size, shape and physiology of a range of plants (Soffe et al., 1977; Cracker and Seibert, 1982; Holsteijn, 1981). It is widely known that temperature affects metabolism and influences plant growth (Sutcluffe, 1977) and is the main determinant of growth rate during the exponential phase (Scaife, 1973). In a constant environment the growth of lettuce has been shown to be almost exponential for at least half of crop life (Dullforce, 1962; Nichols, 1971).

In this study, the relative growth rate during the exponential growth phase was similar between cultivars, daylengths and temperatures even though total plant dry weight and leaf area were higher for plants grown at 30/20°C and 14 h daylength. This suggests that lettuce plants grown at 30/20°C and 14 h daylength enter the exponential growth stage sooner than plants grown at 25/15°C under shorter daylengths. It should be noted that the difference between temperatures used in the present study was only 5°C (day and night). Such a small temperature differential combined with a high irradiance level might have caused the lack of difference in relative growth rate between treatments as shown by other workers (Scaife, 1973; Wurr *et al.*, 1981; Knight and Mitchell, 1983).

In Thailand, consumer acceptability of lettuce plants when they reach marketable size is very important, and is based on usually well defined visual criteria. In leaf lettuce, the consumer normally prefers young and fresh lettuce plants. The whole plant is harvested when it is well developed, though it may often be cut for sale when it is still only half grown if the market demand is good. At the advanced stages of vegetative growth or by the time the plants have begun floral development, the leaves are tough and bitter (Shoemaker, 1953).

The present study showed that plants grown at 25/15°C had a better "market acceptability" than plants grown at 30/20°C at any daylength. At 25/15°C plants were yellow green in colour, compact and fresh while plants grown at 30/20°C were pale green and excessively soft. The optimum harvest time of lettuce plants was 30 d under a 14 h daylength; 30 to 40 d under a 12 h daylength and 40 d after sowing under a 10 h daylength at both temperatures

Although plants grown at 30/20°C and 14 h daylength produced higher vegetative growth than at 25/15°C, such rapid growth was generally associated with tissue 'softness', bolting and tipburn, particularly in the Thai and Grand Rapids cultivars 40 d after sowing. Slobolt however was still vegetative at this stage but eventually became 'oversized' with low marketable value. Plants grown at 25/15°C and 14 h daylength at 40 d after sowing still remained vegetative, but decay of the older leaves often resulted in the production of lettuce plants which were unmarketable. Under these conditions plants were also generally 'overmature' in terms of market quality.

Temperature and daylength were also found to influence floral development and flowering in leaf lettuce. Long days (14 h) and high temperatures (30/20°C) enhanced stem elongation, flower induction and flowering, while short days (10 to 12 h) and low temperatures (25/15°C) delayed these characteristics in all three cultivars. Slobolt produced a shorter main stem and was significantly later in bolting than Thai and Grand Rapids. This cultivar is even reported to be slow in bolting after vernalization (Thompson and Kosar, 1948).

The cultivars used in this study differ in the rate of seed stalk formation. Although lettuce cultivars have been variously shown to be either long day plants or day neutral (Ryder, 1979), flowering in Thai and Grand Rapids was influenced more by high temperatures than by long photoperiods whereas Slobolt required both long days and high temperatures before becoming reproductive. Rappaport and Wittwer (1956b) also reported that Grand Rapids flowered on either warm nights (21°C) or in long photoperiods (16 h).

Lettuce is normally a quantitative long day plant at high temperature and a day neutral plant at low temperature (Vince - Prue, 1975). The Thai, Grand Rapids and Slobolt cultivars used in this experiment can be considered as quantitative long day plants at both 25/15°C and 30/20°C. However, the daylength response was only operative at 14 h daylength in Thai and Grand Rapids while Slobolt was responsive across all daylengths. Such lettuce cultivar differences in their response to daylength (Bremier, 1931; Thompson, 1938; Cytovic, 1967a; Hiraoka, 1967a) and to temperature and daylength (Thompson and Knott, 1933; Rappaport and Wittwer, 1956a,b) have been widely reported. However, previous work has tended to only emphasize the onset of floral initiation as it is affected by temperature and photoperiod and has generally involved studies in head lettuce. Relatively few papers appear in the literature detailing work with leaf lettuce and even fewer seem to have included studies on subsequent seed development and production.

After lettuce plants produce their first flower, flowering proceeds through an increase in numbers until they reach a peak. The time taken to reach this peak of flowering varies between cultivars and is influenced by the environment, particularly temperature. Over about a 50 d flowering period, two major peaks of flowering occurred in each cultivar. This 'double peak' flowering pattern occurred in plants irrespective of daylength and temperature. The exception was in Slobolt at 25/15°C under 10, 12 or 14 h daylengths. In these treatments Slobolt plants did not reach their first peak flowering until the plants of the other cultivars had reached their second peak flowering. This delay was due to slowness of bolting in this cultivar. This delay resulted in insufficient time for the development of a second peak flowering before the termination of the experiment after 160 days.

