REGULATION OF CURD INITIATION IN THE SUMMER CAULIFLOWER

by

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I am a part of all that I have met;
Yet all experience is an arch wherethrough
Gleams that untravelled world, whose margin fades
For ever and for ever when I move.
How dull it is to pause, to make an end,
To rust unburnished, not to shine in use,
As though to breathe were life.

Ulysses : (Tennyson 1809-1892)

ABSTRACT

Factors regulating curd initiation in the summer cauliflower were examined with special attention given to responses to change in environment.

Low temperature treatments of four weeks at 5°C accelerated curd initiation, reducing the number of leaves initiated before the curd. A reduction in vegetative growth was associated with earlier curd initiation. The extent of the low temperature effect was dependent on genotype, temperature, treatment duration and the plant's stage of development when low temperature treatments commenced.

A distinct juvenile phase was observed when plants were incompetent to perceive chilling as a vernalization stimulus. Phase transition from the juvenile to the mature, competent form was associated with the initiation of a specific number of leaves. These were 14 and 18 leaves for cvs Perfection and White Fox respectively, leaf number being higher in the later season cultivar. The duration of phase change itself was short, lasting approximately two plastochrons. Increase in leaf initiation rate was associated with phase transition.

Rate of leaf initiation increased with increasing temperature. Duration of the juvenile phase, measured chronologically, was therefore shorter at higher temperatures. Shoot dry weight was linearly related to leaf number in plants examined here; this characteristic would also be a stable marker for phase transition. Chilling imbibed seed proved ineffective in accelerating curd initiation.

Reduction in total irradiance receipt delayed curd initiation in plants grown under warm conditions. Associated with this delay were reductions in rate of leaf initiation and stem dry weight increment. Photoperiods of 16 h following sub-optimal vernalization allowed faster curd initiation than photoperiods of 8 h and 24 h. A minimum stem dry weight at curd visibility was achieved under this regime.

Reciprocal of leaf number subtending the curd, denoting the rate of progress towards curd initiation, was shown to be linearly related to temperature under controlled environment conditions. Curd initiation rate in cv Perfection increased after treatment in the temperature range -1.25°C to 5.5°C and decreased after treatment over the range 5.5°C to 23.5°C. Similarly, in cv White Fox, curd initiation rate increased following

treatments at temperatures of -3.0°C to 8.6°C and declined over the range 8.6°C to 31.5°C. Linear regressions also adequately described the relationship of rate of curd appearance on temperature. Rate of curd appearance in cv Perfection increased following treatment at temperatures of -4.5°C to 12°C and declined over the range 12°C to 29.5°C. In cv White Fox rate of curd appearance was shown to increase following treatment over the range -3.5°C to 15.8°C and decline from 15.8°C to 28.3°C. The different cardinal temperatures from those established for curd initiation were probably the result of examining not one process but two: curd initiation and early curd growth. Their two distinct optimum temperatures would account for the observed parabolic trend.

The relationship between leaf number subtending the curd and thermal time established under controlled environment conditions was extrapolated to predict curd initiation time in the field. Thermal times of vernalization for plants grown under field conditions showed close agreement with controlled environment figures at early transplantings, but not for late transplantings. This drift was probably due to irradiance receipt whereby increasing irradiance would partially substitute for low temperature in accelerating curd initiation.

Curd growth and morphology were clearly influenced by post-chilling temperature conditions. Linear functions adequately described regression of Log_e curd diameter or curd weight on thermal time. Thermal requirement for a specified curd diameter could therefore be calculated.

Increasing supply of mineral nitrogen accelerated curd initiation in unchilled plants. Curd initiation in chilled plants, however, was not affected by nitrogen applications. Increasing nitrogen increased both leaf area and dry weight. A minimum leaf dry weight below which curd initiation could not occur was indicated. Both larger module size for plant growth and increased nitrogen levels increased the number of leaves initiated during propagation. Increased nitrogen during propagation accelerated curd initiation in the field. Severe water stress also accelerated curd initiation and reduced leaf growth.

Application of GA_{4+7} to unchilled plants accelerated curd initiation more than applications of GA_3. GA_{4+7} generally increased stem dry weight and decreased leaf dry weight. The hypothesis was proposed that GA_{4+7} accelerated curd initiation by redirecting assimilates to apical regions of the stem. Curd initiation under field conditions was also accelerated by GA_{4+7}.

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ABBREVIATIONS

ABA - Abscisic acid

a.i. - active ingredient

°C d - Thermal time, degree days

cm - centimetre

cv - cultivar

d - day

d.f - degrees of freedom

dwt - dry weight

GA - gibberellic acid

g - gramme

HLRG - High pressure mercury vapour lamps

h - hour

Jm^{-2} - Joules per square metre

MJ - Megajoules

Mpa - Megapascals

PAR - Photosynthetically active radiation

S.E - Standard error of means

S.E.D. - Standard error of the difference between means

SON/T - High pressure sodium lamp

T - Temperature

T_b - Base temperature for a process

T_m - Maximum temperature for a process

T_o - Optimum temperature for a process

t - time

wk - Week

$W.m^{-2}$ - Watts per square metre

$\Psi leaf$ - Leaf water potential

Chapter 1

INTRODUCTION
and
LITERATURE REVIEW

Cauliflowers are produced virtually all-year-round in the UK, with regional specialization for particular times of the year. Worcestershire and Lancashire are the main production centres for container-raised early summer cauliflowers. Lincolnshire is the major production centre for the late summer and autumn crops, with lesser production in early summer. Winter hardy Roscoff cauliflowers are grown in the relatively mild winter climates of Cornwall, Devon, Dyfed and parts of Kent with winter hardy spring heading cauliflowers produced mainly in Lincolnshire and Kent (Anon, 1982). In 1985 total cauliflower production in the UK yielded some 331,700 tonnes with a value of 71.2 million pounds. Summer and autumn cultivars constituted over 85% of the total production. This thesis concentrates on the summer cauliflower.

The early summer cauliflower group is grown from an autumn sowing and overwintered under cold glass or polythene prior to field planting in the spring. Seed is normally sown between September 26 and October 12, although it may be sown in heated glasshouses in January providing a continuity of harvest into July. The late summer group can be produced by direct drilling into the field or by transplanting seedbed raised plants 6 to 8 weeks after sowing. Seed of the late summer cauliflower is traditionally sown in frames from February to April, whereas field sown crops are drilled in April or early May. Bare-root transplants, although still widely used are being replaced following recent advances in the development of modular raised transplants (Hiron, pers. comm; Symonds, 1984; Anon, 1985a).

The production of early and late summer cauliflowers is beset by two major interrelated problems: buttoning and a lack of crop uniformity.

Buttoning is defined as the production of curds with a diameter of less than 9 cm (Anon, 1980). This was originally regarded as a premature heading phenomenon (Robbins et al. 1931), but further research has led to a re-appraisal of this view.

Carew and Thompson (1948) showed that buttoning was controlled by several factors, and in particular demonstrated that plants growing in nitrogen deficient conditions produced buttons. They considered buttoning not as "premature heading" but to be a consequence of reduced leaf expansion allowing early curd visibility. Low nitrogen did not influence the time of head formation as was inferred by Robbins et al. Carew and Thompson concluded factors having the most influence on buttoning were nitrogen levels in the field, and the age of plants at transplanting.

Jensma (1957) defined a buttoned plant as having small leaves, low leaf number and a small curd. Again implicit in this definition is the association between buttoning and premature heading, as indicated by the reduced leaf number. Jensma concluded that larger transplants were more prone to buttoning as these were reproductive at the time of transplanting. Buttoning was affected by three factors: sowing distance in the seedbed, age of transplant and the variety. Crowded plants and young transplants gave the lowest percentage of buttons. The later 'LeCerf' type was less susceptible than the early 'Alpha' cultivar. Jensma therefore proposed that plants should be grown on a dry seedbed of poor soil, under crowded conditions and concluded that under such unfavourable conditions the plants could grow "old" and remain vegetative. These recommendations are analagous to the principles behind the current practice of modular raised transplants.

Extensive studies on buttoning (Wiebe, 1981,1983; Wurr and Fellows, 1984) have shown that it is not always due to premature curd initiation, as was the case with Jensma's plants. Growth chamber experiments carried out by Wiebe (1981) have shown that buttoning can be the result of retarded leaf growth and independent of curd initiation. Experiments using transplants raised under different growing conditions for different times have shown that buttoning cannot be predicted on the simple basis of transplant size, or diameter of the stem apex. Prediction is better based on leaf weight and size. Wiebe (1983) concluded that the larger the seedlings were at transplanting, the more liable they were to buttoning. Retarding vegetative growth by restricted watering or by storage at 2°C in darkness for up to two weeks helped to prevent buttoning. A temperature of 20°C inhibited curd differentiation, increased growth and hence the risk of buttoning. The use of large pots or high nitrogen rate during propagation had the same effect. Manipulation of vegetative growth by these means is likely to influence the size of the leaves and the degree to which they compete with the curd for assimilates. Post transplanting disturbances in growth increased the incidence of buttoning, while continuous growth, and an adequate water and nutrient supply after planting prevented buttoning. Wurr and Fellows (1984) studied the effect of transplanting plants of different sizes on the time of curd initiation, the growth of plant parts and the extent of buttoning. Larger plants transplanted later produced more buttons, but did not initiate curds earlier. Larger plants at transplanting had a lower leaf weight than smaller plants after curd initiation and consequently produced a smaller leaf area. Initiation before transplanting was not a prerequisite for buttoning. In fact there was a slight tendency for the reverse to be true, which was

consistent with the view of Carew and Thompson (1948) that the use of the term 'premature' in relation to curd initiation is unjustified.

The reduction in leaf growth which was greater with later transplanting and plant size is likely to be the predominant factor in determining the degree of buttoning (Wurr and Fellows, 1984),. Further studies indicated that relative growth rate changes in plant parts are not necessary to induce buttoning. A lower weight of leaf and subsequently smaller leaves gives rise to more buttoning, whereas larger leaves allow the curd to become bigger before it is exposed. This would also explain the increased susceptibility to buttoning in earlier cultivars, as earlier cultivars initiate curds at a lower leaf number. In conclusion, although it has been shown (Wurr and Fellows 1984) that initiation prior to transplanting is not a prerequisite for buttoning, it seems likely that reduced growth close to the time of curd initiation will adversely affect leaf growth and consequently increase the incidence of buttoning.

The production of predictable yields is desirable in all crops, but with cauliflower the problems are particularly difficult due to poor uniformity in curd maturity. Harvesting the crop is currently a manual procedure which accounts for 20-40% of total production costs (Wheeler and Salter, 1974). Mechanical harvesting would significantly reduce costs but as any mechanical harvesting system is likely to be non-selective, a high percentage of curds would have to be marketable at a given time. This would facilitate clearance of the crop on one occasion. Lack of crop uniformity at present means several harvests are required spread over as many as three to four weeks. Studies on cropping characteristics and uniformity, measured as spread of harvest within a crop, are therefore of considerable interest (Martin, 1985; Booij, 1986).

Most of the studies undertaken to date have been agronomic and have indicated factors likely to influence crop uniformity. These can be divided into genetic and envionmental components. Crisp (1984) concluded that cauliflowers appear inherently variable in maturity time and curd size: coefficients of variation for maturity time and yield are consistently higher than in crops of other Brassicas such as Brussels sprouts and cabbage. Indeed, the notable advances in uniformity and yield of Brussels sprouts and cabbages which have accompanied the breeding of F1 hybrid cultivars have not been obtained in cauliflowers. In a study of factors causing small curds in cauliflowers, Crisp (1984) suggested that differences within cultivars in maturity and curd size may not be genetic. Breeding to eliminate or reduce this condition may not therefore be possible. These other Brassica crops are harvested in the vegetative state whereas cauliflowers are reproductive. This would suggest that transition to the reproductive state is the key variable.

Most of the annual summer maturing cultivars are self compatible and are substantially inbred; in contrast to the biennials which are largely open pollinated out breeding types (Watts 1965; Crisp and Hardwick, 1985). This again is evidence that high variability in crop maturity is not associated with increased outbreeding. More uniform crops of cauliflower cannot be expected in F1 hybrids or further inbred cultivars. The limited introduction of F1 hybrids has, to date, shown this to be the case (Crisp, 1984). Inbred lines may themselves differ substantially in their variability, suggesting that genetically controlled stability to microenvironmental variation is important. Minor differences in growth during the "juvenile" phase may be magnified into large differences in maturity time if different plants within a crop become responsive to environmental stimuli at

different times. Salter (1969) established that the length of the maturity period in crops was related to the length of their curd initiation period. This suggested that environmental factors operating before curd initiation occurs can influence the maturity characteristics of the crop. The time of curd initiation has been correlated with the temperature experienced after the initiation of the 19th leaf, corresponding to the end of the proposed juvenile phase. The variation in the time at which the different plants started to initiate curds was closely correlated with the variation in the time at which the heads were ready for harvesting (Booij, 1984; 1986). Monitoring crop growth in the cultivar White Fox at four sites in Lincolnshire over the period 1983 to 1985 resulted in similar observations (Wurr, 1986). Wurr concluded that when the time of curd initiation is determined by crop dissection it becomes apparent that the time from curd initiation to curd maturity is relatively stable and varies much less than the time from transplanting to curd initiation. Clearly the key to manipulating cauliflowers to avoid buttoning, or to improve the degree of uniformity, is to understand more of the environmental factors which induce curd initiation (Salter, Ward and Whitwell, 1972).

The remainder of this chapter presents a critical review of previous published work relevant to curd initiation in the cauliflower. It will serve both to identify areas in which knowledge is sparse and to examine those experimental techniques and approaches used eleswhere, in many cases with other plants, that could be adapted for use in the current project.

Cauliflowers have either a qualitative or quantitative cold requirement for curd initiation (Haine, 1959; Gauss and Taylor, 1969; Sadik, 1967; Wiebe, 1972b). However, the effectiveness of any cold treatment in bringing about curd initiation is largely dependent on the time at which

cold is experienced relative to the plants' development (Sadik, 1967; Wiebe, 1972a), and by inference, the duration of a juvenile phase. It therefore seems pertinent to review the literature with respect to juvenility before attempting to understand how the cauliflower responds to changes in environmental conditions.

The phenomenon of phase change or juvenility has been reviewed extensively in recent years by a number of authors (Doorenbos, 1965; Leopold and Kriedemann, 1975; Schwabe, 1976; Wareing and Frydman, 1976; Ross, Pharis and Binder, 1983; Hackett, 1985) as has the relation of juvenility to flowering (Wareing, 1961; Zimmerman, 1972; Wareing, 1987).

Juvenility has been defined as that phase of growth during which flowering cannot be induced by any treatment (Leopold and Kriedemann, 1975; Vince-Prue, 1975) and a phase when the plant is capable of exponential increase in size, when flowering processes cannot be readily induced and when the plant develops characteristic morphological forms of leaves, stems and thorns. Whilst this second definition is often the case with woody species, morphological differences between juvenile and adult (mature) forms are usually much less distinct in herbaceous plants. Transition to the reproductive state occurs in many plant species after completion of the juvenile phase, without exposure to any particular stimulus, whereas others require an appropriate environmental trigger. In this context the term "ripe-to-flower" is often used for plants which have completed the juvenile phase, but not experienced the correct conditions for flowering. They are "competent" to respond.

In most woody plants the juvenile phase lasts several years and can be as long as 30 to 40 years in some trees. Most herbaceous species however are rarely juvenile for more than a few days or weeks. In extreme cases

the juvenile stage is very short, if present at all, since flower primordia are found in the seed. Flowering is often the key character associated with phase change to maturity and transition from the juvenile to the adult phase has usually been defined in terms of the plant attaining the ability to flower (Stokes and Verkerk, 1951; Zimmerman, 1972; Schwabe, 1976; Wareing and Frydman, 1976). Once competence has been attained the plant may flower as long as the required environmental stimuli are present. It has been pointed out however in a recent review (Zimmerman, Hackett and Pharis, 1985) that although flowering may indicate transition to the adult phase, a delay in occurence of the requisite environmental conditions will only delay flowering itself, and not necessarily phase transition. Also although flowering indicates maturity it does not necessarily indicate when transition occurred.

In Brussels sprout the juvenile and mature forms can be distinguished by both physiological and morphological characteristics. Flowering follows chilling as long as the number of nodes totals approximately 30 (Stokes and Verkerk, 1951). With woody perennials situations may arise whereby enviromental factors trigger precocious flowering but then flowering does not occur again for many years (Ross et al., 1983). Zimmerman, Hackett and Pharis (1985) therefore concluded that the ability to flower is a necessary but not sufficient condition to mark the beginning of the adult phase. Phase change has occurred only if the plant will then continue to flower in its natural environment without the application of any "artificial" stimulus that may have originally induced flowering. Although applicable to woody plants, the last statement would not be applicable in the case of a monocarpic species such as the cauliflower where the definition of Stokes and Verkerk (1951) is adequate, juvenility comprising that phase during which seedlings cannot be induced to flower.

In cases were seed vernalization is effective it can be assumed that the duration of the juvenile phase is very short. Seed vernalization has been reported in most Brassica groups with the exception of Brussels sprouts (Friend, 1985b). Reports on the effectiveness of seed vernalization are inconsistent which may be attributable to differences in techniques and duration of exposure to low temperature as well as to differences between cultivars. When long periods of exposure to low temperature are required it is possible that the little growth achieved during the treatment is sufficient to complete the juvenile phase. This has been proposed as the explanation for successful seed vernalization of some cold requiring biennials such as carrots and turnip (Lang, 1965). Where full sensitivity to seed vernalization is evident in cold requiring annuals the evidence is that most effective seed vernalization takes place during very early embryogenesis. In some cases the ripening embryo can be vernalized while attached to the mother plant or when excised, this has been demonstrated in several winter cereals and certain members of the leguminosae (Gregory and Purvis, 1938; Lang, 1965; Reid and Murfet, 1977). Embryo sensitivity is greatest at the early stages, one or two weeks after pollination.

Most cold requiring perennials do not show a vernalization response to cold treatments of the imbibed seed. They possess a distinct juvenile phase marked by a variable amount of vegetative growth. This is also evident in many species which possess a so-called "direct" response to chilling such as Brussels sprouts and cabbage (Stokes and Verkerk, 1951; Lang, 1965). Seed vernalization was reported for the cauliflower cultivar Nozaki-Wase (Fujime and Hirose, 1979) although chilling was required for 30 to 40 days and the amount of growth achieved during this period was not indicated. They also noted that under field conditions the time of curd

formation was hardly advanced by chilling of the seeds, although a slight reduction in leaf number below the curd was reported. A similar duration of exposure to low temperature is required in other Brassicas were seed vernalization has been reported, or seed chilling is further augmented by vernalization of the plant or exposure to a specific photoperiodic regime (Friend, 1985b). Further evidence for the variability of Brassicas to seed vernalization is shown by the work of Wiebe (1972a). Seed vernalization at 1°C for 0 to 12 weeks in cauliflower was totally ineffective when measured against the time of curd initiation. Wiebe concluded from further experiments that termination of the juvenile phase was associated with the production of 4 and 8 leaves that were longer than 1 cm for the cultivars Aristokrat and Sesam respectively. This requirement for a period of early vegetative growth before becoming responsive to low temperature was demonstrated in cabbage as early as 1918 by Gasner, as reported by Friend (1985b).

In Brassicas, as with other plant species, the transition to maturity may be marked by various morphological criteria such as the production of a minimum leaf number (Wiebe, 1972a) or a minimum stem diameter. In herbaceous species the number of nodes to first flower is often used as a measure of the length of the juvenile phase. This concept of a minimal leaf number was first postulated by Purvis (1934). Although Purvis and Gregory (1937) found that this number is not easily defined rigidly, and may be modified by events at the apex, it is a useful marker in those species which lack other morphological markers associated with phase transition. Chronological time is not satisfactory as a marker for the duration of the juvenile phase as factors controlling the rate of leaf initiation will vary the duration of this phase.

In one of the few studies on juvenility in a non-woody species Zeevaart and Lang (1962) demonstrated that Bryophyllum daigremontianum, a long short day plant (LSDP) required the development of at least 10-12 pairs of leaves before it was capable of responding to photoperiodically inductive conditions. Studies on seven cultivars of Brussels sprouts (Thomas, 1980) showed that although competence for glasshouse grown plants of all cultivars was reached at different chronological ages, they all flowered in response to low temperature treatment given when they had produced about 15 true leaves and a further 13 to 15 initials. A similar requirement for the initiation of a certain number of leaves has also been reported for cauliflowers, although the number has seldom been accurately determined. Sadik (1967) reported a juvenile stage in cauliflower cv Snowball M marked by the initiation of 16 true leaves and 18 in the cultivar February-early-March. This difference in duration of the juvenile phase with cultivar has been further reported for cauliflower (Wiebe, 1972a; Wurr, 1981) and for other Brassica species (Friend, 1985b). Salter and James (1974) proposed that individual plants in the same cv may not enter the inductive phase at the same leaf number, which would account for the lack of uniformity observed in many crops. Further examples of a minimal number marking the end of the juvenile phase can be found in the Hop, Humulus lupus L. (Thomas and Schwabe, 1969) and the woody species Ribes nigrum (Schwabe and Al-doori, 1973). The latter being a short day plant (SDP) was found to require a minimum of twenty nodes before flowering would occur even when grown under inductive short day conditions.

The physiological significance of these observations is unclear as there is no evidence that leaf number in itself is a determinant of flower initiation. It is also unclear how size may affect physiological processes.

Experiments with Ribes nigrum (Robinson and Wareing, 1969) determined whether the attainment of a minimum size is necessary for phase change. The shoot tips of seedlings were removed whilst they were still juvenile. These were rooted as cuttings, grown on and the shoot tips removed again. This process was repeated twice. The final series of plants which had been derived in this manner initiated flowers in response to short days and thus had attained the adult condition, although at no stage had any of the successive rooted cuttings attained the minimum size (measured as stem length and number of nodes) for phase change in this species. Size per se, is not therefore the primary factor determining the stage at which phase change occurs.

One possibility proposed for certain woody species is that the determining factor is the attainment of a certain length of stem between the root and shoot apices. It has been proposed that endogenous gibberellin may be implicated in maintaining the juvenile condition in Hedera (Frydman and Wareing, 1973a), where nodal roots associated with prostrate growth habit are a source of gibberellin and therefore maintain the juvenile condition. Similarly aerial rooting in plants of Ribes nigrum cv Wellington XXX with more than 20 nodes inhibited flower initiation (Schwabe and Al-doori, 1973), apparently due to roots supplying inhibitory gibberellins to the shoot apex. In contrast to the role proposed for gibberellin in woody species increased availablility of gibberellins in cauliflower appears to enhance curd initiation (Leshem and Steiner, 1968; Hassib, 1972; Thomas, Lester and Salter, 1972; Wurr, Akehurst and Thomas, 1981). It is likely that the hormonal and nutritional status of the plant will influence the attainment of maturity. Allsop (1954) advanced the hypothesis that the rate of apical development is clearly controlled by the supply of nutrients.

Reduction in the supply of nutrients below a certain level leads to a reversion of apical development with a gradual return to an increasing juvenile condition. This reversion is usually accompanied by a decrease in the apex size. Change in size and configuration of the apex have been associated with the transition from the juvenile phase in several Brassica species. In Brassica oleracea var Italica cv coastal (calabrese) time of differentiation was based on such changes (Gauss and Taylor, 1969). Stokes and Verkerk (1951) working with Brussels sprouts noted a change in apical configuration, the apex becoming more pointed on completion of "puberty", however these changes were observed in association with a cold treatment and therefore may be a result of early floral evocation rather than completion of juvenility. Further evidence for intrinsic differences between juvenile and adult apices was obtained in grafting experiments on cauliflower carried out by Sadik (1967). He showed that the flowering stimulus was not transmitted through a graft union to vegetative plants, although this assumed such a graft would permit the transmission of any stimulus. The basis of these intrinsic differences has recently been reviewed (Wareing and Frydman, 1976; Zimmerman, Hackett and Pharis, 1985; Wareing, 1987).

Low temperature has been shown to be one of the factors regulating curd initiation in the cauliflower (Parkinson, 1952; Iwama, Hamashima and Motai, 1953; Haine, 1959; Austin, 1968; Wiebe, 1972a and 1984b).

Two distinct types of low temperature effect on flowering have been claimed (Kagawa, 1957; Salisbury, 1963, Bernier, Kinet and Sachs, 1981). In vernalization, low temperature induction is apparently only expressed on returning plants to higher temperature. This occurs in those plants such as the Chinese cabbage where slowly germinating seed can be vernalized

(Eguchi, Matsamaru and Koyama, 1963) and winter cereals (Gregory and Purvis, 1938; Lang, 1965). Vince-Prue (1975) proposed that the term vernalization is best restricted to this "after-effect" where flower initiation is promoted by a previous cold treatment. The second type of low temperature effect is seen in Brussels sprouts (Stokes and Verkerk, 1951) and some bulbous plants such as Iris cv Wedgewood (Hartsema, 1961; Elphinstone, 1986) and onion (Hartsema, 1961). This is claimed to be a "direct-effect" as no "after-effect" of low temperature has been reported. Plants that have not initiated an inflorescence at the time of transfer to growing temperatures remain vegetative. Another distinction claimed is that the "direct-effect" is able to proceed at higher temperatures than the "after-effect", with the optimum temperatures being 10-15°C and 5°C respectively (Kato, 1964). In a study of cabbage (Heide, 1970), temperature requirements for vernalization could not be separated from those of flower initiation. Temperatures of 15°C caused devernalization whilst exposure to 12°C caused further vernalization. This is analagous to the situation observed in the cauliflower cultivars Sesam and Aristokrat (Wiebe, 1972c) where the vernalization stimulus continued up to 17°C whereupon further increase resulted in increased vegetative growth. Other varieties of cauliflower remain vegetative when grown at 21°C (Sadik, 1967) or above 10°C (Haine, 1959). Friend (1985b) suggested that in certain cases the distinction between direct and after-effect vernalization may be semantic rather than physiological and concluded that the direct type of response displayed by Brussels sprouts and some cultivars of cauliflower be included in the term vernalization although other workers would not consider this to be a true vernalization reponse (Chouard, 1960; Evans, 1971; Vince-Prue, 1975). The view that the two types of response

may be considered as extreme ends of a continuum is further supported by work cited in Bernier, Kinet and Sachs (1981). In many plants demonstrating the "after-effect" type of response, initiation of flowers may proceed during the cold treatment, constituting a "direct-effect" if the cold treatment is sufficiently long. Examples of this are the biennial Lunaria annua (Pierik, 1967) and Daucus carota (Hiller and Kelly, 1979; Basher, 1984) and the perennial Geum urbanum (Chouard, 1960). Thus the type of response exhibited by those plants is dependent on the duration of the cold treatment and any distinction is simply one of degree. This further suggests that low temperature action is basically the same in both cases and accordingly all promotive effects of low temperature on flowering may be regarded as vernalization. This view is adopted throughout this thesis.

The majority of cauliflower cultivars display a quantitative response to low temperature, eventually initiating curds at high temperatures. Little attempt has been made however to quantify their vernalization response. The length of chilling treatments and range of temperatures that are effective with brassicas appear to vary between cultivars. One to three months between 0 and 10°C is usually required for complete thermoinduction (Bernier, Kinet and Sachs, 1981). Wiebe (1974a), working with cauliflower cultivars Aristokrat (early) and Sesam (late), demonstrated that Sesam had a greater vernalization requirement and a lower inductive temperature range for curd initiation than Aristokrat. Further varietal differences related to season of production have been recorded for both cauliflower (Haine, 1959; Sadik, 1967; Salter and James, 1974; Wurr, 1981; Wurr, Kay and Allen, 1981b) and Brussels sprouts (Thomas, 1980). In studies of the cauliflower cultivars Lero and Lawyna (Wurr, Akehurst and

Thomas, 1981) concluded that due to varietal differences it is unlikely that a standard cold treatment could be developed commercially without further effort to identify and quantify the factors modifying the cold treatment effect. With the exception of studies by Wiebe (1972b) no attempt has been made to determine the relative effectiveness of different temperatures in bringing about curd initiation. Friend (1985b) found the optimal duration of exposure to low temperature difficult to determine accurately because increasing duration of exposure to low temperature becomes less effective in promoting flowering as the optimum is approached, and as a rule the optimum temperature decreases as duration increases. From this Lang (1965) concluded that any temperature in the effective range results finally in the same maximal response provided the duration of the treatment is sufficiently extended. As this work failed to consider the rate of progress towards flowering, it is not surprising that the effects could not be differentiated.

The site of perception for the vernalization stimulus is the shoot apex. It was reported (Ito, Saito and Hatayamo, 1966) that shoot pieces of cabbage seedings could be reduced in length from 25 to 3 cm with little reduction in the effectiveness of vernalization. Curtis and Chang (1930) demonstrated that chilling in celery is perceived at the crown by the shoot apical meristem and/or the surrounding young leaves. Successful reciprocal graft transfers of shoot tips between vernalized and unvernalized Hyoscyamus and Althaea rosea, and vernalization of excised shoot tips of cabbage and carrot, demonstrate the perceptive role of the shoot apex (Kruzhilin and Shvedskaya, 1958; Harada, 1962; Lang, 1965). In several studies on the perception of the vernalization stimulus, Wellensiek (1961 and 1962) demonstrated that both isolated roots and leaves of

Lunaria biennis can be vernalized, as is observed from the flowering of the plants regenerated from these cuttings. Wellensiek concluded that dividing cells are necessary for the action of low temperatures, no matter where in the plant they occur. Further evidence to support this hypothesis was provided in later studies by the same author (Wellensiek, 1964). When temperatures experienced by plants exceed the maximum for vernalization not only will further vernalization cease, but partial vernalization may be completely or partially reversed. This is referred to as devernalization. With some plants such as celery and chrysanthemum effective vernalization can take place when plants are exposed to moderate non-vernalizing temperatures for part of the day, provided the highest temperature coincides with the daily light period (Thompson, 1947; Schwabe, 1950; Evans 1960). In other plants such as winter rye and cabbage (Purvis and Gregory, 1952; Heide, 1970) high temperature interruptions of the cold treatment greatly reduce its effect. The complexity of this temperature response is illustrated by the work of Picard on Oenothera biennis (cited in Bernier, Kinet and Sachs, 1981). This plant will not flower after continuous exposure to temperatures of 11 or 3°C, but requires a discontinuous cold treatment with daily alternation of 11 and 3°C. Periods of 15 or 18°C completely abolish the effect of preceding vernalization treatment. The devernalization effect of high temperature is dependent on the time and duration of exposure relative to previous vernalizing temperatures. Although high temperatures may lead to devernalization in the early stages of chilling, the vernalized condition is usually extremely stable once established (Vince-Prue, 1975). Devernalizing temperatures are usually in the range 20 to 40°C but temperatures as low as 18 to 25°C may be effective in some plants (Lang,

1965). Often temperatures around the maximum for vernalization are neutral in that they neither add nor detract from the vernalization process.

Devernalization in cauliflowers has previously been reported as being in the range 20 to 25°C, although lower temperatures are more effective when plants are held in darkness (Sadik and Ozbun, 1968). Devernalization may also occur when a few days at low temperature are alternated with high temperature, as in cabbage (Ito and Saito, 1961; Heide, 1970) or when low temperature days are alternated with high temperature nights, as in cauliflowers (Fujime and Hirose, 1980; 1981). Studying the effect of high temperature on curd initiation Wiebe (1974b) concluded that when high temperature experienced by cauliflowers is not sufficiently high for devernalization, circa 20°C, the effects of low temperature are additive. Under those conditions however increased growth of bracts was recorded by Haine (1959). The possible effects of devernalization on curd formation in cauliflower and broccoli were also studied by Fujime and Hirose (1980) who concluded that the low temperature stimulus is reduced when a low temperature day is followed by a high temperature day. Their observation that the low temperature effect was accumulated despite intercalation of high temperatures may be an important consideration when attempting to predict the effect of low temperature on curd initiation. Whether devernalization would be expected under field conditions when warm daytime temperatures are interposed with low night temperatures would depend on the stability of the vernalized state.

The vernalization response may be influenced by environmental factors other than high temperature. One of the most important is light, as both an independant floral stimulus and as a moderator for the cold response. In the context of this review, light will be considered separately in terms firstly of photoperiod and secondly irradiance.

Vernalization is closely associated with photoperiodism and in some plants one process can substitute for the other in the induction of flowering (Bernier, Kinet and Sachs, 1981). The view could be taken however that these are all photoperiodic plants and that low temperature merely allows early completion of the juvenile phase (Schwabe, 1971). Short days can often substitute either partly or completely for chilling in plants which flower in response to LDS. However in some species there is an obligate requirement for both processes, vernalization preceding photoperiodic induction, as with kohlrabi (Lang, 1965). Friend (1985b) provides an extensive list of flowering responses to photoperiod exhibited by Brassica species. Species of Brassica have either LD or DN photoperiodic responses, this response as with vernalization may be either obligate or preferential.

Many of the studies investigating photoperiodic effects in Brassicas are related to development of the flower stalk. Extensive studies of this type have been carried out with chinese cabbage, Brassica parachinensis (Zee, 1975; Elers and Wiebe, 1984; Moe and Guttormsen, 1985) and oilseed rape (Myers, Christian and Kirchner, 1982). However, this is not analagous to the curd initiation phase in cauliflowers, where studies on possible photoperiodic effects are few. In all cases reported cauliflowers appear to be day neutral after vernalization (Eguchi, 1947; Sadik, 1967; Wiebe, 1981). This is further supported by the work of Carew and Thompson (1948) and Parkinson (1952) which showed daylength was of no importance in the regulation of curd initiation in the cauliflower. In an extensive study on curd yield in relation to crop growth and development Khan (1967) also found no effect of photoperiod on curd initiation. Gauss and Taylor (1969) did find an effect of the length of the light period on the number of leaves produced before the curd of sprouting broccoli, however, increase in

photoperiod here was confounded by an increase in the total amount of daily radiation. Chaisuwan (1974) working with the summer cauliflower Cluseed major, concluded that there was no effect of daylength on the time of curd initiation when plants were grown at 15°C; at 20°C initiation took place most rapidly with a 16 h photoperiod, but at 25°C more rapidly with a 12 h photoperiod. In both cases plants were grown at an energy level of 21 joules cm^{-2} hr^{-1} in the visible part of the spectrum.

Irradiance is another component of the light environment that has been shown to regulate flowering. Recently Krekule (1987) stated that any attempt to understand the physiology of light effects should attempt to distinguish firstly between those light actions mediated by a modification of the vernalization process, and those that are independent of it.

Although several studies to date have investigated the role of irradiance on curd growth and final yield (Salter 1960a), there is a paucity of information concerning the role of irradiance in curd initiation. Regardless of species or other environmental requirements it is widely observed that flower initiation has a higher photon flux density (PFD) requirement than continued vegetative development (Bernier, Kinet and Sachs, 1981). Evidence for the implication of photosynthesis in floral initiation is that high PFD in the photosynthetically active region (PAR) may override the photoperiodic requirement in certain LD species. This phenomenon has been observed in Sinapis (Bodson, King, Evans and Bernier, 1977), and in Brassica campestris (Friend, Deputy and Quedado, 1979), where flower initiation takes place once a certain number of hours of light have been received over the range 4-24 hours. Fewer hours of light are required at higher photon fluxes. The effect of PFD on flowering is at least in part mediated by photosynthesis because CO_2 or a substitute

carbon source is required during the light period. However there is a critical non-photosynthetic component of high PFD (Quedado and Friend, 1978). In Anagallis they showed the flowering response not to be saturated by light until the PFD is about three times higher than that required to saturate CO_2 fixation.

In one of the few studies examining the effect of light energy at supra-optimal temperatures for vernalization, Chaisuwan (1974) observed that in the summer cauliflower Cluseed major grown at 20°C the time to curd initiation decreased with increasing energy up to 336 joules cm^{-2} day^{-1}. Beyond this level, no further acceleration of curd initiation was observed, nor was there any further reduction in leaf number before initiation of the curd. In a study of the effect of illuminance level before and during vernalization, Wiebe (1974b) concluded that there was no difference between 2.5, 5.0 and 10 klux prior to cold for the subsequent vernalization response. With diminishing illuminance in the same range during vernalization, leaf number as a marker of the rapidity of induction increased slightly at 12°C, in contrast to the results at 20°C, where no effect was apparent.

One of the aims of this thesis is to develop a technique for the prediction of curd initiation in the field using a knowledge of the environmental factors that regulate initiation. Comparison of plant development from year to year in the field is difficult because of variable climatic conditions. This can be overcome by the use of cumulative measurements of the main climatic variables as time scales, as employed by Salter (1960a) in a study of cauliflower curd development. He used two time scales; accumulated solar radiation and accumulated temperature. The time from seed sowing to curd maturity was more closely related to

accumulated temperature than any other climatic factor when edaphic factors were non-limiting.

The use of heat sums as a predictive system has been widespread (Brown, 1960; Dickson, Reiger and Peterson, 1961; Cross and Zuber, 1972; Brewster, 1987). Dickson et al. attempted to predict bolting in carrots using such a system based on accumulated day degrees below 10°C. In this example the assumption that all temperatures below 10°C are equally effective in induction is false (Basher, 1984). In studies of the cauliflower cultivars Aristokrat and Sesam, Wiebe (1972b) concluded that in the temperature range 2 to 17°C vernalization occurred in the form of an optimum curve. The optimum temperature for the shortest duration (8 days) required to complete vernalization, lay between 7 to 12°C. At temperatures of 2 and 17°C respectively Wiebe found that prolonged exposure was needed to satisfy the vernalization requirement. This established the link between temperature and the duration of exposure, time.

The term "heat sums" is misleading as it is temperature, and not heat, that is measured (Roberts and Summerfield, 1987). Monteith (1981a) favoured the term "thermal time". This is not the amount of heat which is transferred from the environment to the plant, but time perceived by the plant as a function of temperature (Gallagher, 1976; Ong and Baker, 1982). The basis for the calculation of thermal time is that completion of a particular developmental process requires that the plant receive a characteristic number of thermal time units, expressed as day degrees (deg C d). Early use of this concept has been much criticised on various grounds (Wang, 1960; Landsberg, 1975). Selection of an appropriate base temperature is often arbitrary and few controlled experiments have

demonstrated the precise relationship between temperature and the rate of a developmental process. The use of the thermal time procedure is therefore only justified if firstly a linear relationship exists between temperature and the rate of development. Such a linear relationship allows establishment of three cardinal temperatures, namely the base and maximum temperatures below and above which the rate of development is zero, and the optimum temperature at which rate of development is at its maximum. Linear responses to temperature have been observed in a number of developmental processes including seed germination (Bierhuizen and Wagenvoort, 1974; Garcia-Huidobro, Monteith and Squire, 1982a, 1982b and 1985c), vegetative growth (Gallagher, 1979a; Ong, 1983a; Milford, Pocock and Riley, 1985) and reproductive development (Ong, 1983b; Basher, 1984; Elphinstone, 1986). A second precondition claimed for the use of thermal time is that the rate of development should be a function of the temperature currently experienced by the plant and not the plant's thermal history. However thermal history has been demonstrated to affect development in Iris (Elphinstone, 1986) and vernalization is a "thermal history" effect, as seen in carrots (Basher, 1984). Part of this thesis will determine cardinal temperatures for curd initiation and attempt to use these as the basis for a predictive model using thermal time.

Cauliflower and brassica growers frequently claim that nitrogen supply and water stress have major effects on curd development in their crops. Scientific evidence for such claims is however somewhat sparse.

The role of nitrogen has received some experimental attention in the cauliflower but has been largely restricted to curd development and final curd yield (Cutcliffe and Munro, 1976; Dufault and Water, 1985). Parkinson (1952) reported that shortage of nitrogen delayed curd initiation and

maturity in the cauliflower. A recent study (Wurr, Cox and Fellows, 1986) using the late summer and autumn cultivars, White Fox and Snowy River respectively, demonstrated that although differing levels of nitrogen given during propagation in modular trays resulted in transplants which differed with respect to dry weight, number of leaves formed, and percentage dry matter, these pre-transplanting effects were soon lost when plants were set in the field. There were no significant effects on the time of curd initiation, final leaf number, or the time to 50% curd maturity.

In most plants where nitrogen deficiency has been shown to delay the appearance of flower buds, the time of floral initiation has frequently proven to be unaffected (Purvis, 1934; Naylor, 1941). This has led to the claim that inorganic nutrients can affect the time of flowering through effects on flower development but that they have very little influence on floral initiation (Leopold, 1951).

Important exceptions to this observation exist however. Von Denffer (1940) showed that in spring barley and wheat flowering was accelerated and leaf number markedly reduced by low nitrogen, as was also the case with Mustard (Chailakhyan, 1944). In carnation Blake and Harris (1960) found low nitrogen treatment retarded development of successive leaf pairs, whilst the final leaf number below the flower initials was increased. The effects of nitrogen and inorganic nutrition on floral initiation are most pronounced under conditions otherwise unfavourable to flowering. This was also demonstrated by Brewster (1983) in the onion, where reduction in the nitrate concentration of the nutrient solution accelerated inflorescence initiation, particularly in photoperiods and temperatures not conducive to rapid initiation.