Jones (1927) and Soffer and Smith (1974a) both previously reported the occurrence of double flowering peaks in lettuce plants. Jones (1927) observed that flowering rate was influenced by fluctuations in temperature while Soffer and Smith (1974a) suggested that light intensity might be the controlling factor involved, particularly when comparing the performance of lettuce plants grown in the field with glasshouse conditions. The present experiment suggests that flowering pattern and flowering rate vary due to differences in cultivar reponse to daylength and temperature. The highest peak of flowering occurred in Grand Rapids and Slobolt plants grown under a 14 h daylength and low temperature (25/15°C). The Thai cultivar was the exception, reaching its highest flowering peak in plants grown at 12 h daylength and 25/15°C. Unfortunately there were not enough plants remaining in the 12 h daylength treatment to continue for seed production studies. This situation occurred because plants from this treatment had been previously used for seed development studies in order to determine optimum harvesting time.

The effect of temperature and daylength on seed numbers and seed set was more obvious at 30/20°C than at 25/15°C. At

30/20°C, the number of seeds per head and percentage of seed set were both higher at 14 h daylength than at 10 h daylength while at 25/15°C, daylength effects were relatively unimportant. Koller (1962) reported that good seed set in Grand Rapids was only obtained at night temperatures between 17 and 23°C under short day conditions (8 h). This trend is supported by the present results which show that all three cultivars 'set' seed better at 25/15°C than at 30/20°C under 10 h daylength. However, long days (14 h) brought about a higher peak flowering, seed number and seed set at both temperatures.

The production of high seed yields and high seed quality in lettuce is possible if plants are harvested at the right time. By delaying harvest, much of the seed yield can be lost because of shattering (Hawthorn and Pollard, 1954; Pokanan, 1981). On the other hand, if harvesting is too early, much of the seed would be immature and fail to germinate. It has been shown by a number of workers that seed weight increases towards maturity (Globerson, 1981) and that the size of lettuce seed is positively correlated with plant develoment (Smith et al., 1973b; Soffer and Smith, 1974b; Renard, 1978). High temperatures have also been found to hasten seed maturity and shattering, with seed developing and maturing about 12 d after anthesis (Jones, 1927) or 14 to 16 d after anthesis (Globerson, 1981) depending on cultivar. Seed colour changes occur about 8 to 9 d after anthesis (Globerson, 1981).

Most of the information on lettuce seed development in the literature has been carried out under field and glasshouse conditions. Under the controlled environmental conditions used in the present study, seed of the three cultivars reached their maximum dry weight (physiological maturity) 11 d after anthesis at 30/20°C and 13 d after anthesis at 25/15°C. At this stage, no seed shattering was observed and the pappus was beginning to protrude out of the capsule. The seed head was brownish-green in colour. Seeds harvested at this time would not suffer from lack of viability since the maximum percentage of germination was reached 9 d after anthesis at 30/20°C and 11 d after anthesis at 25/15°C. In both cases this was about 2 d before seed reached physiological maturity.

The precise date at which seed must be harvested does not seem to be critical in plants grown at 25/15°C. This was because of the 4 to 6 d interval between the time seed had completed its physiological development and the onset of shattering. However, in plants grown at 30/20°C, shattering was first observed only 2 d after seed maturity (13 d after anthesis). This suggests that in higher temperature environments harvest timing may be more critical to ensure yields are not severely depleted by seed loss.

Seed colour change in lettuce, is not considered to be a particularly reliable indicator of seed maturity because colour change to black (Thai and Grand Rapids) or light brown (Slobolt) occurred some time (about 4 d) before seed reached physiological maturity. Such seeds, although they showed a high germination percentage are likely to be of low vigour (Pollock and Roos, 1972) and shortened storage life (Hyde et al., 1959).

Thai, Grand Rapids and Slobolt cultivars all showed a similar seed development pattern even though the rate of seed development was influenced by temperature. The higher the temperature the quicker seed matured and shattered. The present results suggest that the optimum time of harvest for seed of these cultivars is not when the seed looks ripe as a result of seed colour change or when the seed head has opened and shattering has commenced. Probably the easiest way to determine optimum harvest time by eye appraisal is when the seed heads turn slightly brown and about 50% of the pappus appears through the bracts. At this stage the seed head still retains its cupped shape and full seed retention.

The correct time of harvest to obtain high seed yield is the most important single variable influencing seed yield provided that seeds have reached physiological maturity. The present experiment showed that the optimum harvest time was about 13 d after peak flowering at 30/20°C and 20 d after peak flowering at 25/15°C. This was about 2 - 3 d later than had been expected from the results of the previous seed development study. However, it should be noted that plants were grown in a growth room enviornment which did not take acount of the effects of wind or rain. Some seeds from the early stages of growth remained in the seed head rather than shattering as would be likely to be the case in the field. This probably resulted in higher than expected seed yields at the later harvest.

Highest seed yield was obtained at 15 - 20 d after the second peak flowering in Grand Rapids under 14 h daylength at 25/15°C. This maximum seed yield of 64 g/plant was obtained 139 to 144 d after sowing and was mainly due to the ability of Grand Rapids plants to produce extremely high flower numbers at the second flowering peak. The maximum seed yield in the Thai cultivar was obtained from plants grown under 14 h daylength and 30/20°C (39 g/plant, 113 d after sowing) while Slobolt produced up to 40 g/plant at either 12 h daylength, 25/15°C (146 d after sowing) or 14 h at 30/20°C (104 or 135 d after sowing).

It is possible that the 'two peak' flowering characteristic of leaf lettuce could be most fully exploited commercially by using a 'double harvest' system involving removal of maximum seeds from the first peak flowering on the standing plant. A second harvest could then be carried out after seeds from the second peak flowering had completed their development. In Grand Rapids this would have resulted in a maximum cumulative (two harvest) yield of over 100 g/plant (25/15°C, 14 h daylength) compared with comparative maximum yields of 80 g/plant in Slobolt (30/20°C, 14 h daylength) and about 67 g/plant in Thai (either 25/15°C or 30/20°C. 14 h daylength).

The results show that Grand Rapids has a higher seed yield potential than the other two cultivars. This suggests that, particularly under 14 h and 25/15°C conditions, Grand Rapids is a most suitable cultivar while Slobolt is well suited under 14 h and 30/20°C. Slobolt however, was not as visually acceptable as Thai and Grand Rapids cultivars in terms of its vegetative growth and visual appearance. The Thai cultivar is also highest yielding under a 14 h daylength at either 25/15°C or 30/20°C. The Thai and Grand Rapids cultivars are very similar in both growth and appearance. This is possibly because they are related, since they are reputed to have both originated from Black Seeded Simpson (Wittwer et al., 1965). However, it might be argued that the Grand Rapids is more suitable than the Thai cultivar under a 14 h daylength since it produced a significantly higher seed yield (78 g/plant, 117 d after sowing) at 30/20°C. The Thai cultivar, however, appears to be more adapted to relatively shorter days. This might reflect its continued cultivation over many years in the relatively shorter daylengths (11 to 12 h) in Thailand.

This short day response (12 h) in seed yield was also apparent in Slobolt. The advantage of this cultivar in producing its highest seed yield at 25/15°C and 12 h daylength (40 g/plant) was more than offset by the delay of about 30 d in bolting of Slobolt plants compared to the other two cultivars. Such delay might be expected to reduce the chances of Slobolt producing a second peak flowering - a characteristic which has been demonstrated to be normal and attainable in both Thai and Grand Rapids. Although Thai and Grand Rapids seed yields were obtained from plants grown at 12 h daylength only from the first peak flowering in the present study, plants of these cultivars did show the capacity to produce a second peak flowering (Chapter 4). At 25/15°C the Thai cultivar in particular, produced the highest number of flowers at its second peak flowering. This suggests that Thai has the potential to produce comparable seed yields to Grand Rapids at 25/15°C and 12 h. If this is correct then the

Thai cultivar could continue to be favoured for seed production under these conditions.

In the case of plants of all three cultivars grown in a 10 h daylength, relatively high yields of seed were obtained. This was principally due to the ability of plants to produce higher numbers of flowers at peak flowering under such short days. Grand Rapids grown at 25/15°C produced more seed (69 g/plant) than the other two cultivars. Maximum seed yields of 47 - 50 g/plant were obtained in the Thai cultivar at both temperatures. Slobolt, despite its approximately 20 -50 d delay in reaching maximum seed yield, produced about 52 g/plant at 30/20°C and 18g/plant at 25/15°C respectively.

These variable seed yields however, were mainly determined by the numbers of flowers present at peak flowering in each cultivar. By comparison branch numbers were relatively insensitive to differences in temperature or daylength although maximum secondary branches were produced under 14 h daylength. This environmental insensitivity was particularly reflected in tertiary branch numbers.

Leaf lettuce is very popular in tropical countries like Thailand yet seed production is rarely attempted successfully. The present study has shown, however, that seed production is feasible and controllable under a wide range of temperature and daylength conditions. The production of two flowering peaks make this crop well suited to hand harvesting methods where labour is cheap. Such a production system would increase domestic seed yield and enable growers to avoid the need to import lettuce seeds from other countries.

Thailand is a tropical south-east Asian country located between latitudes 5° - 22°N. Temperatures vary considerably within the country from 35/25°C in the dry summer season (March to May) and wet season (May to October) to 25/15°C in the cool dry season (November to February). At higher altitudes, the temperature is lower, particularly at night; dropping to about 5°C in the coldest months of December and January. The daylength varies from 11 h (December) in the dry season to 13.5 in the wet season (June).

In certain areas of Thailand with more reliable climate, lettuce can be grown for the market throughout the year. However, conditions which are likely to be favourable for seed production generally only occur during the cool dry season (November - February) and hot dry summer (March - May) where daylengths are about 11 h (December) to 12.5 h (April). Seeds then could be raised in the nursery or greenhouse in September or October and transplanted into the field late in the rainy season (October - November). This would allow plants to develop seed stalks and flower while the temperature is still high and yet develop seed during the dry season (November - March). Such management timing should enable lettuce plants to produce a first peak flowering during December - January and a second peak flowering in February. The seeds harvested during these periods are likely to be of high quality since seed weight and seed germination are not affected by either temperature or photoperiod.

If planting is carried out earlier, plants might not survive due to heavy rain (June - September). On the other hand, if planting is delayed until early in the dry season, plants might not be able to develop their second peak flowering due to problems caused by the onset of the rainy season. Areas which are likely to be most suitable for lettuce seed production in Thailand during the dry season (November - May) would be some areas of the central region and the lowlands of northern and north-eastern Thailand (latitudes 14 - 22°N.) Thai or Grand Rapids are considered to be suitable cultivars for these areas.

The results of this study have proved the feasibility of leaf lettuce seed production in a range of environments. Such information should allow seed growers to choose the climatic conditions most likely to result in high seed yields and quality.