In certain species nitrogen nutrition may have qualitative effects on the inductive requirements. Cold requiring plants such as Dactylis

glomerata lose their need for low temperature in the presence of high nitrogen levels (Calder and Cooper, 1961). The SDPs Pharbitis and Lemna Paucicostata 6746 will flower under long days with low nitrogen levels (Wada, 1974; Tanaka, 1986). In this context it has recently been argued (Trewavas, 1983) that the status of nitrate in physiological and morphogenetic studies should be upgraded from that of nutrient to growth regulator. It is probable that where nitrogen deficiency retards floral initiation this is due to a reduction in the level of metabolites at the stem apex. Acceleration of floral initiation may be due to removal of growth centres normally in competition with the primary site of initiation. Thus in the case of barley and wheat flowering is hastened whilst tillering is suppressed. In the presence of high nitrogen, tillers go on to produce their own inflorescences. The concept that certain metabolites were more readily available to the primary apex under conditions of nitrogen deficiency is central to the nutrient diversion hypothesis of floral initiation (Sachs, 1977).

The possible regulation of curd initiation by water stress has to date received little attention. Salter (1960b), in studying the effects of different soil moisture conditions during the seedling stage on the growth and yield of early summer cauliflowers observed that 'dry' conditions reduced the final leaf number, although results were not consistent between trials. Parkinson (1952) obtained a similar effect on leaf number by subjecting the young plants to a 16 day dry period, whereas Aamlid (1952) found that dry conditions increased final leaf number. Although in Salter's study plants had fewer leaves at the stage of curd initiation this stage was not reached in a shorter time, initiation occurring approximately 5 days later than plants from the 'wet' treatments.

Although many observations suggest that stress may be of importance in floral initiation, definitive conclusions have seldom been reached. Water stress has however been shown to control flowering in Geophila renaris, a perennial herbaceous plant of the tropical rain forest (Bronchart; cited in Bernier, Kinet and Sachs, 1981). There is evidence to show that the case of Geophila is not exceptional as water stress has been implicated in the flowering of citrus (Southwick and Davenport, 1986) and from in vitro studies on Cichorium intybus (Chicory), a biennial plant (Bouniols, 1974).

An interesting parallel between water stress and chilling is that both reduce growth and result in starch and protein hydrolysis with consequential increase in soluble carbohydrate availablity and acids, especially proline. The amino acid proline is a component compound for osmoregulation in plants submitted to water stress and low temperature. Changes in amino acid content appear early during the transition from the vegetative to the generative state in an early cabbage (Shvedskaya and Kruzhilin, 1964).

A secondary aim of this thesis was to examine processes that might mediate the effects of the environment on curd initiation. Gibberellins have been shown to mediate the flowering response in a wide range of species, and extensive reviews have appeared on their role in flowering (Bernier et al., 1981; Zeevaart, 1983) and reproductive development in general (Pharis and King, 1985; Looney and Pharis, 1986). Considerable emphasis has been placed on the role of gibberellins in cold requiring plants, after Lang's original discovery that GA treatment induced growth and flower formation in non thermoinduced biennial Hyoscyamus niger (Lang, 1965).

Several studies have investigated the role of gibberellins in curd initiation in the cauliflower (Leshem and Steiner, 1968; Hassib, 1972; Salter and Ward, 1972; Thomas et al., 1972; Wurr et al., 1981). Investigations into the levels of endogenous gibberellins throughout early vegetative growth and subsequent curd initiation (Thomas et al., 1972; Wurr et al., 1981) indicated high levels of gibberellin in the young seed and then a decline with age. Gibberellin levels increased in apices after 6 weeks with a further peak after 9 weeks, both peaks were enhanced by cold treatment (Thomas et al., 1972). It was therefore concluded that increased gibberellin synthesis occurred during the low temperature induction period, with a direct correlation between temperature, gibberellin synthesis and curd initiation.

Increases in endogenous gibberellins associated with vernalization have also been reported in wheat (El-Antably, 1977) and radish (Suge, 1970), Brassica napus (Chailakhyan and Lozhnikova, 1962) and carrot (Hiller, Kelly and Powell, 1979). In winter wheat seedlings this increase in gibberellin level occurs in all tissues but is greatest in the shoot apices (El-Antably, 1977). However, in several studies changes in gibberellin occur early during the cold treatment before the requirement for flower initiation is satisfied, suggesting that they may be insignificant transients or be part of a sequence of events required for evocation (Bernier, Kinet and Sachs, 1981). Exogenous gibberellin has also been shown to promote curd initiation maximally in combination with a cold treatment (Leshem and Steiner, 1968), although the role for gibberellin under non-inductive or field conditions is not yet clear (Salter, Salter and Ward, 1972; Booij, 1984).

Gibberellin is almost always causally associated with stem elongation, a process which, although separable from flower initiation, as

was shown for cauliflower (Leshem and Steiner, 1968) is normally connected to the onset of reproductive growth in many species. Stem elongation in both rosette and caulescent species is a function of sub-apical meristematic activity, and added gibberellin substitutes well for the naturally occurring substances which normally regulate this process (Sachs, 1956; Sachs, Bretz and Lang, 1959).

The possible role of carbohydrates in vernalization has been reviewed extensively (Bodson, 1984; Bodson and Bernier, 1985; Sachs, 1987). The theory of assimilates being the primary controlling factor in floral initiation is the basis of the nutrient diversion hypothesis first proposed by Sachs and Hackett (1969, 1983) and Sachs (1977), in which changes in source sink relationships favouring the apex are seen as the major prerequisite for floral transition, whatever the nature of the induction.

Carbohydrate content of the shoot tip has been implicated in the floral transition of several Crucciferous species such as Sinapis (Bodson, 1977; Bodson and Outlaw, 1985), broccoli (Fontes and Ozbun, 1972) and cauliflower (Sadik and Ozbun, 1968). Whilst assimilates are essential for flowering they are only part of a complex controlling system in which other regulating agents also operate such as various substrates and growth substances (Bernier, Kinet and Sachs, 1981; Bernier, 1984). The view that flowering might be controlled by a balance of hormones has been reviewed at length (Vince-Prue, 1975; Zeevaart, 1976; Bernier, 1984; Bernier and Kinet, 1986). Chailakhyan (1986) has stated that at no stage has the hormone concept of flowering been based on the presence or absence of one hormone.

Abscisic acid (ABA) has been implicated in the diversion of assimilates to developing reproductive structures such as the barley grain

(Tietz, Ludewig, Dingkuhn and Dorffling, 1981), tomatoes (Dorffling, 1970), apple (Beruter,1983) and pea (Browning, 1980), and has been demonstrated to have a promotive effect on the rate and the time of floral initiation in some species (El-Antably and Wareing, 1966; Kandeler and Hugel, 1973) whilst inhibiting others (Aspinall and Hussain, 1976; King and Evans, 1977). It has been suggested that the basis of ABA induced promotion of flowering is the inhibition of vegetative growth (El-Antably, Wareing and Hillman, 1967). Changes in the shoot : root ratio as a consequence of ABA application have been demonstrated in Zea (Watts, Rodriguez, Evans and Davies, 1981) and cauliflower (Biddington and Dearman, 1982).

It was the intention of this chapter to provide an overview of both environmental and chemical factors that may regulate curd initiation in the summer cauliflower, and that have a bearing on the subsequent chapters of this thesis. This was not an exhaustive review of all factors influencing transition to the floral state, and it is recognised that other events associated with floral transition have been neglected (Bernier, 1971; Bernier, Kinet and Sachs, 1981; Bernier, 1984).

The objectives of the present investigation on summer cauliflowers are summarised as follows:

- to determine and measure curd initiation responses under various environmental, chemical and cultural conditions.

- to characterise and quantify the exent and duration of the juvenile stage in the summer cauliflower.

- to develop techniques for predicting curd initiation in field crops of cauliflower.

- to suggest mechanisms mediating those conditions influencing curd initiation.

Chapter 2

GENERAL MATERIALS and METHODS

Introduction

The experiments described in this thesis were carried out at the University of Nottingham, School of Agriculture, Sutton Bonington. Field trials during the summer of 1986 were sited at Kirton Experimental Horticulture Station, Kirton, Boston, Lincolnshire. Precise details of the field trials are described in Chapters 6 and 7. All experiments described were completed during the period October 1984 to September 1987.

In this chapter those materials and methods either for specific techniques or common to more than one experiment will be described. Any modification or alteration to the materials and methods used in particular experiments will be described in the relevant chapter.

2.1 Glasshouse and controlled environment experiments

2.1.1 Propagation and general maintenance of experimental plants

Graded seeds of cauliflower (Brassica oleracea var botrytis L.) cultivars Perfection and White Fox were obtained from Elsoms Seeds Limited, Spalding and Breeders Seeds Limited, Ormskirk, respectively. Other cultivars used in a preliminary experiment were cvs Dok, Alpha Cliro, and Abundantia, obtained from Samuel Yates Limited, Macclesfield.

The experimental plants were raised from seeds thinly sown in trays containing Levington Universal Compost (Fisons Horticulture Limited, Ipswich). Trays were covered with black polythene and the seeds germinated in the glasshouse at an average temperature of 20°C. When the cotyledons had expanded seedlings were pricked out individually into 12 cm diameter pots containing Levington Potting Compost. The plants

were then grown in a glasshouse (day temperature 20°C, night temperature 16°C, with ventilation at 24°C). Plants were grown under natural glasshouse irradiance conditions, with supplementary lighting from high pressure sodium lamps (SON/T) providing an additional 55 to 65 Wm^{-2} during the winter months. Durations of supplementary lighting are described in the individual experiments. Throughout the growing period plants were watered regularly to maintain normal healthy growth. Plants were fed daily with liquid fertiliser of the formulation 1 : 1 : 1 ($N : P_2O_5 : K_2O$) to provide 200 ppm N, P_2O_5 and K_2O. Feeding commenced on expansion of the second true leaf.

Those experimental plants that were raised coincident with the emergence period for cabbage root fly (Delia radicum), April to September, were treated by the incorporation of insecticide granules (Twinspan; a.i. chlorpyriphos with disulfoton, Pan Britannica Industries Limited) into the compost. Further control measures for the eradication of caterpillars (Ambush; a.i. permethrin, Imperial Chemical Industries Limited), and peach-potato-aphid (Myzus persicae) (Lindane; a.i. gamma-HCH; Pan Britannica Industries Limited) were undertaken as required. In all cases applications were carried out in accordance with manufacturers' and government recommendations (Anon, 1984; Anon, 1986).

2.2 Constant temperature treatments

Constant temperature treatments were given in controlled environment rooms and Saxcil growth cabinets (Fisons Ltd) maintained to within $\pm$ 1°C. The precise nature and duration of individual temperature treatments are described in the relevant experimental chapters. Temperatures were monitored throughout using screened thermometers and

thermograph chart recorders. In addition "Squirrel" multi channel data loggers (Grant Instruments (Cambridge) Limited, Cambridge) were used, recording controlled environment temperature every fifteen minutes. Illumination during the temperature treatments was provided by a bank of 80W warm white fluorescent tubes giving an irradiance level of 50 to 55 Wm^{-2} incident at plant height for 12 h each day.

On completion of temperature treatments plants were usually returned to the glasshouse and maintained there until termination of the experiment. When the natural daylengths fell below 10 h, 400W SON/T lamps were used both to extend the photoperiod to 12 h, in line with the controlled environments, and to supplement natural irradiance throughout the natural day. The additional irradiance provided was from 55 to 65 Wm^{-2} at plant height.

2.3 Shading treatments

Natural light levels were reduced, when required, by using shading of green 'Rokolene' netting (Rokolene KDA, Rokocontainers, Nottingham) suspended over the benches on cane frames. The frames stood 1 m in height above the bench top, with their widths and lengths corresponding to those of the bench measurements. Layers of netting were suspended all around the frames to enclose the plants. When experimental treatments required different levels of natural irradiance the number of layers of shade netting was changed. By this method irradiance levels of between 35% and 60% of natural irradiance in the glasshouse were achieved.

Irradiance levels at the top of the canopy within each shading, as well as the levels of natural irradiance within and outside the glasshouse were determined using a cosine corrected pyranometer with a selenium

sensor (T.J. Crump, Scientific Instruments Limited, UK). Using these values, the total irradiance receipt during the treatments was calculated from the daily records of the meteorological station at Sutton Bonington. Total energy sums expressed in Megajoules (MJm^{-2}) were verified using tube solarimetry (Monteith, 1959; Szeicz, Monteith and Dos Santos, 1964).

2.4 Imposition and measurement of water stress

2.4.1 Water stress treatment

Water stress was imposed on pot-grown plants by witholding irrigation for different periods until the desired level of plant stress had been achieved. This was followed by re-watering to pot capacity. In contrast to this cyclic stress, plants were also maintained under relatively constant stress conditions by reduced rates of irrigation.

2.4.2 Measurement of imposed stress

Stess under both cyclic and constant stress conditions was determined periodically by measuring the leaf water potential (Ψleaf, MPa) using a pressure bomb (PMS Instruments Co., Oregon, USA). Measurements were made on fully expanded leaves taken from similar positions on the plant to avoid confounding effects of leaf age with respect to cuticular development. All measurements were made around mid-day. The leaf was cut off the plant ensuring a clean edge. The petiole was inserted into the pressure seal which was in turn fixed into the lid of the pressure chamber. The leaf lamina was then placed into the pressure chamber, and the lid through which the cut end of the petiole protruded was locked in place. Pressurised nitrogen gas was then released into the

chamber slowly and the pressure at which water was exuded from the xylem at the cut end of the petiole was recorded (Barrs, 1968; Tyree and Hammel, 1972). In all cases the pressure chamber was lined with damp material in order to minimise transpirational losses from the leaf. Similarly losses resulting from a possible delay in placing the leaf in the chamber were overcome by wrapping the leaf in cling film and then removing this before insertion. This standard procedure was adopted for all measurements throughout the investigation. All measurements were replicated four times and the mean leaf water potential calculated. Leaf water potential was also determined at the end of a stress treatment to ensure that it had returned to the level of that in control plants.

2.5 Nitrogen nutrition

In all experiments on nitrogen nutrition, plants were grown in compost containing no base nitrogen fertilizer. The constituent parts of this modified potting compost are shown in Table 2.1.

Table 2.1 Composition of nitrogen free compost

A.	Bulk constituents	
	75% peat	
	25% fine sand	
B.	Base fertilizers (g per 0.04 m^3)	
	single superphosphate	29.66
	sulphate of potash	27.00
	Dolomite lime	93.45
	chalk or ground limestone	93.45
	Frit Wm255	14.83

Nitrogen was supplied as a liquid feed in the form of ammonium nitrate (NH_2NO_4) at concentrations from 0 to 400 ppm at differing rates. Potassium supply was maintained at a constant 200 ppm K throughout the course of the experiment. Micronutrients were provided in the form of 'Frit WM253' incorporated into the nitrogen free compost.

2.5.1 Determination of total plant nitrogen

Total nitrogen content of plant material was determined using Macro-Kjeldahl digestion modified from the Kjeldahl-Gunning method (Bradstreet, 1965).

Samples to be analysed were air dried and milled to a fine powder and about 1 g was accurately weighed and placed into a Kjeldahl flask. To this was added 20 ml A.R concentrated sulphuric acid (H_2SO_4) and two "kjeltabs" (Thompson and Capper, Liverpool) to act as the catalyst. This was then boiled for about 45 minutes in order to fully digest the sample. After cooling 90 ml of distilled water was added to the flask while still warm. A further cooling period was followed by the distillation procedure. Sodium hydroxide (NaOH, 80 ml) was cautiously added to the Kjeldahl flask containing the digested sample plus a small amount (spatula end, c. 300 mg) of "Devadas alloy". The flask was then reheated to boiling. During this process ammonia was distilled and condensed into a conical flask containing 50 ml of saturated boric acid with 40 drops l^{-1} mixed indicator. When the sample had boiled for 10 to 15 minutes the delivery tubes were disconnected from the condensers and the pH of the condensate was checked with red litmus paper. When the paper no longer turned blue, indicating the absence of ammonia the reaction was over and heating was stopped. The contents of the conical flask, now pale blue, were titrated

with 0.2 M hydrochloric acid (HCl). The titration was complete when the first pink colouration reappeared. Calculation of the % nitrogen in the dried sample was performed using the following equation:

$$\frac{(\text{Titre} - 0.2) \times 0.28}{\text{sample weight (g)}} = \% \text{ N}$$

0.2 = blank titration value

2.6 Plant measurements and growth analysis

Throughout experiments in both controlled environments and the field, measurements were made on growth and development. Particular interest was given to the time of curd initiation, both temporally as measured by days from sowing to initiation or completion of treatment to initiation and developmentally as measured by the number of leaves present below the curd. Leaf number was also measured during the course of treatments and taken as a measure of the rate of development. The determination of leaf number entailed the removal and counting of the larger leaves plus any leaf scars, and then dissection of the shoot tip under a binocular microscope (X 50) to count small leaves and leaf primordia. Curd initiation was said to have taken place at an apical diameter of 0.6 mm (Salter, 1969; Wiebe, 1974) and when secondary meristems were present in the axils of the primordia; prior swelling of the apex representing the transitional phase (Plate 1).

Attention was also given to other parameters of shoot development to allow possible correlations between these and curd initiation to be studied. Plants for destructive measurements were taken at random from each treatment. Fresh weight of the various shoot components was measured immediately on harvesting and leaf areas were

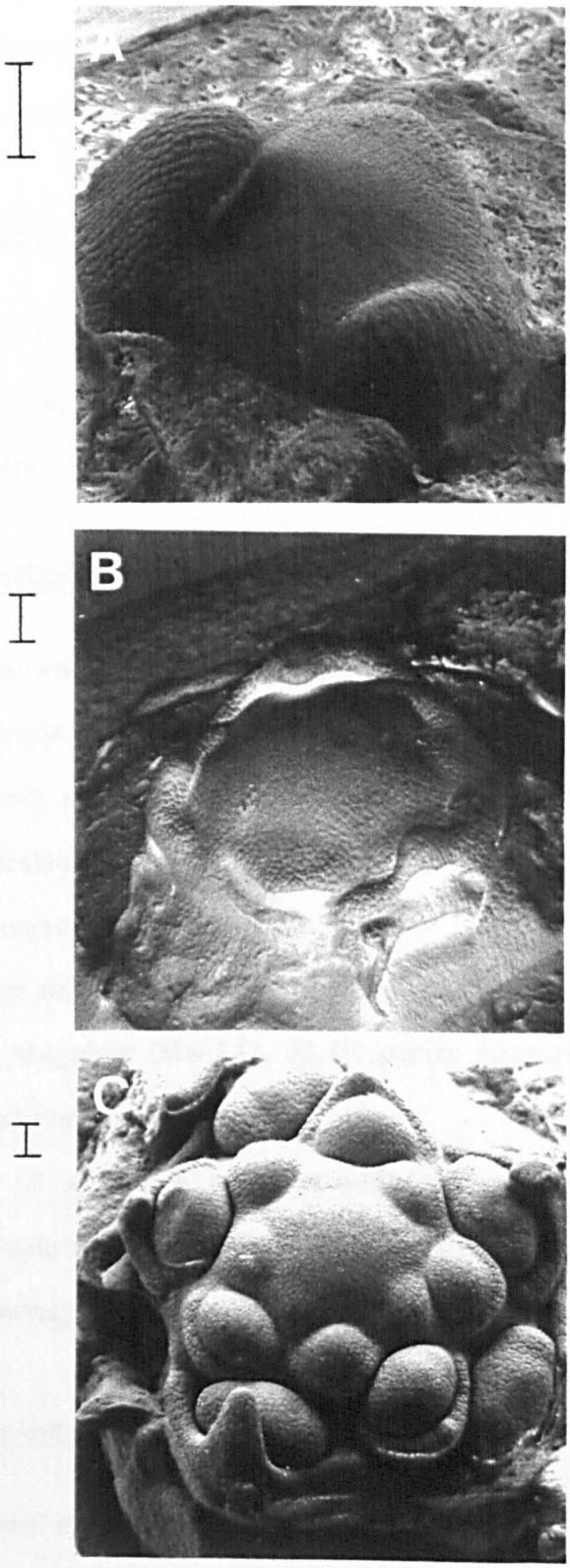
Plate 1 Stages of apical development

A Vegetative

B Transitional

C Reproductive

I = 0.1 mm


A
B
C

determined using a leaf area meter (ΔT Devices, Burwell, Cambridge). Dry weights were determined by placing shoot components into individual paper bags or aluminium cans and drying in an oven at 80°C until constant weight was achieved. This usually occurred after 48 hours' drying. The stem length was taken as that length from the cotyledons to the apex.

2.7 Preparation and application of gibberellins

The gibberellins used in the experiments here were GA (gibberellin A3; Sigma Chemicals Co. Limited) and gibberellin A4+7, 'Regulex' (Imperial Chemical Industries Limited).

2.7.1 Preparation of gibberellin solutions

Aqueous solutions of GA were prepared by dissolving a known weight of anhydrous GA (Mw 346.4, purity 90% gibberellin A3) in a small volume of ethanol and then making up to a know volume with distilled water. The solution was then stirred on a magnetic stirrer at room temperature to ensure complete dissolution.