CONCLUSIONS

This experiment has shown that temperature and photoperiod greatly influence both the vegetative and reproductive development of lettuce plants. Warmer temperatures and longer photoperiods are required for seed production than for market vegetable production. Although the three leaf lettuce cultivars used in this study were fairly well suited to growth at higher temperatures (30/20°C), better quality lettuce was obtained when plants were grown at 25/15°C. High temperatures and long days however, accelerated vegetative growth - a characteristic which was associated with early bolting. Both of these cause reduced product marketability.

The results suggest that commercial growers should choose cooler growing areas for market production. Slobolt is more productive and remains vegetative longer than the Thai and Grand Rapids cultivars because of its delayed bolting character. It is, however, not a popular cultivar compared to Thai or Grand Rapids in terms of visual appearance.

The temperatures and photoperiods used in this study appear to be suitable for seed production of these three lettuce cultivars. Floral initiation and flowering are hastened by high temperatures as well as long photoperiods. Long days tend to increase branch numbers, flower numbers at peak flowering and percentage of seed set. High temperatures however, hasten seed maturity and the onset of shattering.

Within the confines of the two temperature combinations and three daylengths used in this experiment, it is possible to make some suggestions concerning the best climatic conditions for high seed yield in the three cultivars studied. The present study has shown that Thai and Grand Rapids produce best under long days (14 h) at either 25/15°C or 30/20°C whereas Slobolt needs long days (14 h) at 30/20°C or 12 h daylength at 25/15°C to express high seeding potential. High seed quality however, is obtained under a wide range of growth conditions and the optimum harvest time occurs when the majority of seed heads are slightly brown in colour.

The results of the study are discussed in the context of climatic areas likely to be most suitable for seed production of leaf lettuce. The production of maximum cumulative (2 harvest) yields of up to 100 g/plant suggests there is tremendous potential for the application of these results. This is particularly true in countries like Thailand where seed yields as low as 3 - 10 g/plant have been reported. This suggests that continued studies to examine seed yield and quality effects under field conditions could be a particularly rewarding area of seed research.