Aqueous solutions of GA4+7 were prepared by simple dilution of the formulation 'Regulex' (Mw 333, 92.4% purity mixture gibberellins 4 and 7) to the required concentration.

Tween 20 at 0.05% a.i. was added to each solution to act as a surfactant. All solutions were stored at 5°C in darkness prior to use, for a period not exceeding seven days.

2.7.2 Application of gibberellins

Solutions were applied as foliar sprays to the whole shoot of the plant. Under controlled environment conditions gibberellins were applied

by hand sprayers and sprayed directly onto the shoot until run-off. The number and frequency of applications are described in the relevant experimental sections.

2.8 Extraction and measurement of endogenous ABA

2.8.1 Extraction procedure

The method that was used during the extraction of abscisic acid from cauliflower tissue is based on that used by Taylor and Rossall (1982). Plant material collected was instantly frozen in liquid nitrogen. The fresh weight of tissue was typically 50 g per sample. All samples were stored at -15°C until extraction.

The samples were blended for 2 minutes with a polytron PCV-2 homogenizer in 150 ml of 80% aqueous methanol containing 2 ml of glacial acetic acid and 20 mg of butylated hydroxy toluene (BHT) per litre. The samples were then filtered (Whatman No 1) to remove plant debris prior to the removal of the organic solvents at 30°C *in vacuo*. The resultant aqueous residue was adjusted to pH 8.2 with 40% (Aq) sodium hydroxide and then stored at 4°C for one hour to reduce the lipid content. The resulting precipitate was removed by centrifugation on an MSE Centaur 2 (3,000 rpm). The supernatant was partitioned three times against an equal volume of diethyl ether. The aqueous phase was retained and adjusted to pH 3.5 with 30% hydrochloric acid and partitioned three times against equal volumes of diethyl ether. The bulked organic phase (250 ml) was evaporated to dryness and the residue redissolved in ethanol (20 ml). The ethanol was then removed at 30°C *in vacuo* and the sample taken up in 0.5 ml of methanol. Samples were then stored at -15°C until analysed.

2.8.2 ABA analysis

Samples were analysed using reverse phase high performance liquid chromotography. Isocratic separation was achieved using a 250 x 4.6 mm I.D. sphericarb 5 µm ODS column with methanol : 5% aqueous formic acid (1 : 1, v/v) as mobile phase. 10 µl of each sample (in methanol) was injected and a flow rate of 1.5 ml min^{-1} was maintained using a Pye-Unicam LC-XPD pump and ABA was detected with a Pye-Unicam LC-UV variable wavelength detector set at 252 nm. At a flow rate of 1.5 ml min^{-1}, the retention time of abscisic acid was around 402 seconds.

2.9 Experimental design and statistical analysis

All experiments were either in the form of a completely randomised design or randomised complete blocks. Each treatment was replicated three times with a minimum of three plants per replicate. The GENeral STATistics package was used throughout to analyse the raw data to give treatment means and a full analysis of variance (ANOVA). The use of GENSTAT also facilitated the construction of correlation matrices and the fitting of first and second order polynomials using the method of least squares (Draper and Smith, 1966; Ridgeman, 1975). Tests of significance refer to change of probability at the five percent level unless otherwise stated. Results were presented in the form of tables or graphs.

Chapter 3

SHOOT ENVIRONMENT

Introduction

A better understanding of those environmental factors which induce and determine curd initiation has been suggested as the key both to avoidance of buttoning and to improvement of uniformity (Salter, Ward and Whitewell, 1972). Whilst temperature has been shown to have an important regulatory role (Parkinson, 1952; Haine, 1959; Austin, 1968; Wiebe, 1972c and 1983), other climatic variables such as irradiance receipt and photoperiod have received relatively little attention.

This chapter describes experiments designed firstly to clarify further the role of low temperature in curd initiation under controlled conditions and secondly to investigate other environmental conditions likely to influence curd initiation, either independently, or in association with, low temperature. Particular attention was given to the role of light in terms of both irradiance receipt and photoperiod.

3.1 Varietal differences in the vernalization response to chilling

Low temperature accelerates curd initiation in many cauliflower cvs (Sadik, 1967; Wiebe, 1972b). The effectiveness of any cold treatment is thought to depend on genotype, plant age and the duration and degree of cold (Sadik, 1967; Wiebe, 1972a; Wurr, 1981; Wurr et al., 1981).

The first two experiments in this chapter investigate responsiveness of five cauliflower cvs at different ages to chilling at 2 and 5°C.

Time of curd initiation was assessed both as leaf number subtending the curd and days to macroscopic curd visibility. Attempts were also made to correlate other changes in the development of the leaves with time of curd initiation.

3.1.1 Materials and methods

Four cvs were used in the first experiment, these were sown and germinated as described in section 2.1.1. The cvs Perfection and Alpha Cliro represented the early summer cauliflowers, whilst Dok and Abundantia were of the mid/late summer grouping (Anon, 1986; Thompson, pers. comm.). Sequential sowing dates provided plants aged six, four and two weeks at the commencement of chilling on 16 November 1984.

Chilling treatments, applied in controlled environment rooms (section 2) consisted of zero, one, two or four weeks at 2 or 5°C ± 1°C. Temperatures were selected as those used in previous low temperature studies; 2°C (Salter and Ward, 1972; Salter and James, 1974) or proposed as being close to the optimum for vernalization in the cauliflower; 5°C (Wiebe, 1972b).

Throughout the low temperature treatments plants received a 12 h photoperiod from HLRG lamps, providing an irradiance of c. 50 ± 5 Wm^{-2} incident at plant height. Dates when plants were transferred to or from chilling are summarised in Table 3.1(a).

Control plants were retained under glasshouse conditions for the duration of the experiment at a daily temperature of 20 ± 4°C. Natural irradiance was supplemented with 400W SON/T lamps, giving an additional irradiance of c. 60 ± 5 Wm^{-2} at plants height for 12 h each day, starting at dawn. The natural November photoperiod of 9 h was therefore extended to

Table 3.1 Dates of sowing and transfer to and from chilling

(a) Exp 1

Plant age at start of chilling (weeks)	Sowing date	Start of chilling	Chilling treatments 2 or 5°C	
			Duration (weeks)	Finish
6	5.10.85	16.11.85	1	23.11.85
			2	30.11.85
			4	14.12.85
4	19.10.85	16.11.85	1	23.11.85
			2	30.11.85
			4	14.12.85
2	2.11.85	16.11.85	1	23.11.85
			2	30.11.85
			4	14.12.85

(b) Exp 2

8	9.11.85	4.1.86	1	11.1.86
			2	18.1.86
			4	1.2.86
6	23.11.85	4.1.86	1	11.1.86
			2	18.1.86
			4	1.2.86
4	7.12.85	4.1.86	1	11.1.86
			2	18.1.86
			4	1.2.86
2	21.12.85	4.1.86	1	11.1.86
			2	18.1.86
			4	1.2.86

12 h in line with the photoperiod of plants receiving low temperature treatments. On completion of low temperature treatments all plants were returned to the glasshouse and randomised with unchilled control plants.

Plant development was measured before the start of low temperature treatments and at the end of the experiment. Measurements taken and techniques used were as described in the preceding sections 3.1 and 2.6 respectively.

The later summer cv White Fox was used in the second experiment. Treatments were as described in the preceding section, with the single addition of eight week old plants at the commencement of chilling treatments. The dates of sequential sowings, and transfer to and from low temperature treatments are summarised in Table 3.1(b).

The combination of four cvs with three sowing dates and three durations at either 2 or 5°C gave a total of 72 treatments in the first experiment. These were arranged in a completely randomised design with nine plants per treatment for sampling at macroscopic curd visibility. Nine additional plants of each cv per sowing date were sampled at the commencement of chilling. Similarly, the 24 treatments in experiment two with cv White Fox used a completely randomised design. The number of plants sampled and the time of sampling were as described above.

3.1.2 Results

As the two experiments consisted largely of the same treatments the results will be presented together to minimise repetition.

3.1.2.1 Leaf number at curd visibility Four weeks' chilling accelerated curd initiation measured as a reduction in the number of leaves beneath the curd (Fig 3.1) relative to unchilled controls, in all cvs tested. A greater

response was, however, recorded in the early summer cultivars Perfection and Alpha Cliro. Acceleration of curd initiation was apparent when plants were chilled at either 5 or 2°C, although exposure to 5°C generally had a greater effect. The degree to which curd initiation was accelerated depended on the chronological age of plants at chilling and on the duration of chilling.

Maximal acceleration of curd initiation in the early summer cvs Perfection and Alpha Cliro was recorded when six week old plants, with 19 and 18 leaves respectively, were chilled for four weeks at 5°C (Fig 3.1a and b). No further leaves were produced then prior to initiation of the curd. This was in contrast to unchilled control plants which produced 55 and 52 leaves in cvs Perfection and Alpha Cliro. Whilst significant, the reduction in leaf number following chilling of four week old plants for four weeks at 5°C was less marked than that recorded in older plants. Leaf numbers of 31 and 32 were recorded for cvs Perfection and Alpha Cliro respectively in contrast to 48 and 45 for unchilled control plants. Chilling two week old plants had no significant effect on leaf number beneath the curd. Effects of chilling plants at 2°C were generally similar to those observed at 5°C apart from when two week old plants were kept at 2°C for four weeks, where approximately 50% of the plants died.

Fifty per cent of those surviving this treatment failed to initiate curds by the end of the experiment (134 days after the commencement of chilling). Similar effects of chilling at 2°C were evident in cv Dok.

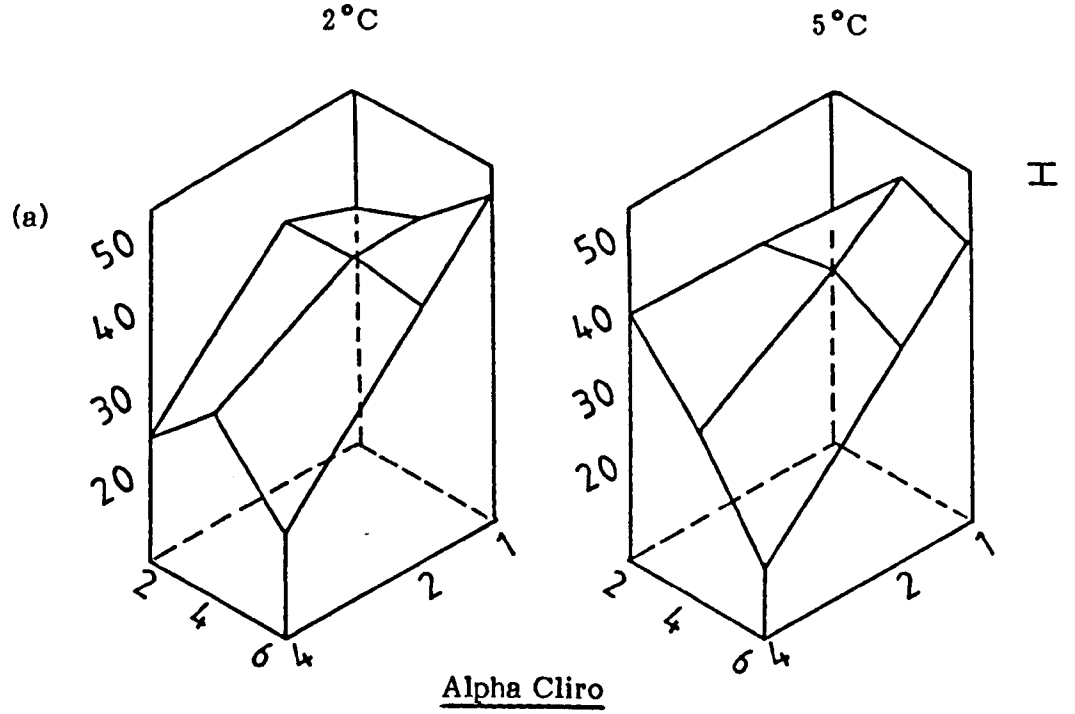
Maximum reduction in leaf number beneath the curd in the late summer cvs Dok and Abundantia occurred after six week old plants were chilled at 5°C for four weeks (Fig 3.1c and d). However the reduction in leaf number following chilling was not as great as that observed in the

Fig 3.1 Relationship between genotype, plant age and number of leaves subtending the curd following different durations of low temperature treatment

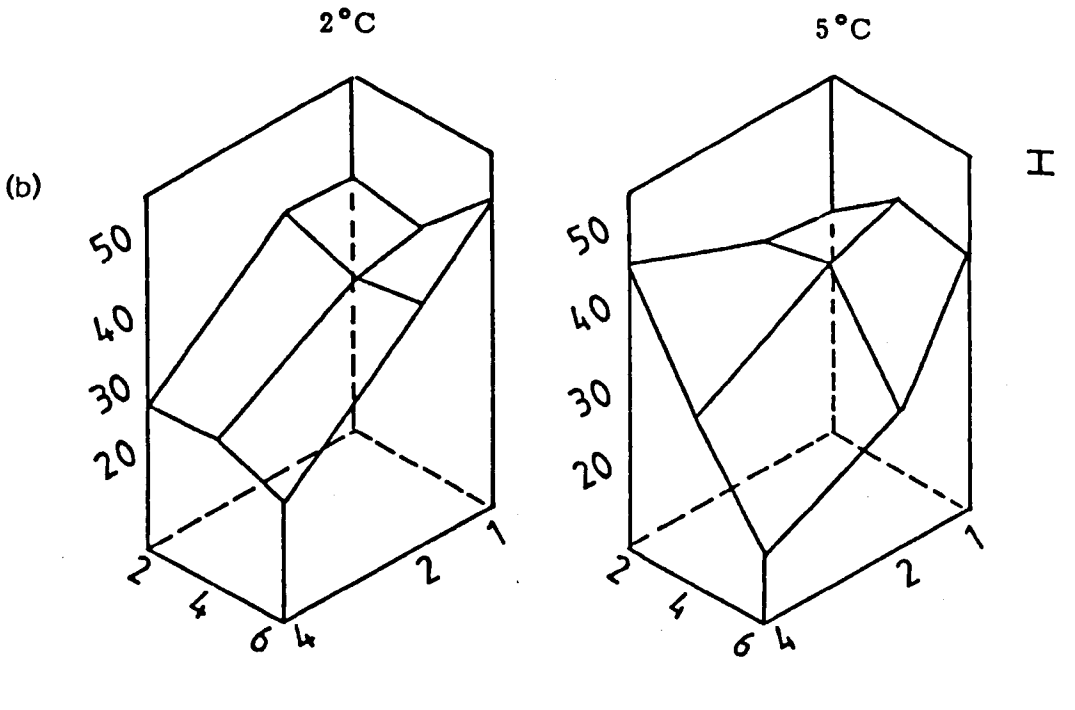
Leaf number in control (20 °C) plants at curd initiation

			Perfection
1st sowing	(6 wks)	=	55
2nd sowing	(4 wks)	=	48
3rd sowing	(2 wks)	=	39
			Alpha Cliro
1st sowing	(6 wks)	=	52
2nd sowing	(4 wks)	=	45
3rd sowing	(2 wks)	=	41

I SED (d.f. = 618)


2°C
5°C
(a)
50
40
30
20
2
4
6
4
2
1
H

Alpha Cliro


2°C
5°C
(b)
50
40
30
20
2
4
6
4
2
1
H

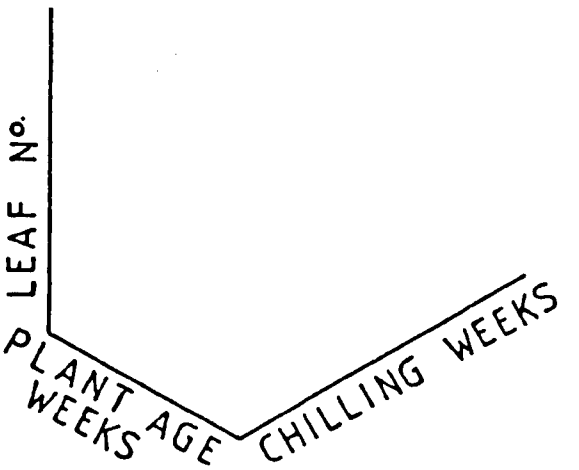

LEAF No.
PLANT AGE WEEKS
CHILLING WEEKS

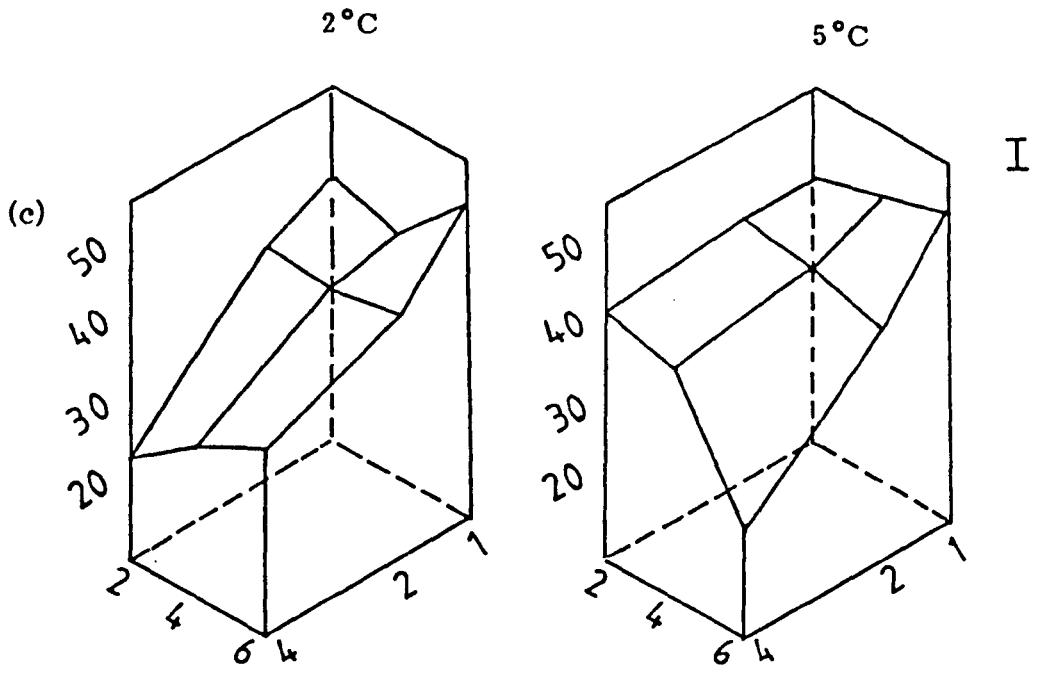
Fig 3.1 (continued)

Leaf number in control (20 °C) plants at curd initiation

			Dok
1st sowing	(6 wks)	=	51
2nd sowing	(4 wks)	=	43
3rd sowing	(2 wks)	=	45
			Abundantia
1st sowing	(6 wks)	=	47
2nd sowing	(4 wks)	=	49
3rd sowing	(2 wks)	=	39

I SED (d.f. = 618)

Dok



Abundantia

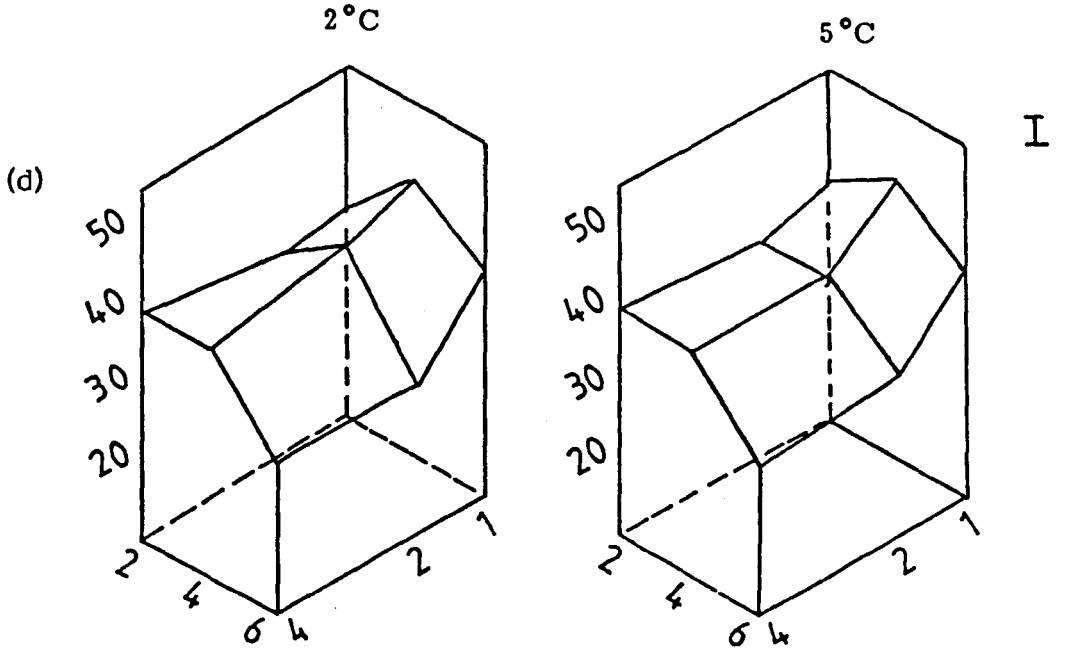


Fig 3.1 (continued)

Leaf number in control (20 °C) plants at curd initiation

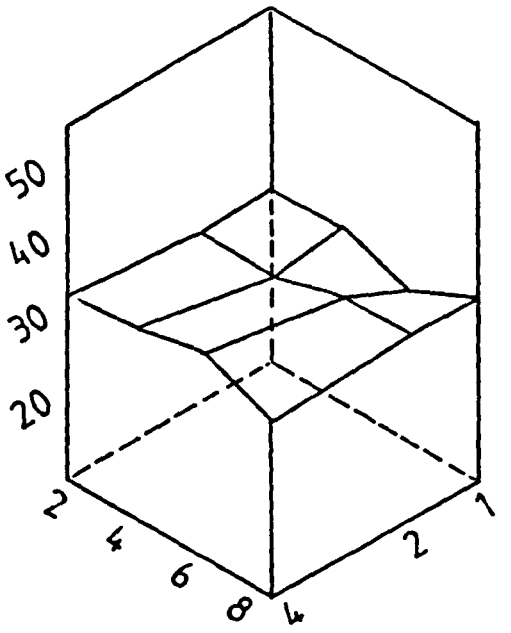
			White Fox
1st sowing	(8 wks)	=	36
2nd sowing	(6 wks)	=	29
3rd sowing	(4 wks)	=	28
4th sowing	(2 wks)	=	25

I SED (d.f. = 209)

White Fox

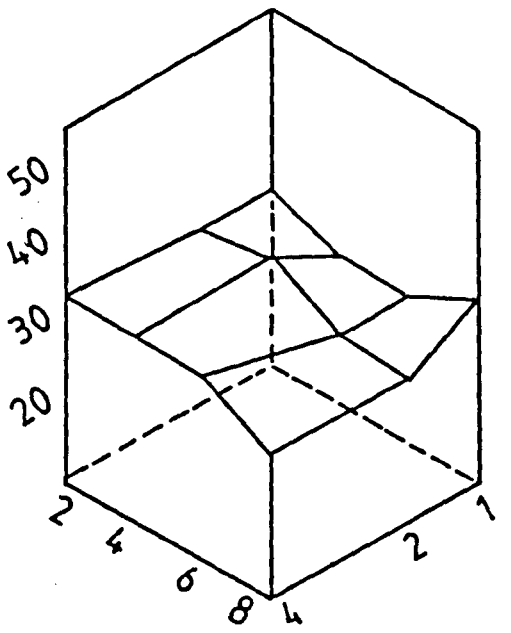
2°C

(e)



I

5°C



early summer cvs. Chilling four week old plants with eleven leaves (Table 3.2) produced a less significant reduction in leaf number than chilling six week old plants. Abundantia displayed a significant reduction in leaf number after only two weeks exposure at 5°C, whereas cv Dok failed to respond following four weeks' treatment. Two week old plants of both late summer cvs showed no promotion of curd initiation in response to chilling. Treatments at 2°C again had largely similar effects to those at 5°C.

The promotory effect of chilling White Fox was confined to two or four weeks at 5°C applied to eight week old plants (17 leaves, Table 3.2). This small response to chilling may indicate a juvenile phase terminated by the initiation of 17 leaves or more. Prolonged exposure (4 weeks) to either 2 or 5°C appeared to retard curd initiation as marked by a significant increase in leaf number beneath the curd (Fig 3.1e).

Any attempt to utilize the quantitative effect of low temperature in predicting curd initiation would be facilitated by a non-destructive means of assessing development. Days to macroscopic curd visibility was examined for this purpose (section 2.6).

3.1.2.2 Days to macroscopic curd visibility The number of days to macroscopic curd visibility was measured either from the date on which seeds were sown, or as the promotion or retardation of curd visibility as compared with unchilled control plants (Table 3.3).

The response was similar to that described above for leaf number. Curd visibility in cv Perfection was accelerated by 17 days following four weeks at 5°C (Table 3.3). The remaining treatments delayed curd visibility most significantly when two week old plants were chilled. Similar results were recorded in the other early summer cv, Alpha Cliro where the fastest

Table 3.2 Age and corresponding leaf number in plants at the start of chilling

Cultivar	Sowing date	Age (weeks from sowing)	Leaf number (including primordia)
Perfection	5.10.84	6	19
	19.10.84	4	12
	2.11.84	2	6
Alpha Cliro	5.10.84	6	18
	19.10.84	4	9
	2.11.84	2	6
Dok	5.10.84	6	19
	19.10.84	4	11
	2.11.84	2	5
Abundantia	5.10.84	6	31
	19.10.84	4	11
	2.11.84	2	6
White Fox	9.11.84	8	17
	23.11.84	6	11
	7.12.84	4	7
	21.12.84	2	5

Table 3.3 Days from sowing to macroscopic curd visibility, time relative to control plants in parenthesis

Cultivar	Age at chilling weeks (leaf number)	Control plants	Duration of chilling at 2 or 5°C (weeks)					
			2°C			5°C		
			1	2	4	1	2	4
Perfection	6 (19)	105	113 (+8)	112 (+7)	104 (-1)	103 (-2)	101 (-4)	88 (-17)
	4 (12)	107	113 (+5)	136 (+29)	119 (+12)	113 (+6)	101 (-7)	110 (+3)
	2 (6)	119	128 (+10)	133 (+14)	134 (+15)	116 (-2)	132 (+13)	133 (+14)
Alpha Cliro	6 (18)	111	112 (-1)	111 (0)	111 (0)	98 (-13)	97 (-14)	88 (-23)
	4 (9)	117	121 (+4)	121 (+4)	126 (-8)	100 (-17)	113 (-4)	106 (-2)
	2 (6)	123	132 (+9)	134 (+11)	134 (+11)	129 (+6)	132 (+9)	134 (+11)
Dok	6 (19)	107	115 (+8)	113 (+6)	116 (+9)	116 (+9)	111 (+4)	112 (+5)
	4 (11)	124	122 (-2)	125 (+1)	126 (+2)	122 (-2)	124 (0)	126 (+2)
	2 (5)	133	134 (+1)	134 (+1)	134 (+1)	133 (0)	134 (+1)	134 (+1)
Abundantia	6 (31)	70	74 (+4)	78 (+8)	88 (+18)	77 (+7)	75 (+5)	33 (+13)
	4 (11)	84	94 (+10)	93 (+9)	115 (+31)	86 (+2)	92 (+8)	95 (+11)
	2 (6)	93	99 (+6)	120 (+27)	134 (+41)	105 (+12)	106 (+13)	114 (+21)
White Fox	8 (17)	120	123 (+3)	119 (-1)	131 (+11)	117 (-3)	121 (+1)	122 (+2)
	6 (11)	120	124 (+4)	128 (+8)	150 (+30)	121 (+1)	126 (+6)	135 (+15)
	4 (7)	122	131 (+9)	127 (+5)	125 (+3)	124 (+2)	138 (+16)	146 (+24)
	2 (5)	133	141 (+8)	158 (+25)	164 (+29)	133 (0)	136 (+3)	158 (+25)

Perfection, Alpha Cliro, Dok and Abundantia ; SED = 4.7 (d.f. = 619)

White Fox ; SED = 6.8 (d.f. = 209)

curd visibility was associated with chilling six week old plants for four weeks at 5°C. Rapid curd visibility was also observed in four week old plants chilled at 5°C. The retarding effect of prolonged chilling on the youngest plants was probably due to the suppression of early vegetative growth.

The late summer cv Dok showed no consistent change in time to curd visibility after chilling. Only six week old plants chilled for four weeks at 2°C or one week at 5°C showed a significant delay of nine days. Low temperature treatments applied to cv Abundantia (Table 3.3) failed to accelerate curd visibility. However prolonged chilling applied to four and two week old plants delayed curd visibility, particularly in plants chilled at 2°C. The results obtained for cv White Fox also showed no significant acceleration in curd visibility, but marked delays when younger plants were chilled for long periods.

In measuring the number of days to macroscopic curd visibility as an indicator of relative curd initiation time and comparing different genotypes, it is assumed that the rate of early curd growth is the same for all the cultivars under study. Time of curd visibility is also however likely to be influenced by the leaf growth surrounding the curd. The possible role of leaves in influencing time of curd visibility was considered by attempting to correlate leaf growth, measured as dry weight and area, at the time of curd visibility with time to curd visibility itself.

3.1.2.3 Leaf dry weight at curd visibility Leaf dry weight at macroscopic curd visibility was generally lower in plants that had been chilled for longer. The magnitude of the the effect was however both cv and chilling regime dependent (Table 3.4). In cv Perfection significant reductions in leaf dry weight were found in plants chilled for four weeks, the minimum

Table 3.4 Leaf dry weight (g plant^{-1}) at macroscopic curd visibility

Cultivar	Age at chilling weeks (dry wt g)	Control plants	Duration of chilling at 2 or 5°C (weeks)					
			2°C			5°C		
			1	2	4	1	2	4
Perfection	6 (0.50)	7.2	5.7	9.1	2.3	7.7	5.2	4.1
	4 (0.08)	9.8	10.8	9.9	5.3	11.9	6.9	6.6
	2 (0.002)	10.0	9.7	8.1	3.5	9.9	10.2	9.8
Alpha Cliro	6 (1.00)	22.6	11.4	11.3	4.6	9.1	7.6	5.3
	4 (0.10)	17.8	15.9	12.2	4.5	14.4	12.8	8.7
	2 (0.002)	15.7	13.3	14.8	3.8	14.2	15.2	11.5
Dok	6 (0.9)	12.5	9.3	8.0	3.9	9.5	8.1	5.8
	4 (0.12)	16.7	14.5	12.8	6.0	14.1	14.3	13.1
	2 (0.001)	14.6	11.9	12.0	2.7	16.6	15.3	10.4
Abundantia	6 (0.77)	4.8	3.4	2.5	2.5	3.8	2.3	5.3
	4 (0.12)	7.2	5.6	5.4	6.3	6.7	5.2	4.2
	2 (0.002)	5.7	7.3	6.5	9.4	6.8	5.9	8.7
White Fox	8 (0.77)	10.4	11.5	10.0	11.3	10.1	9.6	8.8
	6 (0.13)	10.5	10.9	9.3	14.9	8.2	10.2	3.7
	4 (0.009)	8.3	10.5	7.2	15.6	7.0	11.1	12.1
	2 (0.001)	6.4	10.4	9.5	15.9	9.7	10.8	15.7

Perfection, Alpha Cliro, Dok and Abundantia ; SED = 1.36 (d.f. = 616)

White Fox ; SED = 0.91 (d.f. = 208)

dry weights here were found in the oldest chilled plants. This was in contrast to another early summer cv Alpha Cliro, in which all chilling treatments applied to plants older than two weeks resulted in a significant reduction in leaf dry weight at curd visibility. In cv Dok, except for two week old plants chilled at 5°C for one or two weeks, all chilling treatments resulted in a significant reduction in leaf dry weight at curd visibility. The decrease was greater in older plants exposed to longer duration chilling. Chilling cv White Fox appeared to increase leaf dry weight measured at curd visibility. This effect was most marked in two week old plants chilled for the longer duration.

No clear pattern emerged for cv Abundantia (Table 3.4). Whilst chilling of six week old plants at 2°C reduced leaf dry weight, this was in contrast to a 5°C regime where, with the exception of two weeks' treatment, there was no significant effect on leaf dry weight at curd visibility. A significant increase in leaf dry weight was measured when two week old plants were chilled for four weeks at either temperature.

3.1.2.4 Leaf area at curd visibility Four weeks at either 2 or 5°C reduced significantly leaf area at curd visibility in the cv Perfection (Table 3.5). This was apparent in plants of all ages except two week old plants exposed to 5°C. Six and four week old plants exposed to 2°C displayed a marked reduction in leaf area as did four week old plants at 5°C. Maximum reduction in leaf area was recorded after four weeks' chilling. The effects of chilling on leaf areas of the other early summer cv Alpha Cliro (Table 3.5) were essentially similar to those described for Perfection. Maximum reduction in leaf area at curd visibility followed four weeks' chilling at 2°C.

Chilling the late summer cv Dok (Table 3.5) at 2°C resulted in significant reductions in leaf area in all but four week old plants chilled for

Table 3.5 *Leaf area (per plant cm^{-2}) at macroscopic curd visibility*

Cultivar	Age at chilling, weeks (Area cm^2)	Control plants	Duration of chilling at 2 or 5°C (weeks)					
			2°C			5°C		
			1	2	4	1	2	4
Perfection	6 (172.0)	1684	1494	2107	689	2067	1373	1095
	4 (37.0)	2706	2428	2019	1214	2341	1830	1799
	2 (1.0)	1827	1912	1711	768	1960	1754	1823
Alpha Cliro	6 (297.0)	4092	2552	2227	1072	2276	2042	1293
	4 (40.0)	2756	2244	2244	1067	2681	2543	1783
	2 (0.4)	2267	2271	1942	975	2538	2307	2073
Dok	6 (282.0)	2573	2126	2063	1297	1957	2006	1404
	4 (51.0)	2823	2626	2284	1292	2619	2603	2300
	2 (0.5)	2457	1869	1704	495	2250	2060	1475
Abundantia	6 (292.0)	1734	1070	790	724	1100	855	1382
	4 (52.0)	1898	1515	1738	1620	1743	1705	1717
	2 (1.1)	1554	2125	1492	1563	1968	1853	1813
White Fox	8 (213.0)	1215	1280	1290	1283	1217	1227	1100
	6 (83.0)	1450	1548	1398	2012	1098	1352	1595
	4 (6.0)	1105	1286	926	1914	880	1353	1452
	2 (1.0)	975	1358	1548	2002	1107	1314	1887

Perfection, Alpha Cliro, Dok and Abundantia ; SED = 247 (d.f. = 618)

White Fox ; SED = 103 (d.f. = 209)

one week. The 5°C treatment reduced leaf area in all the six week old plants, but in four and two week old plants decreased leaf area only following four weeks' treatment. This contrasted with cv Abundantia where significant reductions in leaf area following chilling were confined to six week old plants (Table 3.5). Two week old plants grown at 2°C for one week had a significantly higher leaf area at curd initiation. Increased leaf area following chilling was also recorded in cv White Fox (Table 3.5).

3.1.2.5 Possible relationships between leaf growth and acceleration of curd visibility It was possible that interactions of plant age with temperature and duration of treatment described in the preceding sections on leaf area and leaf dry weight, would be paralleled by interactions of the same on time of curd initiation.

Possible relationships between leaf growth and curd initiation, measured as days to macroscopic curd visibility, were examined using regression analysis. Only those plants that displayed a vernalization response to chilling were included in the regressions. This restricted analysis to six and four week old plants of cvs Perfection, Alpha Cliro, Abundantia and Dok and those aged eight and six weeks in cv White Fox.

No significant relationship was established when regressing days to macroscopic curd visibility on either leaf dry weight or leaf area, the only exception being the cv White Fox. In the latter case a linear regression adequately described the relationship between days to curd visibility and leaf dry weight ($r^2 = 0.67$ $p < 0.001$) along with days to curd visibility and leaf area ($r^2 = 0.72$ $p < 0.001$).

In all five cultivars a highly significant relationship ($p < 0.001$) was evident between leaf dry weight and leaf area. Maximum scatter about the fitted line was measured in cv White Fox ($r^2 = 0.73$), whilst the

best fitting line (r^2 = 0.91) was recorded for the cv Perfection. Apart from White Fox, leaf development at the time of curd visibility would seem to be unrelated to the number of days to macroscopic curd visibility.

3.2 The effect of reduced irradiance on curd initiation

Solar radiation receipt has been related to both leaf and curd growth in the summer cauliflower (Salter, 1960a), but has not previously been examined in relation to curd initiation. The objective of the first experiment was to describe the curd initiation response under different solar radiation conditions. Effects on both time and stage of development for curd initiation are considered.

3.2.1 Materials and methods

Seeds of the cvs Perfection and White Fox were sown on 13 May 1986. Germination and general husbandry followed the methods described in section 2.1.1. Prior to experimental treatments starting on 19 June 1986, plants were grown under conditions of natural glasshouse irradiance at a mean daily temperature of 20°C. At the end of juvenile development (14 leaves in cv Perfection and 18 leaves in cv White Fox; see Chapter 4), plants were transferred to shading treatments as described in section 2.3. Layers of 'Rokolene' netting reduced natural glasshouse irradiance incident at plant height to 56 and 35 per cent of the total. A third control treatment comprised unshaded plants.

Plants were removed from the shaded and unshaded control treatments at intervals of 14, 28 and 38 days after commencement of treatments and returned to normal glasshouse conditions.

During the experiment plants were exposed to one of nine light integrals provided by a set time under one of three shading treatments. The light integral received for a specific treatment is summarised in Table 3.6.

Table 3.6 Light integral MJm^{-2} incident at plant height

Duration of shading d	Treatment (layers of shading)		
	0	1	2
14	699	610	567
24	657	511	442
38	594	366	257

External irradiance levels (total shortwave) were measured using a Kipp solarimeter. The percentage transmission of both glasshouse and shading treatments were calculated by taking instantaneous external and internal readings using a cosine corrected pyranometer, measuring irradiance at plant height. Further validation was achieved using tube solarimetry (Monteith, 1959; Sziecz et al., 1964). The solarimeter was calibrated against the Kipp. On removal from shading treatments plants were returned to natural glasshouse irradiance conditions in a second glasshouse. While attempts were made to standardise conditions between the two, the percentage light transmission was found to be slightly greater in the second glasshouse. Increased transmission accounts for the increased light integral achieved by these unshaded plants spending a greater proportion of the experimental period in the second facility.

All experimental plants were harvested after the curd was macroscopically visible on the same date, 2 August 1986. Leaf number

subtending the curd was taken as a measure of the advancement or retardation of curd initiation. Fresh and dry weights of stem and leaves were also determined as described in section 2.6.

The experiment was designed as a randomised complete block with three replications and three plants per cultivar for each removal date in each replicate. This gave a total of nine plants per treatment. Regression analysis was used to fit lines or curves relating final leaf number and changes in shoot components to total irradiance.

3.2.2 Results

No significant difference was evident between blocks and therefore results will be discussed on the basis of treatment effects without further reference to the randomised complete block design.

3.2.2.1 Leaf number subtending the curd Leaf number subtending the curd decreased with increasing total irradiance in both cvs (Table 3.7). In the cv Perfection 55 leaves were produced in the unshaded treatments compared to 64 in the most shaded. The cv White Fox formed 49 leaves in unshaded and 59 in shaded treatments. The highly significant ($p < 0.001$) relationship of leaf number to total irradiance was adequately described by a linear regression (Fig 3.2).