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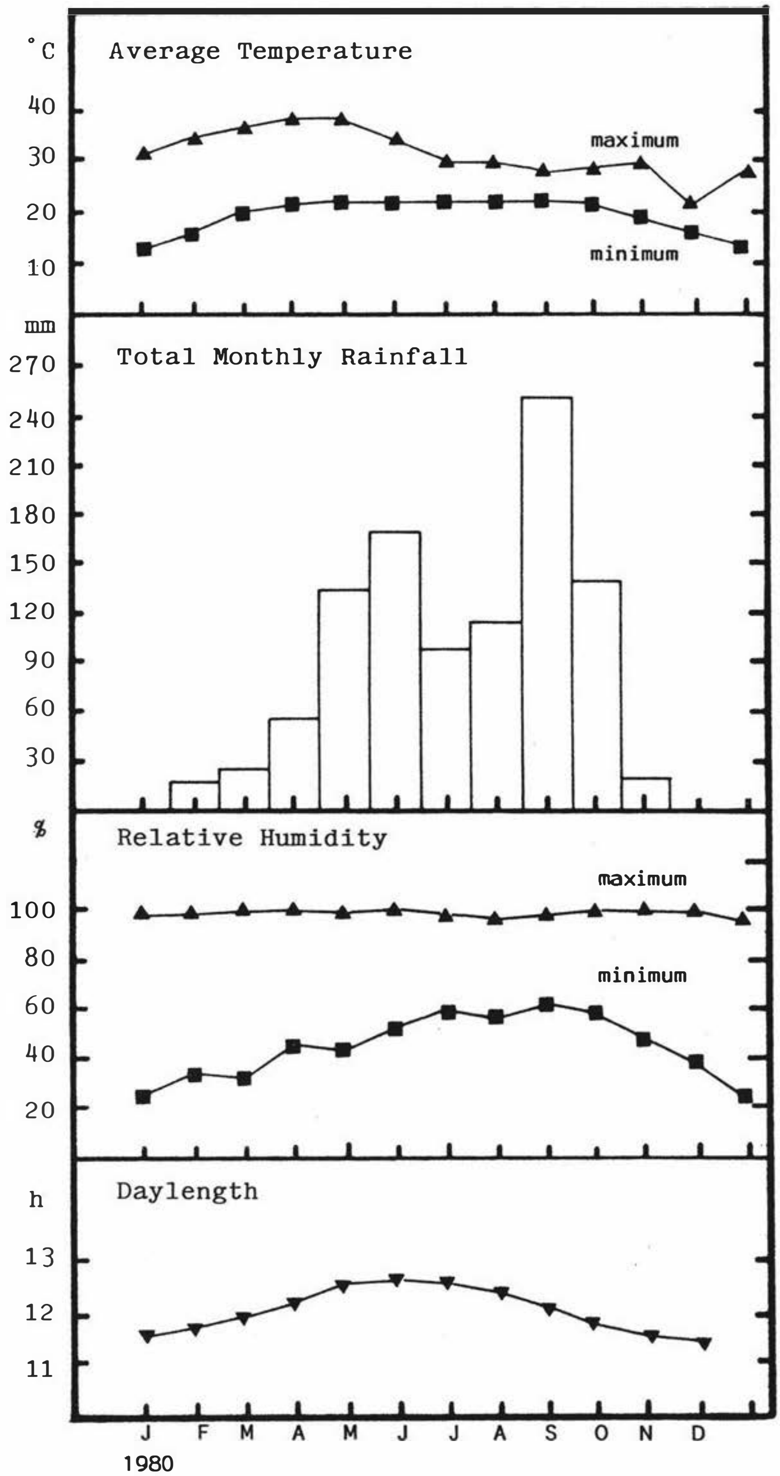
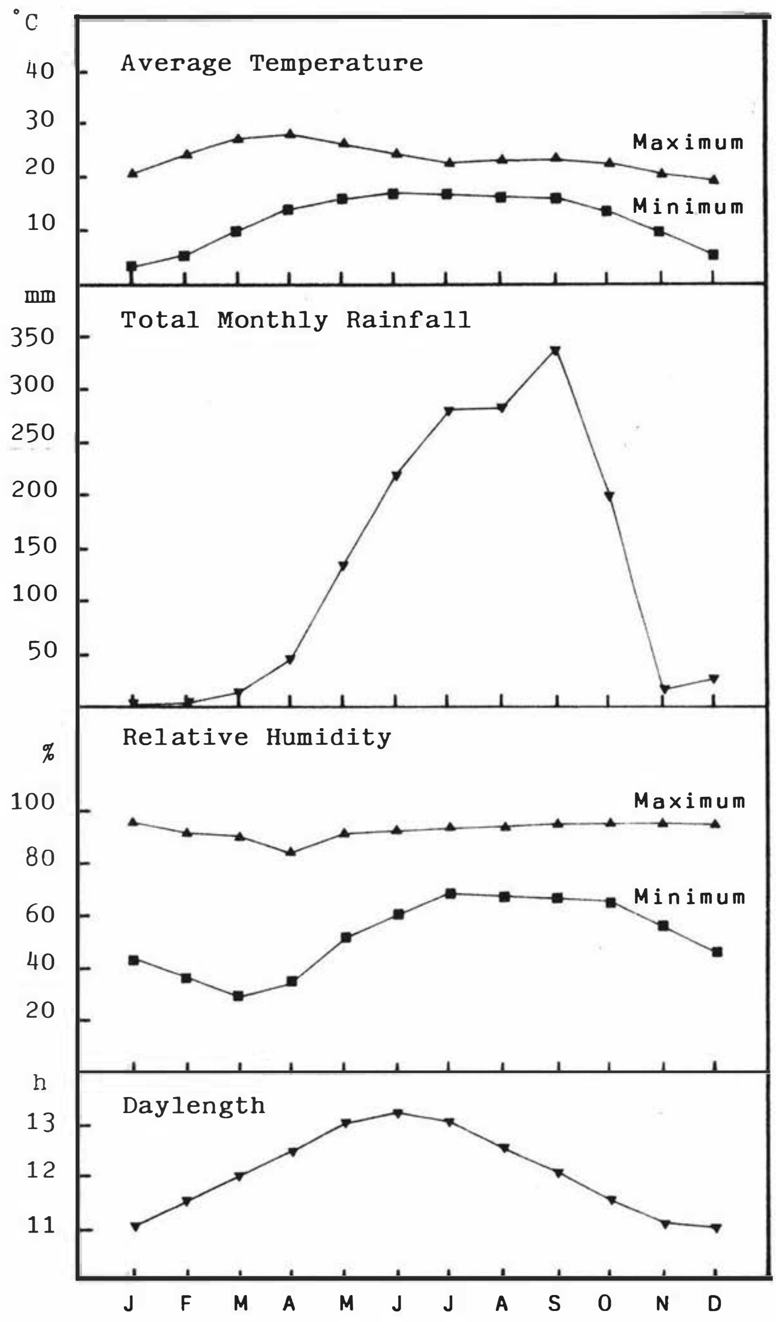
APPENDICES



Appendix 1 Climatic data at Pakchong Horticultural Research station. Elevation: 300m



Appendix 2 Climatic data at Royal Aug Khang Highland Research Station Elevation: 1400 m in 1976 - 1981

Appendix 3 The levels of photosynthetic radiation of each treatment in controlled environment rooms under different temperature and daylength treatments.

Daylength (h)		Pre-Expt.	Post-Expt.	Mean
Photosynthetic irradiance: W/m^2				
10	a	152	147	150
	b	151	149	150
12	a	151	148	150
	b	156	149	153
14	a	153	145	149
	b	151	147	149
Photosynthetic photon flux density: $\mu mol/m^2s$).				
10	a	723	687	705
	b	713	707	710
12	a	707	708	708
	b	738	710	724
14	a	722	683	703
	b	718	696	707

a) 25/15°C temp. regime

b) 30/20°C temp. regime

Appendix 4 Climate Lab - modified half-strength Hoagland's nutrient (g/l)