Calculation of the reciprocal of the slope of fitted lines provided an estimate of the light integral reduction that would increase the leaf number below the curd by one under the conditions employed here. This was 35.7 and 45.0 MJm^{-2} for cvs Perfection and White Fox respectively. This linear response however could not be expected to be maintained at high light levels, as each cv has a minimum leaf number below the curd and increased light integral would not reduce it further. One clearly anomalous

Table 3.7 Effect of irradiance receipt on leaf number beneath the curd for cvs Perfection and White Fox

Duration of shading d	Cultivar	Treatment (layers of shading)		
		0	1	2
14	Perfection	54	57	60
	White Fox	46	46	50
24	Perfection	56	62	68
	White Fox	53	51	54
38	Perfection	55	46	64
	White Fox	48	51	59

SED cv. Shade. Duration = 2.4 (d.f. = 138)
for comparisons within the same shading treatment
SED 2.1 (d.f. = 4)

Fig 3.2 Regression of leaf number subtending the curd on light integral for cultivars Perfection (closed symbols) and White Fox (open symbols)

Data derived from treatments having one (■ □) and two (▲ △) layers of shading plus unshaded (● ○) controls

Data point in parenthesis (■) not included in the fitted regression

Perfection

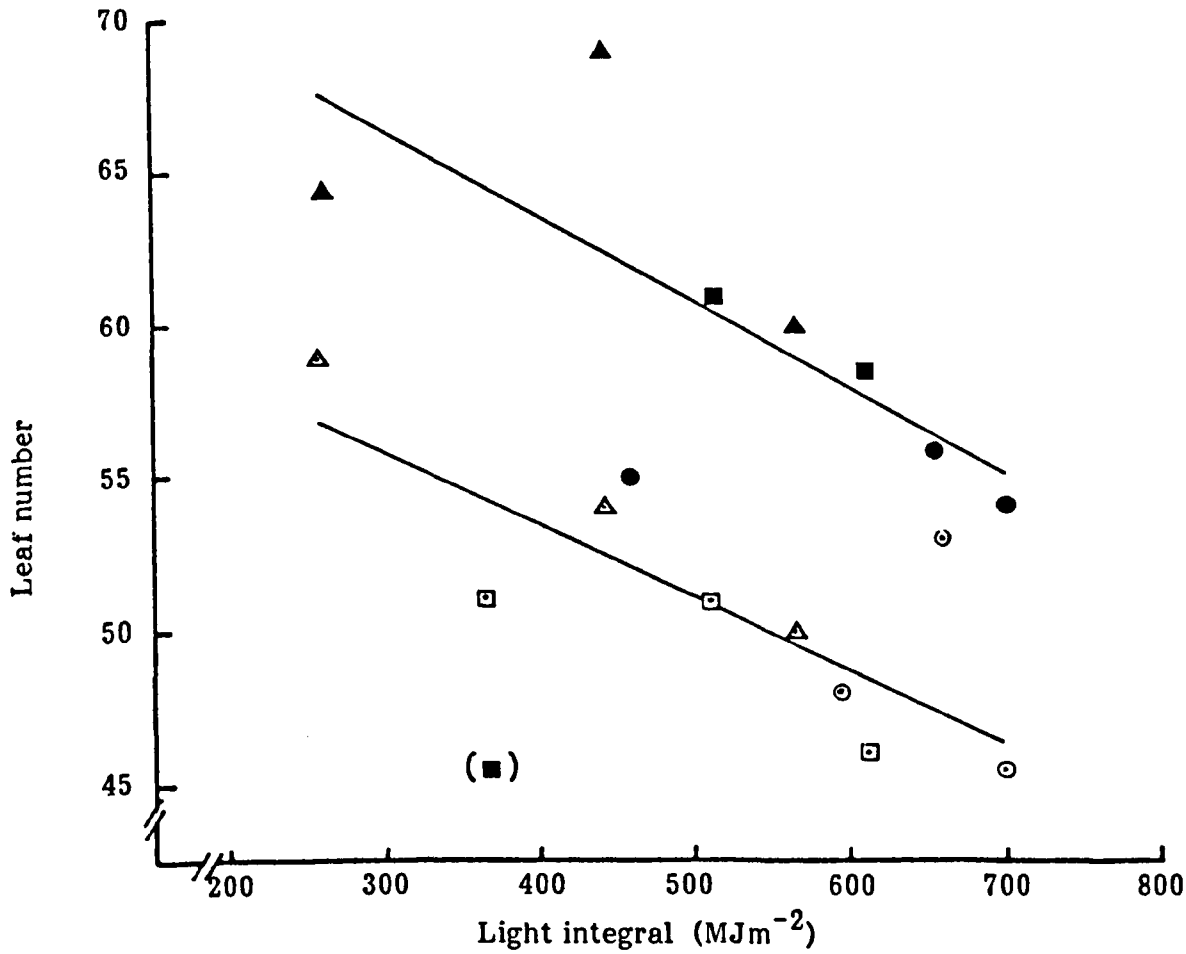
$y = 74.69 + -0.02802\ x$

$r^2 = 0.64$ ($p < 0.01$ d.f. = 6)

White Fox

$y = 62.49 + -0.0222\ x$

$r^2 = 0.59$ ($p < 0.05$ d.f. = 7)


70
65
60
55
50
45
Leaf number
200
300
400
500
600
700
800
Light integral (MJm^{-2})
(■)

data point (Fig 3.2) was omitted when fitting the regression. The reason for this anomaly is not known.

3.2.2.2 Change in shoot components at curd initiation A linear increase in stem dry weight with increasing total irradiance was observed in both cvs Perfection and White Fox (Fig 3.3). This increase was more marked in the cv White Fox where stem dry weight increased two fold as irradiance was raised from 442 to 657 MJm^{-2}, when comparing plants under two layers of shading for 24 days with unshaded control plants. Comparison of the same treatments in Perfection show a 1.5 fold increase in stem dry weight with increasing irradiance. From the fitted line an estimate could be made as to the incident irradiance at plant height required per gramme stem dry weight increase under these conditions. Figures of 104 and 54 MJm^{-2} were calculated for the cvs Perfection and White Fox respectively.

Leaf dry weight also increased with increased light integral (Fig 3.4). A linear relationship accurately defined this response in the cv Perfection ($p < 0.01$). This was in contrast to the cv White Fox where only 29.1% of the variance was accounted for by fitting a linear regression. As with stem dry weight, an estimate of the required irradiance incident at plant height per gramme leaf dry weight increase could be made; this was calculated to be 13.1 MJm^{-2}.

Fig 3.3 Regression of stem dry weight on light integral for cultivars Perfection (A) and White Fox (B)

Pooled data derived from zero (●), one (■) and two (▲) layers of shading

A

$y = 0.46 + 0.00956\ x$

$r^2 = 0.66 \quad (p < 0.05 \quad d.f. = 4)$

B

$y = -1.46 + 0.01844\ x$

$r^2 = 0.58 \quad (p < 0.05 \quad d.f. = 4)$

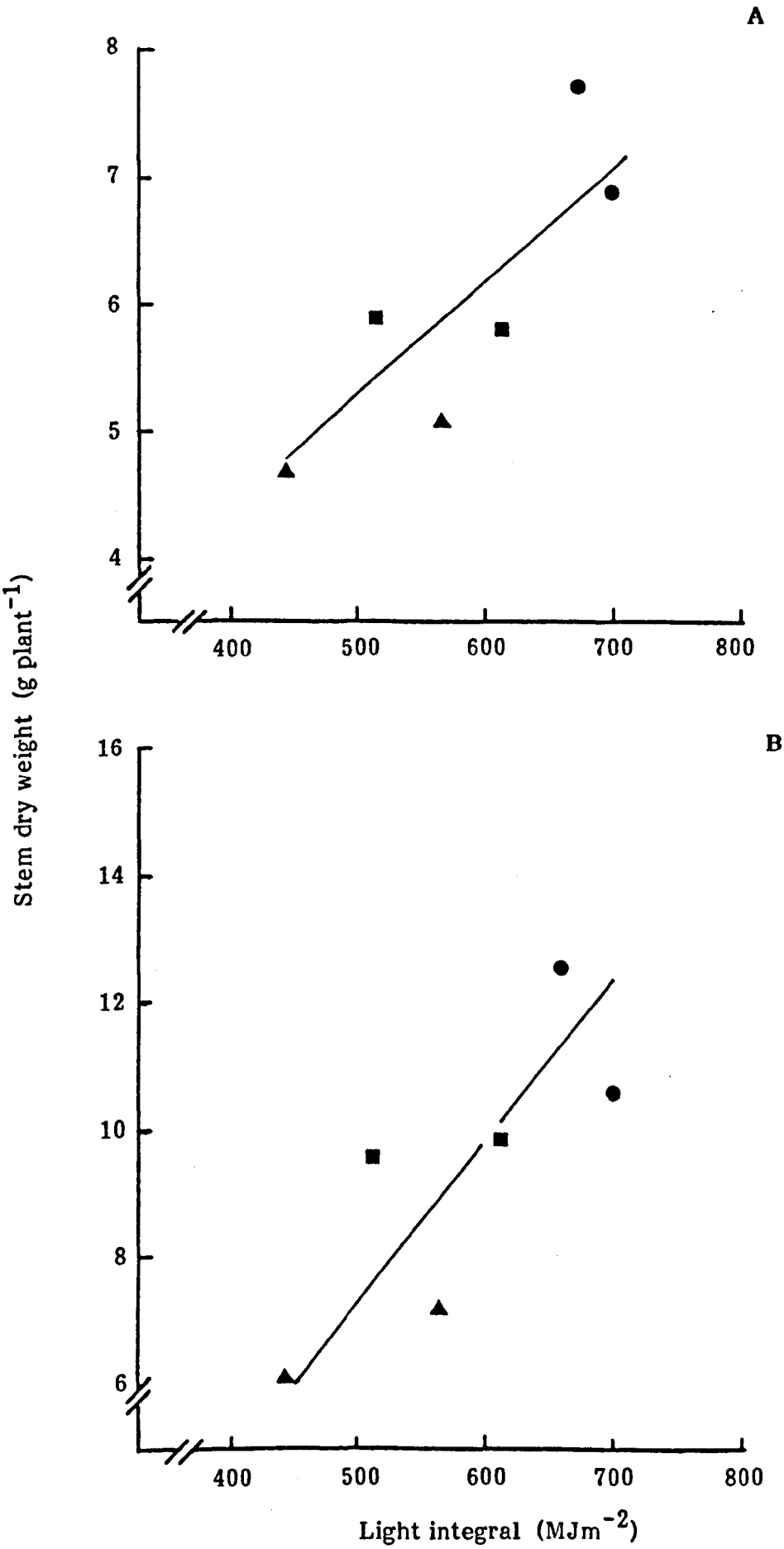
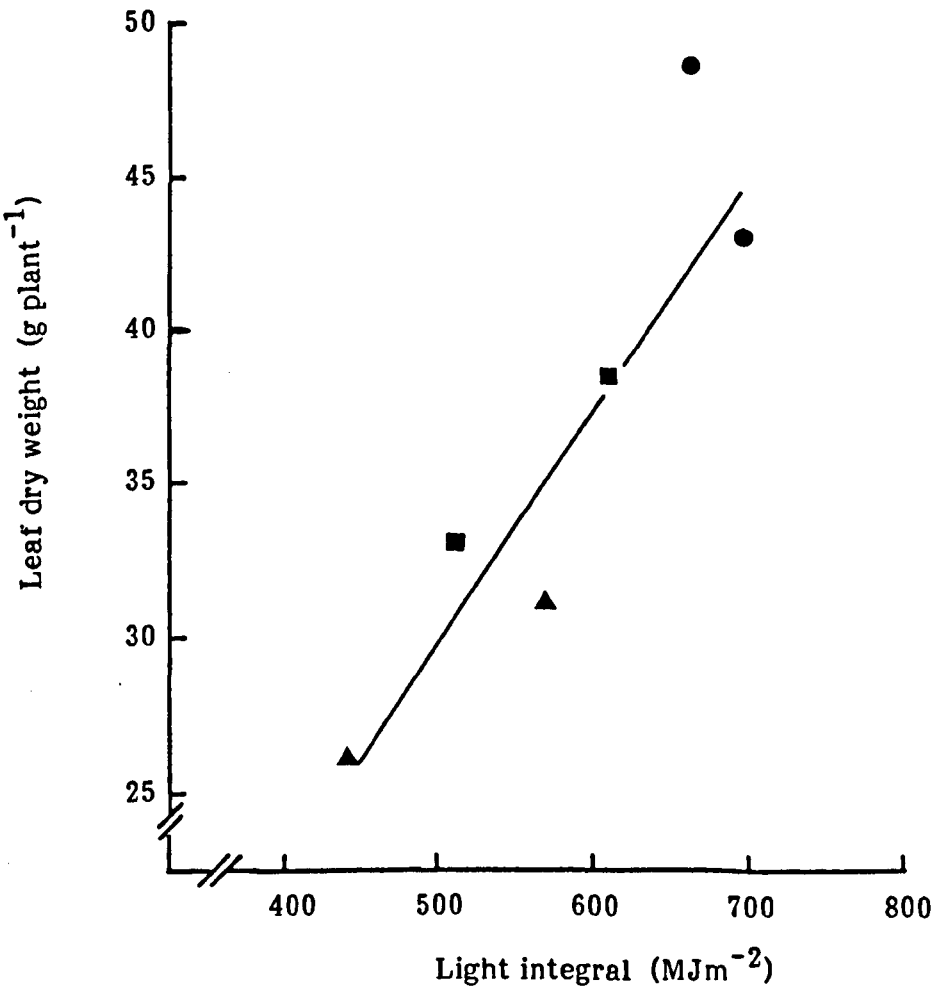

A
B
8
7
6
5
4
16
14
12
10
8
6
400
500
600
700
800
Stem dry weight (g plant^{-1})
Light integral (MJm^{-2})

Fig 3.4 Regression of leaf dry weight on light integral for the cultivar Perfection

Data derived from shaded; one (■) and two (▲) layers plus unshaded (●) controls

$y = -6.9 + 0.0735\ x$

$r^2 = 0.79\ (p < 0.01\ \text{d.f.} = 4)$


50
45
40
35
30
25
Leaf dry weight (g plant^{-1})
400
500
600
700
800
Light integral (MJm^{-2})

3.3 Irradiance and leaf initiation

The previous experiment demonstrated that reduced irradiance receipt delayed curd initiation, as marked by an increase in the leaf number subtending the curd. If effects of irradiance on rate of leaf initiation were known, this would facilitate the use of leaf counts for establishing a time for the start of curd initiation. The next experiment was therefore designed to determine rates of leaf initiation under a range of irradiance levels at warm (20°C) temperatures in the glasshouse.

The possibility that any change in leaf initiation rate may be associated with changes in shoot components was also investigated.

3.3.1 Materials and methods

Seeds of the cvs Perfection and White Fox were sown on 6 July 1986 and propagated following the method described in section 2.1.1. Immediately following transplanting, plants were transferred to shading treatments constructed as detailed in section 2.3. At this stage plants had initiated an average of four leaves. Reduction in total irradiance was achieved to approximately the same degree as in section 3.2.1. Total irradiance was calculated in an identical manner.

Sampling of plants from the different treatments was carried out at selected intervals and total irradiance received by the plants was calculated for this period (Table 3.8).

The experiment was arranged in a randomised complete block design with three replicates and three plants of each cv for sampling in each replicate.

Table 3.8 Light integral received (MJm^{-2}) by plants in shading treatments at selected sampling dates

Sample number	Date	Days from sowing	Treatment (layers of shading)		
			0	1	2
1	3 Aug	28	329	184	115
2	25 Aug	50	518	290	181
3	7 Sep	63	626	351	219
4	23 Sep	79	761	426	266

Regression analysis was used to fit best lines or curves relating leaf initiation, and changes in shoot components to total irradiance.

3.3.2 Results

3.3.2.1 Leaf initiation The rate of leaf initiation was reduced by shading in both cvs Perfection and White Fox, resulting in a significant difference in leaf number by the second sampling date (Table 3.9). Leaf initiation rates were shown to be different in the two cvs with White Fox initiating leaves more slowly than Perfection (Fig 3.5). This interaction between imposed shading, duration of exposure, and cv ($p < 0.001$) demonstrates the effect of increased light integral in accelerating leaf initiation.

The relationship between leaf number and light integral could be described by regressions of leaf number on light integral, MJm^{-2} (Figs 3.6 and 3.7). For the cv Perfection independent regressions fitted to the three shading treatments were shown to be highly significant (Fig 3.6). Comparison of the regressions however showed a significant displacement

Table 3.9 Number of leaves initiated at successive samplings in the cvs Perfection and White Fox

Sample number	Cultivar	Treatment (layers of shading)		
		0	1	2
1	Perfection	13	11	8
	White Fox	11	9	7
2	Perfection	40	24	19
	White Fox	35	24	14
3	Perfection	58	41	24
	White Fox	47	33	18
4	Perfection	*	48	37
	White Fox	*	48	25

* Indicates curd initiation had occurred

SED. cv. Shade. sample = 1.89 (d.f. = 4)

Fig 3.5 Change in leaf number with time in cvs Perfection (a) and White Fox (b) under zero (●), one (■) and two (▲) layers of shading

(a)

● $y = -23.14 + 1.2697x$ $r^2 = 0.99$
($p < 0.05$, d.f. = 1)

■ $y = -10.94 + 0.7626x$ $r^2 = 0.96$
($p < 0.05$, d.f. = 1)

▲ $y = -8.34 + 0.5516x$ $r^2 = 0.97$
($p < 0.05$, d.f. = 1)

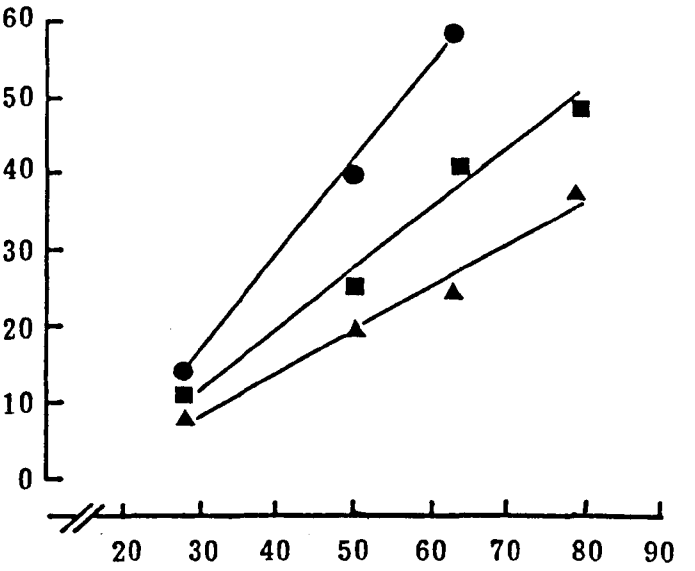
(b)

● $y = -17.65 + 1.0351x$ $r^2 = 0.99$
($p < 0.05$, d.f. = 1)

■ $y = -13.05 + 0.7754x$ $r^2 = 0.99$
($p < 0.05$, d.f. = 1)

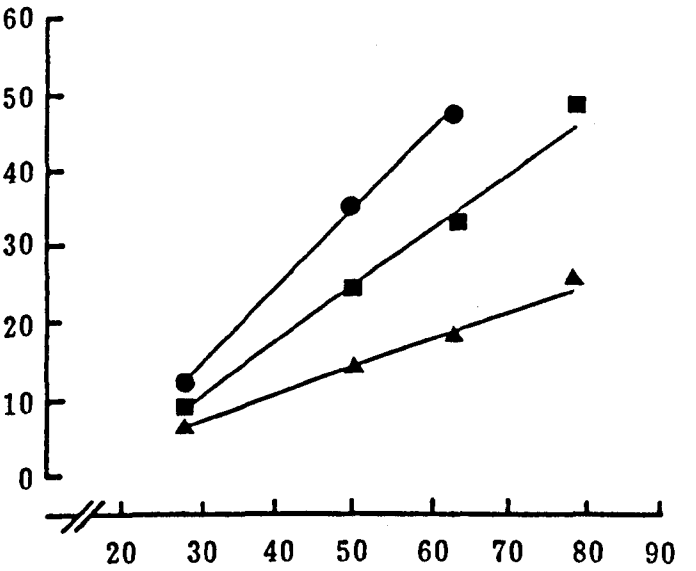
▲ $y = -3.14 + 0.3479x$ $r^2 = 0.99$
($p < 0.05$, d.f. = 1)

(a)



Leaf number

(b)



Days from sowing

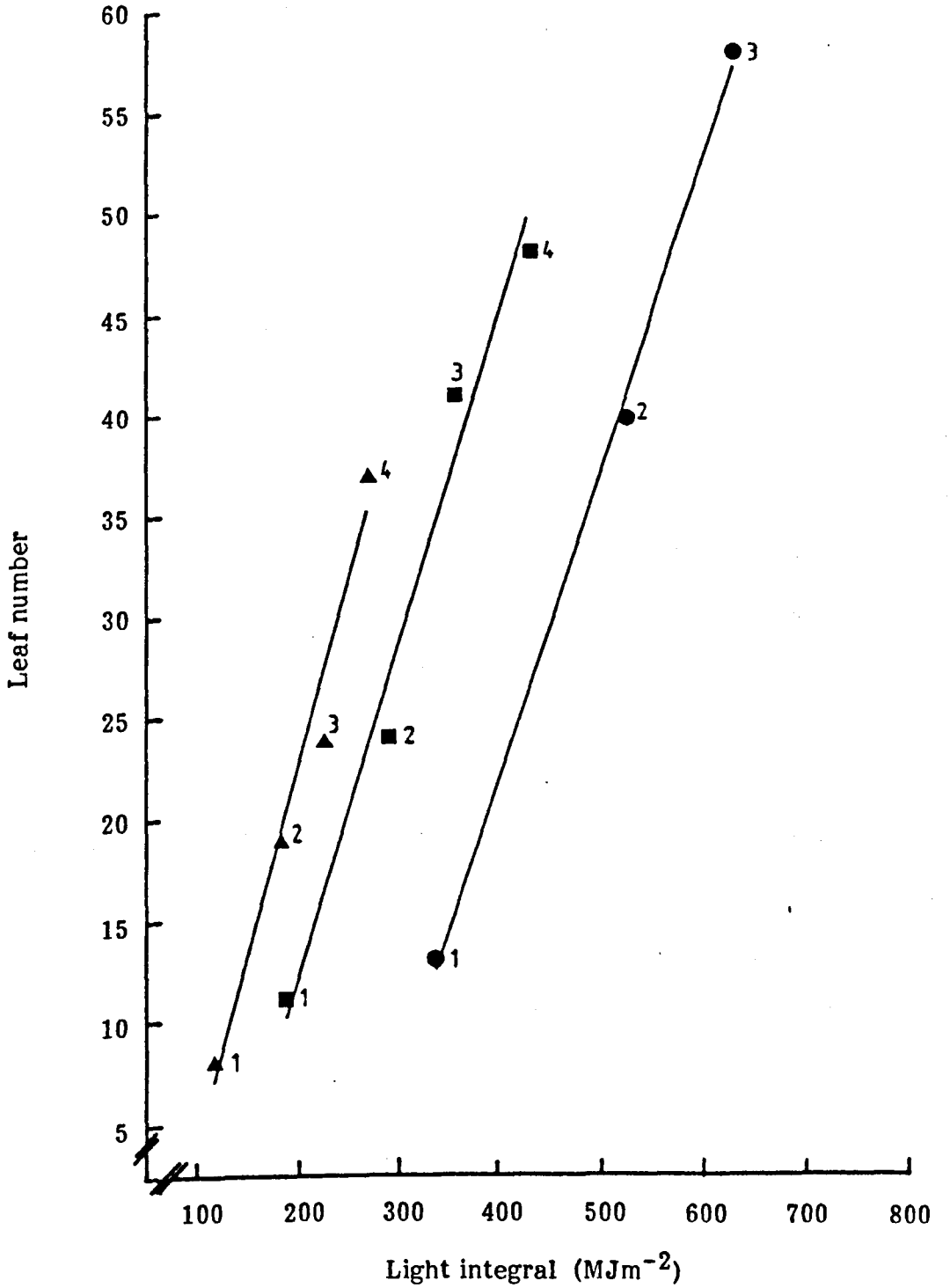
Fig 3.6 Regressions of leaf number on light integral for zero (●), one (■) and two (▲) layers of shading at four sampling dates (1-4) in the cv Perfection

● $y = -36.91 + 0.15054x$ $r^2 = 0.99$
($p < 0.05$, d.f. = 1)

■ $y = -19.25 + 0.1607x$ $r^2 = 0.96$
($p < 0.01$, d.f. = 2)

▲ $y = -14.37 + 0.1863x$ $r^2 = 0.97$
($p < 0.01$, d.f. = 2)

The fourth data point in the unshaded control was omitted from the regression due to curd initiation (Table 3.2)


Leaf number
60
55
50
45
40
35
30
25
20
15
10
5
100
200
300
400
500
600
700
800
Light integral (MJm^{-2})
1
2
3
4

($p < 0.01$) between the three shading treatments. All three lines showed a common slope which suggested that despite differing rates of leaf initiation, the required light integral for the initiation of one leaf remained constant. From the reciprocal of the slope, this was calculated as 6.64 MJm^{-2}.

Comparison of regressions for cv White Fox (Fig 3.7) showed a significant difference in displacement between the lines ($p < 0.001$). However, in contrast to Perfection, a small but significant difference between slopes was also evident ($p < 0.05$).

As the greatest displacement was associated with unshaded control plants, further comparisons of the data sets were made to check this observation. Pooled data derived from one and two layers of shading compared with unshaded controls again resulted in a highly significant difference of the fitted lines ($p < 0.001$), with no significant difference between the slopes. Without the unshaded control, lines fitted to one and two layers of shading were not significantly different. This would suggest that in contrast to the cv Perfection the response of White Fox is common to both one and two levels of shading. Based on these observations a figure of 7.82 MJm^{-2} for the initiation of one leaf was calculated from the reciprocal of the common slope.

Displacement of the regressions for shaded compared with unshaded plants suggests either an effect of the imposed shading on leaf initiation other than a reduction of light integral, or a difference in early growth conditions, prior to sampling, between shaded and unshaded plants.

Air temperature both within and between treatments was monitored throughout the experiment and is summarised in Table 3.10.

Fig 3.7 Regressions of leaf number on light integral for zero (●), one (■) and two (▲) layers of shading at four sampling dates (1-4) in the cv White Fox

● $y = -28.84 + 0.12186x$

$r^2 = 0.99 \quad (p < 0.05, \text{ d.f.} = 1)$

■ $y = -21.26 + 0.1591x$

$r^2 = 0.99 \quad (p < 0.01, \text{ d.f.} = 2)$

▲ $y = -6.94 + 0.11750x$

$r^2 = 0.99 \quad (p < 0.01, \text{ d.f.} = 2)$

The fourth data point in the unshaded control was omitted from the regression due to curd initiation (Table 3.9)

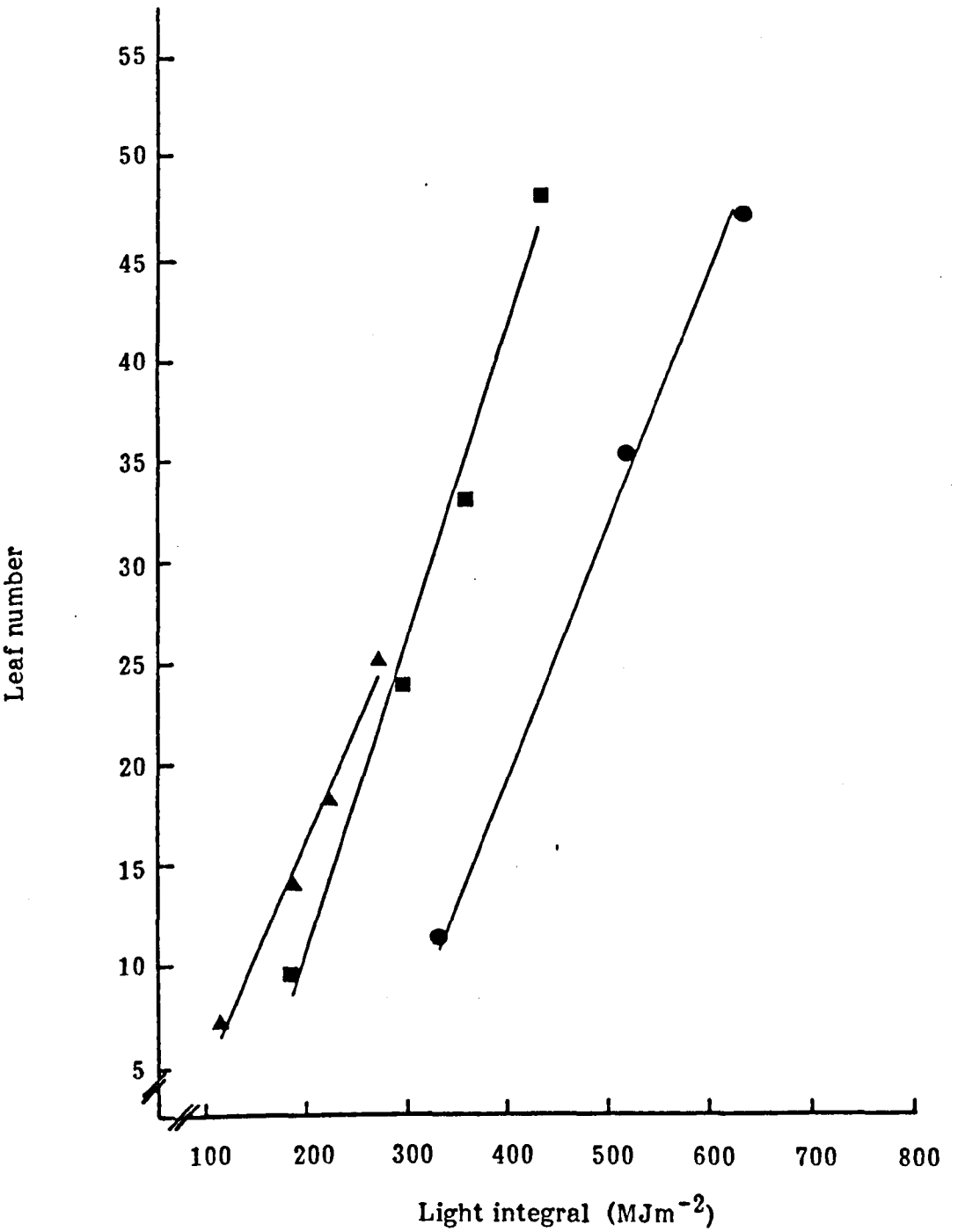

Leaf number
55
50
45
40
35
30
25
20
15
10
5
100
200
300
400
500
600
700
800
Light integral (MJm^{-2})

Table 3.10 Air temperature associated with shading treatments

Layers of shading	Mean air temperature (°C)	Standard deviation
0	22.0	1.8
1	21.0	2.6
2	21.6	2.2

It can be concluded from these measurements that air temperature is unlikely to account for the observed displacement.

Spectral energy distribution had also been measured in previous studies (Basher, 1984; Othman, 1984) using a differential scanning spectroradiometer, LI 1800 (Li. Cor, Inc., USA) and was found not to differ between shaded treatments and normal glasshouse irradiance. Possible causes of the observed displacement will be further discussed.

3.3.2.2 Shoot growth Low light integrals reduced both stem and leaf dry weight and total leaf area (Fig 3.8, a-c). Significant differences between cvs were measured for both leaf and stem dry weight in unshaded plants. Plants under one layer shading differed only at the final sampling, 63 days after sowing. This was in contrast to plants under two layers of shading, where cvs failed to differ significantly.

Rate of increase of all three shoot components was also reduced by low light integral.

Growth in shoot weight and leaf area increased exponentially over the irradiance range 125 to 350 MJm^{-2} but this was not maintained at irradiance integrals greater than 350-400 MJm^{-2} (Fig 3.9, a-c). In both cvs Perfection and White Fox, relative increase in shoot components, derived

Fig 3.8

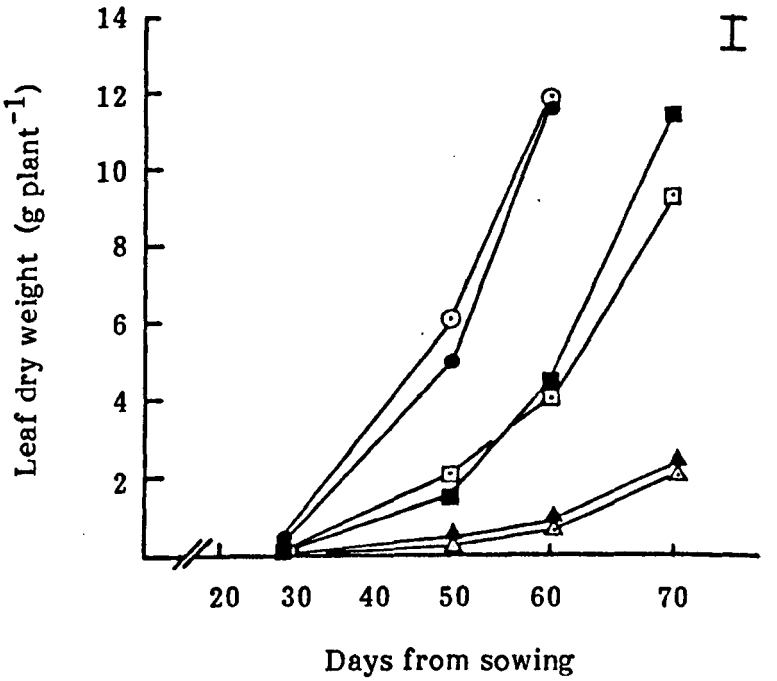
(a) Relationship between leaf dry weight and days from sowing in cvs Perfection (closed symbols) and White Fox (open symbols) for zero (● ○), one (■ □) and two (▲ △) layers of shading

I SED (d.f. = 181)

(b) Relationship between stem dry weight and days from sowing in cvs Perfection (closed symbols) and White Fox (open symbols) for zero (● ○), one (■ □) and two (▲ △) layers of shading

I SED (d.f. = 180)

(a)


Leaf dry weight (g plant^{-1})
14
12
10
8
6
4
2
20
30
40
50
60
70
Days from sowing

(b)

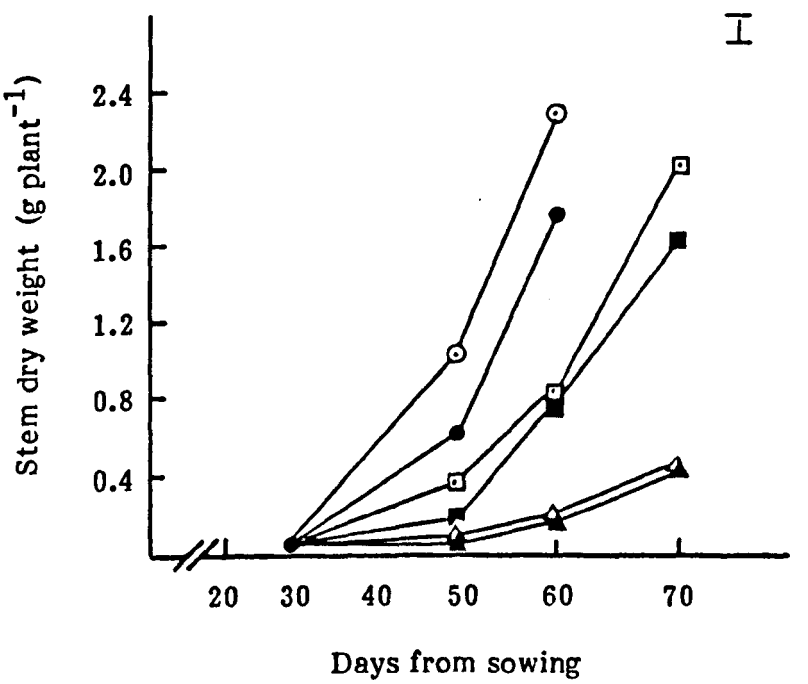

Stem dry weight (g plant^{-1})
2.4
2.0
1.6
1.2
0.8
0.4
20
30
40
50
60
70
Days from sowing

Fig 3.8 (continued)

(c) Relationship between leaf area and days from sowing in cvs Perfection (closed symbols) and White Fox (open symbols) for zero (● ○), one (■ □) and two (▲ △) layers of shading

I SED (d.f. = 181)

(c)

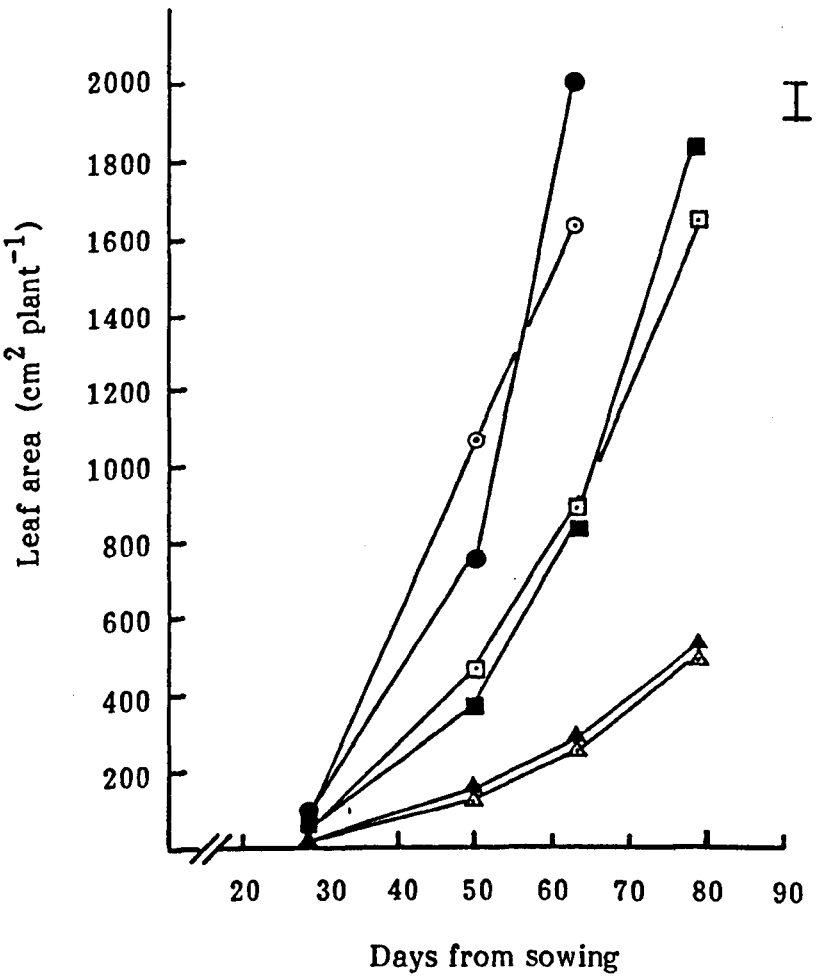

Leaf area (cm^2 plant^{-1})
2000
1800
1600
1400
1200
1000
800
600
400
200
20
30
40
50
60
70
80
90
Days from sowing

Fig 3.9a Regression of Log_e stem dry weight on light integral for cultivars Perfection (A) and White Fox (B) at zero (●), one (■) and two (▲) layers of shading

A $y = -8.30 + 0.0310x + -0.0000280x^2$

$r^2 = 0.71$ $(p < 0.01, \text{ d.f.} = 8)$

B $y = -8.34 + 0.0416x + -0.000072x^2$

$r^2 = 0.79$ $(p < 0.01, \text{ d.f.} = 8)$

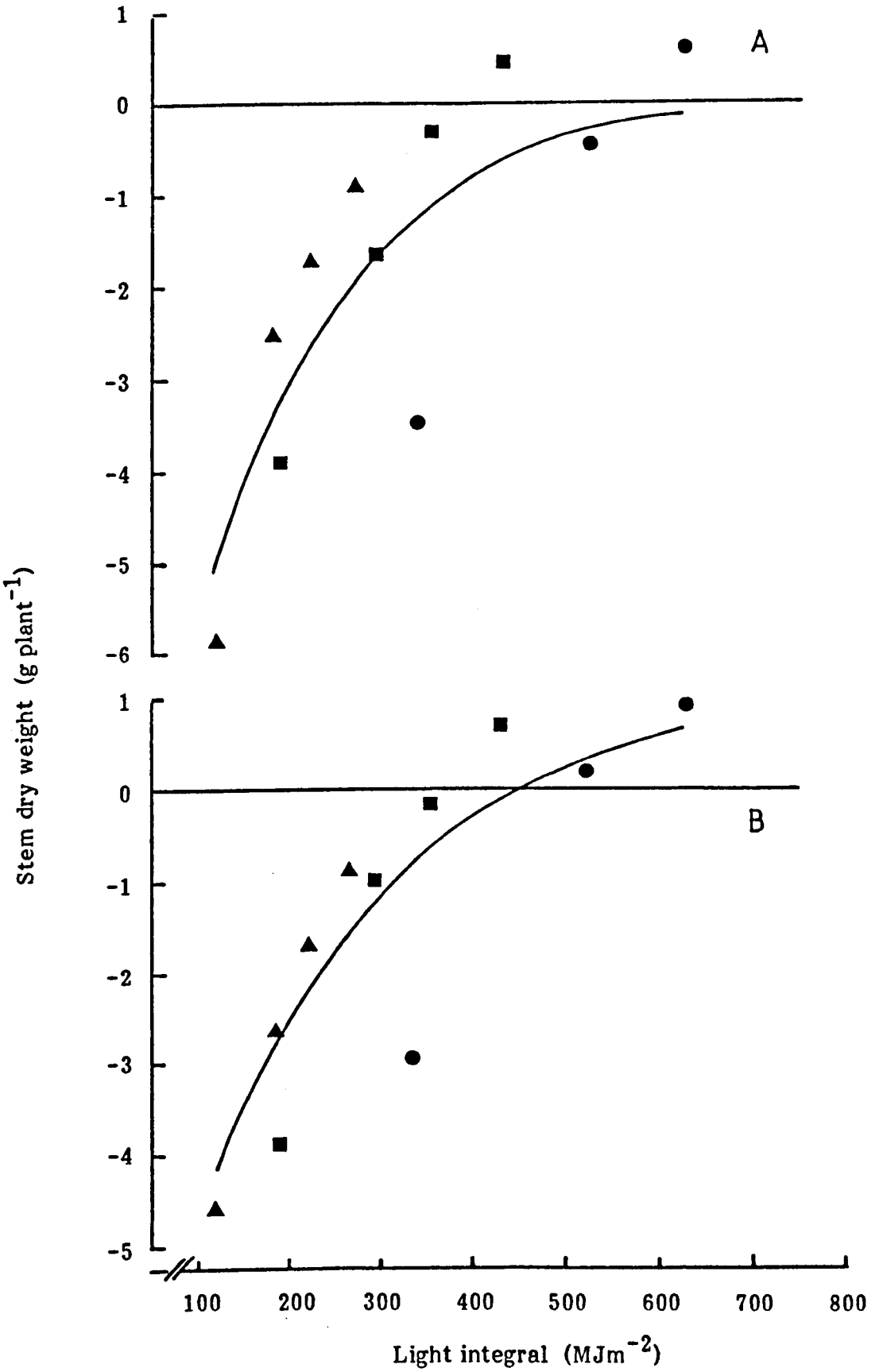

A
B
1
0
-1
-2
-3
-4
-5
-6
100
200
300
400
500
600
700
800
Stem dry weight (g plant^{-1})
Light integral (MJm^{-2})