	Molecular Wt. (g)	Conc.	Final Soln.		PPM
STOCK SOLUTION A:					
Calcium nitrate				Ca	100.20
Ca(NO) x 4H 0	236.15	295.19	.59038	N	70.04
Sequestrene 330				Fe	2.08
10% DTPA NaFe	468.20	10.4	.0208	Na	1.02
STOCK SOLUTION B:					
Potassium phosphate				K	19.55
KH PO	136.08	34.02	.06804	P	15.49
Potassium nitrate				K	97.75
KNO	101.11	126.39	.25278	N	35.02
Magnesium sulfate				Mg	24.32
MgSO x 7H 0	246.5	123.24	.24648	S	32.06
Boric acid				B	0.250
H BO	61.82	0.715	.00143		
Manganese chloride				Mn	0.251
MnCl x 4H 0	197.92	0.4525	.000905	Cl	0.324
Zinc sulfate				Zn	0.025
ZnSO x 7H 0	287.55	0.055	.000110	S	0.012
Copper sulfate				Cu	0.010
CuSO x 5H 0	249.68	0.020	.00004	S	0.005
Sodium molybdate				Na	0.003
Na MoO x 2H 0	241.93	0.0067	.0000134	Mo	0.005
Potassium chloride				K	1.652
KCl	74.56	1.575	.00315	Cl	1.498

Nutrient	PPM	Nutrient	PPM
N	105.06	B	0.250
P	15.49	Mn	0.251
K	118.95	Cu	0.010
S	32.08	Zn	0.025
Ca	100.20	Mo	0.005
Fe	2.08	Cl	1.822
Mg	24.32	Na	1.023

Appendix 5 Relative growth rates of plant dry weight (RGR)[a] and leaf area (RLGR)[b]

Cultivar	Daylength (h)	RGR ($g\ g^{-1}\ d^{-1}$) 25/15°C	30/20°C	RLGR ($cm^2cm^{-2}\ d^{-1}$) 25/15°C	30/20°C
	10	.237	.248	.227	.224
Thai	12	.236	.262	.223	.251
	14	.242	.234	.226	.223
Grand	10	.242	.256	.229	.229
Rapids	12	.246	.256	.229	.229
	14	.248	.223	.240	.214
	10	.209	.257	.232	.243
Slobolt	12	.251	.300	.238	.286
	14	.254	.257	.244	.249

Data within column and rows are nonsignificant according to t-tests, 5% level.

a) The relative growth rates, indicated by changes in dry weight were calculated from:

$$RGR = \frac{Log\,\ell\,(W_2 - W_1)}{T_2 - T_1}$$

where RGR = difference between natural logarithms of whole plant dry weight (gm) at second and fist harvests respectively

$T_2 - T_1$ = Time interval between harvest (days)

b) The relative leaf growth rates, indicated by changes in leaf area were calculated from:

$$RLGR = \frac{Log\,\ell\,(LA_2 - LA_1)}{T_2 - T_1}$$

where RLGR = difference between natural logarithms of whole plant leaf area (cm^2) at second and first harvests respectively.

Appendix 6 Temperature, daylength and cultivar effects on fresh weight (g/plant)

Temperature °C	Cultivar	Daylength (h)	Days from Sowing 10	20	30	40
		10	.066	1.50	17.10	117.60
	Thai	12	.066	1.80	28.90	119.50
		14	.119	5.10	76.10	250.30
25/15	Grand	10	.061	1.5	16.60	120.30
	Rapids	12	.061	1.3	29.00	143.20
		14	.127	4.1	74.20	373.60
		10	.077	1.70	22.90	142.60
	Slobolt	12	.065	2.60	35.30	176.50
		14	.106	4.60	67.40	349.40
		10	.128	2.96	34.25	243.61
	Thai	12	.065	4.11	81.70	272.96
		14	.244	15.15	181.55	484.00
30/20	Grand	10	.122	2.12	46.22	214.00
	Rapids	12	.092	1.36	85.19	333.23
		14	.268	13.72	154.66	416.00
		10	.083	4.04	45.03	270.66
	Slobolt	12	.092	2.26	60.74	305.13
		14	.158	11.72	184.00	591.66

Appendix 7 Temperature, daylength and cultivar effects on dry weight (g/plant)

Temperature °C	Cultivar	Daylength (h)	Days from Sowing 10	20	30	40
25/15	Thai	10	.004	.099	1.00	5.37
		12	.006	.129	1.78	6.17
		14	.010	.316	4.51	13.21
	Grand Rapids	10	.004	.095	1.01	5.74
		12	.005	.086	1.74	7.06
		14	.011	.265	4.23	17.33
	Slobolt	10	.005	.121	1.43	6.83
		12	.005	.166	2.37	9.03
		14	.009	.313	4.08	17.62
30/20	Thai	10	.006	.196	1.92	12.17
		12	.005	.266	4.57	12.30
		14	.017	.996	8.67	20.36
	Grand Rapids	10	.005	.145	2.52	10.47
		12	.008	.390	4.63	15.53
		14	.023	.944	8.29	18.72
	Slobolt	10	.005	.295	2.59	12.81
		12	.002	.146	3.47	15.55
		14	.014	.832	9.68	33.44

Appendix 8 Temperature, daylength and cultivar effects on leaf area (cm^2/plant)

Temperature °C	Cultivar	Daylength (h)	Days from Sowing 10	20	30	40
		10	3.13	56.40	515	2878
	Thai	12	3.08	58.00	585	2409
		14	4.86	158.60	1722	4127
25/15	Grand	10	2.94	55.20	511	2910
	Rapids	12	2.61	45.00	556	2670
		14	4.89	132.00	1723	6236
		10	3.81	70.10	732	3982
	Slobolt	12	3.85	91.80	827	3966
		14	4.59	154.40	1752	7146
		10	5.72	98.99	869	4949
	Thai	12	3.14	123.29	1800	5491
		14	9.92	409.65	3607	8046
30/20	Grand	10	5.65	66.05	1107	4646
	Rapids	12	3.85	205.67	1810	6307
		14	11.28	380.59	2867	7106
		10	4.23	143.15	1262	6826
	Slobolt	12	1.22	184.67	1315	6789
		14	7.46	367.01	4220	13357

Appendix 9 Temperature, daylength and cultivar effects on seed fertility

Temperature °C	Cultivar	Daylength (h)	Floret No. PF1	Floret No. PF2	Seed No. PF1	Seed No. PF2	Seed Set (%) PF1	Seed Set (%) PF2
		10	17.30	15.90	13.75	13.41	79.31	84.3
	Thai	14	17.48	17.55	15.70	14.63	89.82	83.4
		10	18.46	14.79	14.50	12.38	78.51	83.6
25/15°C	Grand Rapids	14	17.43	15.33	13.88	13.14	79.62	85.7
		10	19.81	-	18.73	-	94.65	-
	Slobolt	14	19.72	-	18.74	-	95.00	-
		10	21.15	17.21	14.10	12.41	66.47	72.9
	Thai	14	21.35	17.03	19.42	14.73	90.94	86.1
		10	20.14	16.85	11.88	10.09	58.75	59.9
30/20°C	Grand Rapids	14	20.90	18.98	17.63	16.60	84.49	85.8
		10	19.68	-	15.76	-	80.01	-
	Slobolt	14	22.17	-	20.50	-	92.43	-

Appendix 10 100 seed fresh weight (mg) at different days after anthesis

Days after anthesis	25/15°C Thai	25/15°C Grand Rapids	25/15°C Slobolt	30/20°C Thai	30/20°C Grand Rapids	30/20°C Slobolt
1	18.8	20.5	16.4	20.5	15	21.1
3	75.2	89.2	60.5	86.7	75	106.0
5	84.4	94.7	107.3	103.5	106.4	165.4
7	131.1	100.4	192.8	114.9	155.0	156.3
9	144.0	129.7	167.6	127.8	139.2	159.6
11	153.8	148.3	165.9	127.4	132.5	160.1
13	141.9	135.8	175.6	109.2	111.9	105.8
15	146.6	128.4	148.3	102.6	110.8	106.7
17	102.9	104.4	115.4	90.5	112.1	106.5
19	94.4	93.7	108.0	-	-	109.1
21	91.8	95.2	106.0	-	-	108.4

Appendix 11 100 seed dry weight (mg) at different days after anthesis

Days after anthesis	25/15°C Thai	25/15°C Grand Rapids	25/15°C Slobolt	30/20°C Thai	30/20°C Grand Rapids	30/20°C Slobolt
1	3.3	4	4.1	3.9	4	5.4
3	18.2	18.2	14.3	15.5	15	18.8
5	19.8	20.5	23.5	30.9	37.4	36.9
7	36.1	30.0	47.0	52.5	73.0	66.3
9	53.7	46.3	71.5	75.7	85.9	87.5
11	78.5	79.2	89.1	82.7	100.3	101.3
13	86.5	88.0	105.6	83.5	100.6	99.8
15	89.2	85.9	104.1	84.8	100.1	99.4
17	88.0	86.9	102.8	82.8	100.8	98.6
19	85.3	85.1	102.2	-	-	100.2
21	83.5	86.1	100.6	-	-	100.0

Appendix 12 Moisture content(%) at different days after anthesis

Days after anthesis	25/15°C Thai	25/15°C Grand Rapids	25/15°C Slobolt	30/20°C Thai	30/20°C Grand Rapids	30/20°C Slobolt
1	81.3	80.5	75.0	81	73.6	77.4
3	79.3	79.6	76.2	82.1	79.7	82.2
5	76.5	78.4	78.1	70.1	64.7	77.7
7	72.5	70.2	75.6	54.3	52.9	58.8
9	62.7	64.3	57.3	40.8	38.3	45.2
11	48.9	46.6	46.3	35.1	24.3	36.7
13	38.8	35.2	39.8	23.5	10.1	9.5
15	39.2	33.1	29.8	17.3	9.6	6.8
17	14.5	16.8	10.9	8.5	10.1	7.4
19	9.6	9.2	5.4	-	-	8.2
21	9.0	9.6	6.2	-	-	7.7

Appendix 13 Germination Percentage (Normal Seedlings) at different days after anthesis

Days after anthesis	25/15°C			30/20°C		
	Thai	Grand Rapids	Slobolt	Thai	Grand Rapids	Slobolt
1	-	-	-	-	-	-
3	-	-	-	-	-	-
5	-	-	-	-	43	16
7	6	42	26	78	78	69
9	22	53	61	97	99	98
11	70	75	94	88	96	98
13	98	81	90	91	96	98
15	95	89	98	96	100	98
17	91	88	98	98	99	96
19	94	94	96	-	-	98
21	94	99	93	-	-	99

Appendix 14 Germination percentage (abnormal seedlings) at different days after anthesis

Days after anthesis	25/15°C Thai	25/15°C Grand Rapids	25/15°C Slobolt	30/20°C Thai	30/20°C Grand Rapids	30/20°C Slobolt
1	-	-	-	-	-	-
3	-	-	-	-	-	-
5	-	-	-	46	44	72
7	59	52	54	18	12	14
9	41	30	22	3	1	2
11	5	15	6	12	4	2
13	2	10	10	9	4	2
15	3	11	2	2	-	2
17	5	12	2	2	1	3
19	5	6	4	-	-	2
21	2	1	7	-	-	1

Appendix 15 Seed viability (%) at different days after anthesis

Days after anthesis	25/15°C			30/20°C		
	Thai	Grand Rapids	Slobolt	Thai	Grand Rapids	Slobolt
1	-	-	-	-	-	-
3	-	-	-	-	-	-
5	-	-	-	46	86	88
7	65	94	80	96	90	83
9	63	83	83	100	100	100
11	75	90	100	100	100	100
13	100	95	100	100	100	100
15	98	100	100	98	100	100
17	96	100	100	100	100	99
19	99	100	100	-	-	100
21	96	100	100	-	-	100

<u>Appendix 16</u> Temperature, daylength and cultivar effects on seed yield (g/plant)

Temperature °C	Cultivar	Daylength (h)	Days after PF1				Days after PF2				Cumulative yield (two harvests)
			10	15	20	25	10	15	20	25	
25/15	Thai	10		21.08	23.68	18.85		21.58	23.17	12.66	46.85
		12		11.98	26.94	19.41		-	-	-	26.94
		14		30.03	28.55	36.12		24.73	30.35	11.64	60.38
	Grand Rapids	10		19.82	25.60	36.36		32.58	30.79	16.95	68.94
		12		25.32	20.91	22.15		-	-	-	25.32
		14		35.09	42.95	36.37		63.10	64.93	37.36	107.88
	Slobolt	10		14.01	18.19	10.95		-	-	-	18.19
		12		10.27	28.08	40.90		-	-	-	40.90
		14		26.18	29.40	9.25		-	-	-	29.40
30/20	Thai	10	8.11	19.83	17.44		28.32	30.21	23.14		50.04
		12	8.03	9.06	14.69		-	-			14.69
		14	21.97	22.03	29.65		39.35	30.76	34.67		69.00
	Grand Rapids	10	13.43	11.71	20.71		21.96	23.86	27.65		48.36
		12	10.94	15.53	14.77		-	-			15.00
		14	22.07	22.99	28.24		40.48	49.92	48.62		78.16
	Slobolt	10	12.42	16.67	17.30		18.11	35.23	16.72		52.53
		12	23.22	28.49	12.64		-	-			28.49
		14	20.46	26.47	41.09		33.13	39.15	41.00		82.09

Appendix 17 Temperature, daylength and cultivar effects on germination percentage (Fresh ungerminated seeds in parentheses)

Temperature °C	Cultivar	Daylength (h)	Days after PF1 10	15	20	25	Days after PF2 10	15	20	25
25/15	Thai	10		99.50	98.00	99.00		98.5(7)	98.5(12)	89.75
		12		98.00	97.00	100.00		-	-	-
		14		94.50	98.25	98.00		92.25	95.75	95.25
								-	-	-
	Grand Rapids	10		98.50	98.00	98.50		99.25	99.5	98.25
		12		98.00	97.00	98.00		-	-	-
		14		98.50	98.75	96.75		97.0	97.25	91.75
	Slobolt	10		97.00	96.25	98.50		-	-	-
		12		98.00	95.00(4)	97.00(8)		-	-	-
		14		83.50	97.00	96.50		-	-	-
30/20	Thai	10	97.10	98.75	99.50		98.25	99.5	99.75	
		12	96.00	98.00	100.00		-	-	-	
		14	95.50	98.25	99.25		99.75	99.00	99.25	
	Grand Rapids	10	98.75(3)	99.50(5)	100.00		99.25	99.50(4)	99.50(12)	
		12	99.00	100.00	98.00		-	-	-	
		14	98.00	98.50	98.50		99.50	99.00	99.25	
	Slobolt	10	97.50	98.75	98.25		98.25	99.00	98.50	
		12	98.00	96.00	98.00		-	-	-	
		14	95.75	97.75	96.25		99.75	98.25	99.00	

Appendix 18 Temperature, daylength and cultivar effects on 1000 seed dry weight.

Temperature °C	Cultivar	Daylength (h)	Days after PF1 10	15	20	25	Days after PF2 10	15	20	25
25/15	Thai	10		887	790	853		920	885	975
		12		822	954	857		-	-	-
		14		1013	993	1046		1066	977	877
	Grand Rapids	10		835	725	948		993	900	753
		12		812	903	959		-	-	-
		14		1127	1035	1017		1036	1168	1113
	Slobolt	10		850	853	758		-	-	-
		12		963	1012	1055		-	-	-
		14		1071	983	971		-	-	-
30/20	Thai	10	778	944	974		911	894	880	
		12	754	852	808		-	-	-	
		14	770	787	838		863	775	886	
							-	-	-	
	Grand Rapids	10	884	997	939		961	1001	937	
		12	922	913	971		-	-	-	
		14	820	801	827		819	868	879	
	Slobolt	10	900	914	946		981	928	928	
		12	920	938	1006		-	-	-	
		14	832	830	881		798	940	862	