Fig 3.9b Regression of Log_e leaf dry weight on light integral for cultivars Perfection (A) and White Fox (B) at zero (●), one (■) and two (▲) layers of shading

A $y = -5.32 + 0.02621x + -0.0000226x^2$

$r^2 = 0.80$ $(p < 0.01, \text{ d.f.} = 8)$

B $y = -5.31 + 0.2649x + -0.0000231x^2$

$r^2 = 0.83$ $(p < 0.01, \text{ d.f.} = 8)$

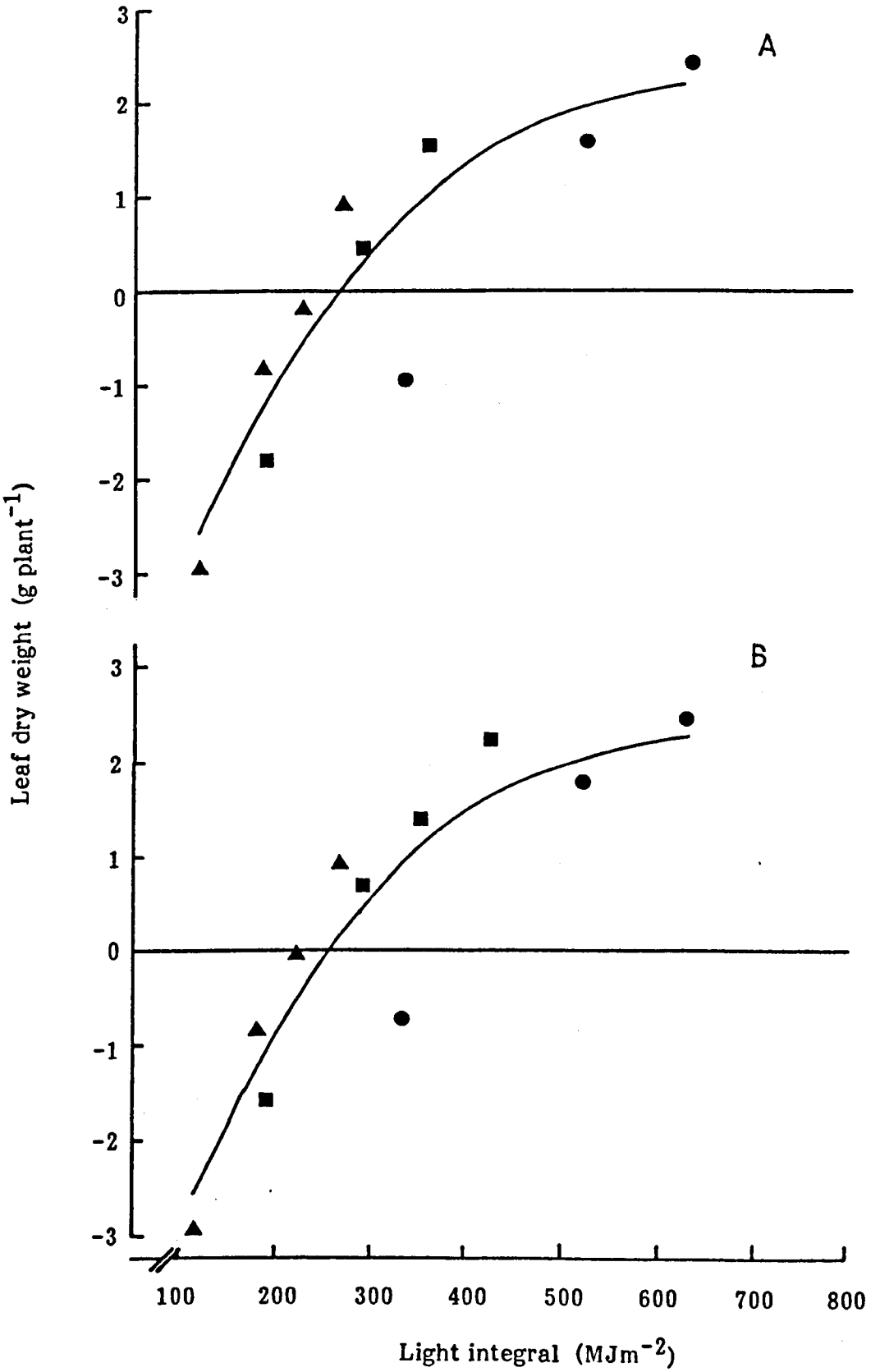

A
Б
3
2
1
0
-1
-2
-3
100
200
300
400
500
600
700
800
Leaf dry weight (g plant^{-1})
Light integral (MJm^{-2})

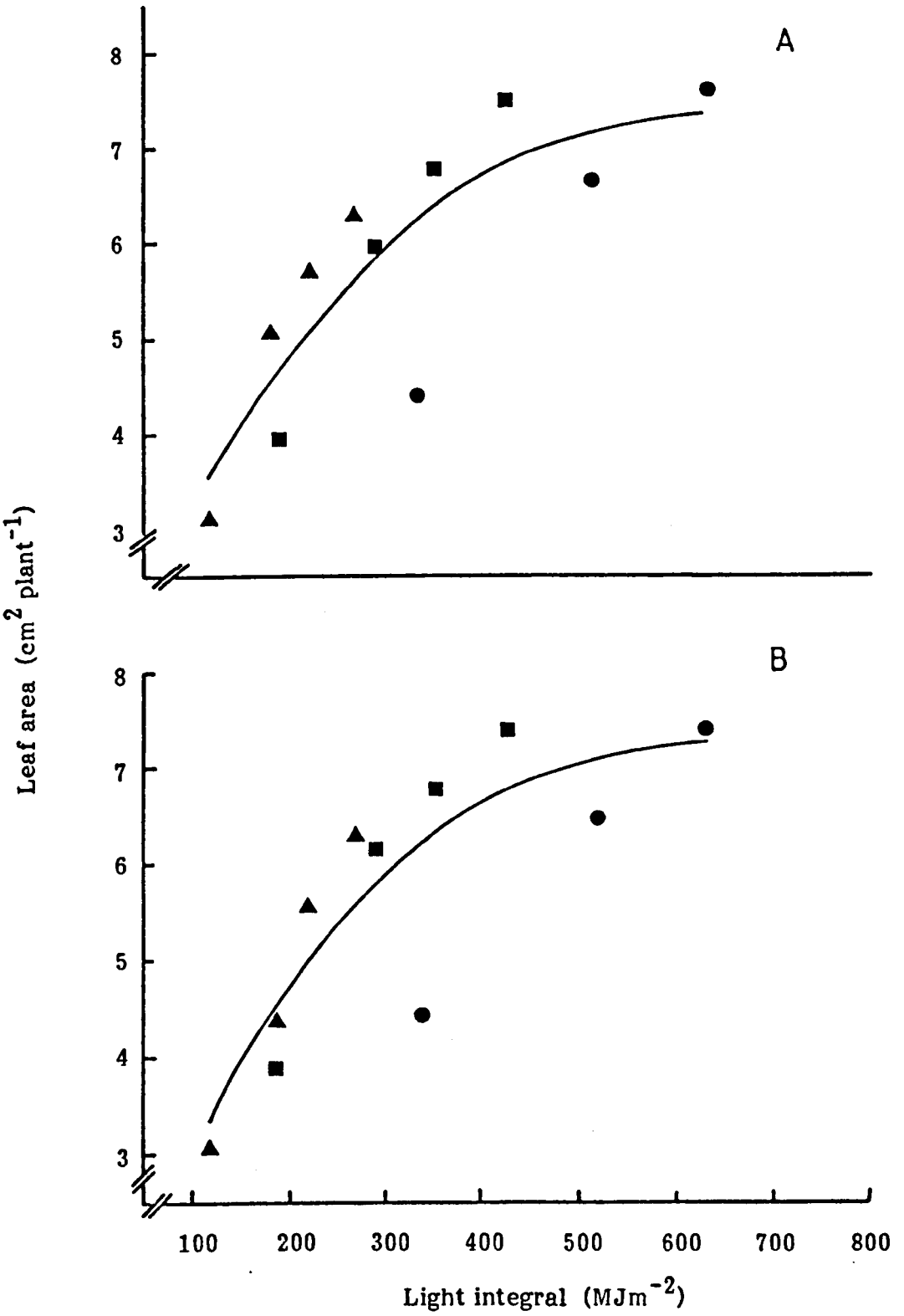
Fig 3.9c Regression of Log_e leaf area on light integral for cultivars Perfection (A) and White Fox (B) at zero (●), one (■) and two (▲) layers of shading

A $y = 1.47 + 0.01974x + -0.0000166x^2$

$r^2 = 0.71$ $(p < 0.01, \text{ d.f.} = 8)$

B $y = 1.11 + 0.02185x + -0.0000192x^2$

$r^2 = 0.75$ $(p < 0.01, \text{ d.f.} = 8)$


A
B
8
7
6
5
4
3
100
200
300
400
500
600
700
800
Leaf area (cm^2 plant^{-1})
Light integral (MJm^{-2})

from the Log_e transform of the data, with increasing light integral was accurately described by quadratic functions (Fig 3.9, a-c).

A comparison of data derived from individual shading treatments comprising the quadratic curves would suggest reduced efficiency of light utilization for both relative dry weight and leaf area increase at higher light integrals.

3.4 The effect of post vernalization photoperiod on curd initiation

Previous studies have reported cauliflowers as being day neutral after vernalization (Eguchi, 1947; Carew and Thompson, 1948; Parkinson, 1952; Sadik, 1967). The possible effects of photoperiod in these studies may however have been confounded by differences in the total radiation receipt in each treatment. It is also unclear in Sadik's study whether curd or floral initiation was studied. Later, Chaisuwan (1974) using constant light energy levels, showed the summer cauliflower cv Cluseed major to have an optimum photoperiod of 16 h for curd initiation at 20°C and 12 h at 25°C. At lower temperatures, 15°C, no effect of photoperiod was evident. These photoperiodic treatments were not preceded by vernalization and the basis for assessing rapidity of curd initiation in these experiments was not clear.

The present study examines curd initiation under 3 differing photoperiods, independent of irradiance reciept following chilling for both optimal and sub-optimal durations (section 3.1). Curd initiation was measured principally as leaf number subtending the curd.

3.4.1 Materials and methods

Seeds of the cv Perfection were germinated, and plants grown under normal glasshouse conditions following the methods described in section 2.1.1. Vernalization treatments comprising one, two or four weeks at 5 ± 1°C in a controlled environment room commenced when plants had attained maturity (Chapter 4) as determined by an assessment of total leaf number. The use of three sowing dates on the 25 September, 9 and 17 October 1986 ensured that all vernalization treatments were completed on approximately the same date, prior to plants being returned to the glasshouse for photoperiodic treatments of 8, 16 or 24 hours. Sowing dates and transfer between treatments are summarised in Table 3.11. Throughout the vernalization treatments plants were maintained under a 12 h photoperiod by a bank of warm white fluorescent tubes providing 60 Wm^{-2} at plant height.

Table 3.11

		Growth at 5°C		
Sowing date		Start	Finish	Duration $weeks^{-1}$
(1)	25.9.86	28.10.86	25.11.86	4
(2)	9.10.86	13.11.86	27.11.86	2
(3)	17.10.86	24.11.86	1.12.86	1

Photoperiod control under glasshouse conditions using an automatic blackout system set to cover all plants at 16.00 h and uncover them at 08.00 h, established a basic 8 h photoperiod. The natural

irradiance during this 8 h was supplemented by 400 W SON/T lamps providing an additional 60 to 65 Wm^{-2} at plant height. When longer photoperiods of 16 h and 24 h were required, the short photoperiod of 8 h was extended by low irradiance (1.2 Wm^{-2}) lighting from incandescent lamps suspended approximately 1.5 m above the plants beneath the blackout for the required period. This arrangement was adopted to reduce any confounding effects of long photoperiod with irradiance level.

Temperatures were monitored in both long and short photoperiods using a Squirrel multi channel data logger (Grant Instruments (Cambridge) Ltd, Cambridge). Differences in air temperature between treatments never exceeded 1.5°C (higher temperatures being recorded in the longer photoperiods).

Development was monitored before and after chilling. A total of nine plants were sampled on each occasion and leaf number, leaf and stem dry weights and leaf area measured (Table 3.12). The same measurements were repeated on completion of the experiment together with an assessment of stem length.

The experimental design used was a randomised complete block with 3 replicates per treatment, each replicate consisting of five plants.

3.4.2 Results

3.4.2.1 Leaf number The degree to which photoperiod influenced leaf number below the curd was dependent on the duration of the preceding vernalization treatment (Fig 3.10a). A significant increase in leaf number with lengthening photoperiod was evident only in those plants previously chilled for one week at 5°C. Here the 24 h regime delayed curd initiation until 37 leaves beneath the curd. This was in contrast to 8 and 16 h

Table 3.12 Shoot characteristics pre-and post-vernalization treatments*

Duration at 5°C week^{-1}	Leaf number	Leaf fresh weight g^{-1}	Leaf dry weight g^{-1}	Stem fresh weight g^{-1}	Stem dry weight g^{-1}	Leaf area cm^2
1	20.6	11.2	1.11	2.3	0.152	235
	(19.0)	(9.1)	(0.78)	(1.6)	(0.083)	(220)
2	23.6	22.3	2.40	3.7	0.288	373
	(17.6)	(6.4)	(0.51	(1.1)	(0.050)	(150)
4	22.9	16.2	1.85	3.2	0.228	266
	(19.1)	(7.1)	(0.50)	(0.9)	(0.054)	(161)
SED	1.16	1.25	0.132	0.349	0.0198	20.1
(d.f. = 24)	(0.6)	(0.68)	(0.056)	(0.115)	(0.0051)	(11.9)

* Figures in parenthesis represent measurements at the commencement of vernalization

photoperiods producing 35 and 28 leaves respectively. Changes in leaf number associated with photoperiod were not significant in plants that had been chilled for either two or four weeks at 5°C.

This highly significant interaction ($p < 0.001$) of photoperiod with duration of chilling suggests an additive effect of short photoperiods for accelerating curd initiation following sub-optimal vernalization conditions.

Within all photoperiodic treatments a significant reduction in leaf number was measured when comparing vernalization treatments of one and four weeks.

3.4.2.2 Shoot components Stem length was increased with increasing photoperiod (Fig 3.10b). Maximum stem extension was observed under a 24 h photoperiod in plants that had previously been chilled for the shortest time. A 1.5 fold increase in stem length to 15 cm was recorded in contrast to 10.5 cm when plants were grown under an 8 h regime. Stem length was, to some degree, under photoperiodic control irrespective of the duration of the preceding vernalization treatment. Only the increase under 16 and 24 h regimes following 2 weeks at 5°C was shown not to differ significantly. As with leaf number, longer periods of vernalization suppressed, or possibly masked the stem extension effect of increasing photoperiod. This interaction was shown to be highly significant ($p = 0.001$).

Leaf number and stem length at the time of curd initiation were highly correlated ($p < 0.001$, d.f. = 7). This may indicate that increasing stem length acted to suppress curd initiation but not vegetative development, resulting in a higher leaf number below the curd (Fig 3.9a).

Where plants were chilled for one or two weeks increasing the photoperiod served to increase stem dry weight. This increase was

significant when comparing 8 and 24 h regimes (Fig 3.10c). However a decrease in stem weight to 0.84 g was recorded when growth at low temperature for one week was followed by exposure to a 16 h photoperiod. As stem dry weight showed a positive correlation with leaf number beneath the curd $r^2 = 0.69$ ($p < 0.01$, d.f. = 7), this may suggest an optimum photoperiod of 16 h for curd initiation following a sub-optimal vernalization period. Positive correlations between both stem length and stem dry weight with leaf number beneath the curd would further suggest competition between stem extension growth and stem apex-curd differentiation.

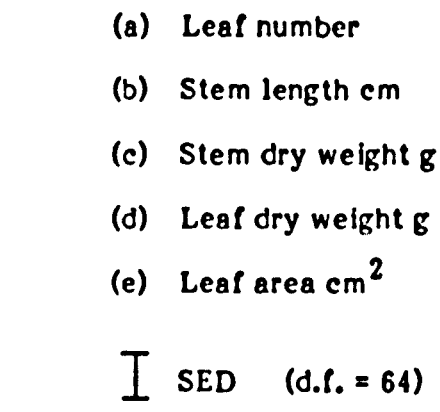
Within the 8 and 24 h photoperiods increased vernalization resulted in a reduced stem dry weight, in contrast to a maximum stem dry weight associated with two weeks' vernalization when growth was continued under a 16 h photoperiod.

Photoperiod had little effect on leaf dry weight except when preceded by vernalization for a period of one week (Fig 3.10d).

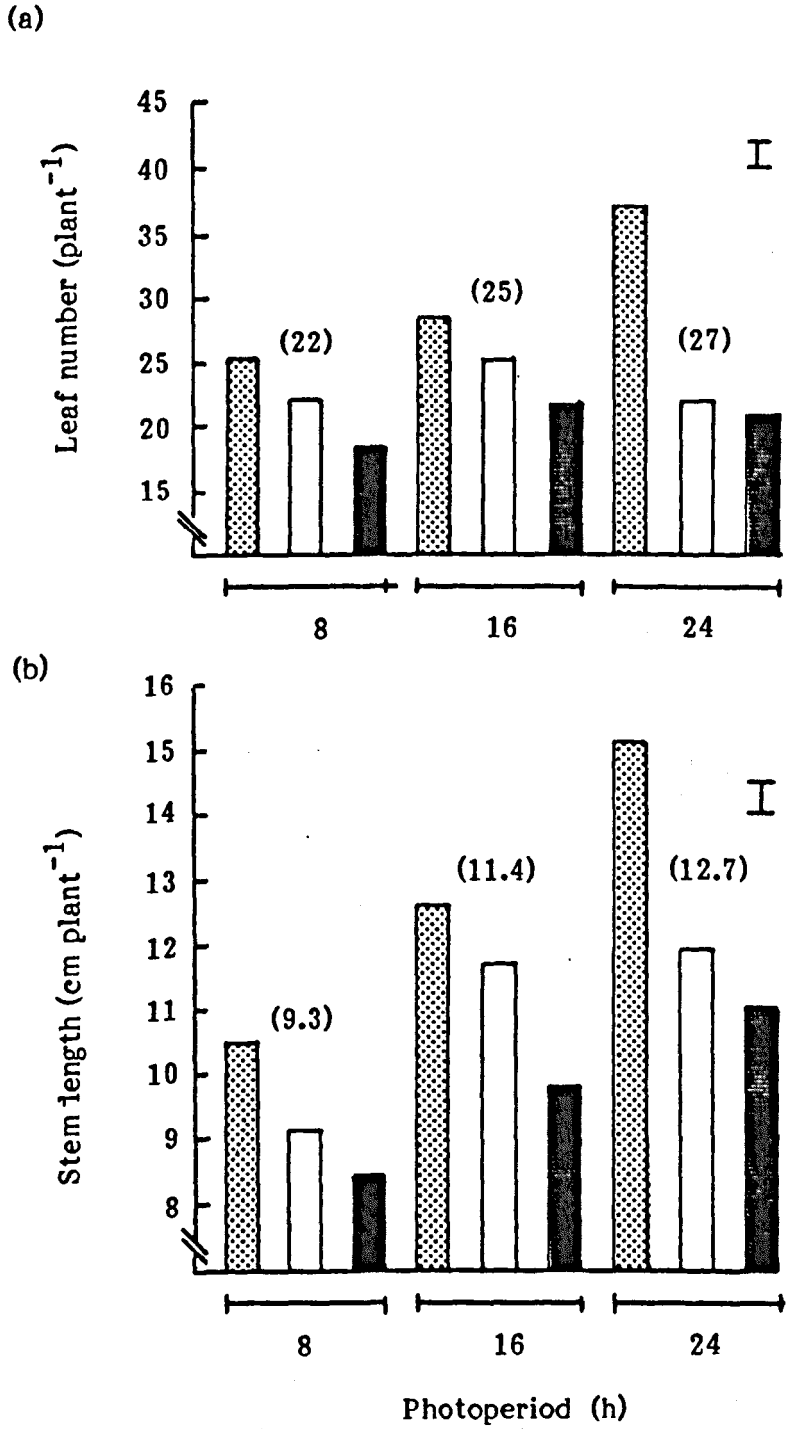
Under these conditions a maximum leaf dry weight of 7.0 g was achieved by plants grown under an 8 h photoperiod. This was in contrast to leaf dry weights of 3.4 and 5.7 g attained under 16 and 24 h regimes respectively. Increasing the duration of vernalization from one to four weeks significantly reduced leaf dry weight within the 8 and 24 h photoperiods, whereas under the 16 h regime a significant increase in leaf dry weight was measured in association with two weeks' vernalization. Changes in leaf dry weight could not be correlated with final leaf number.

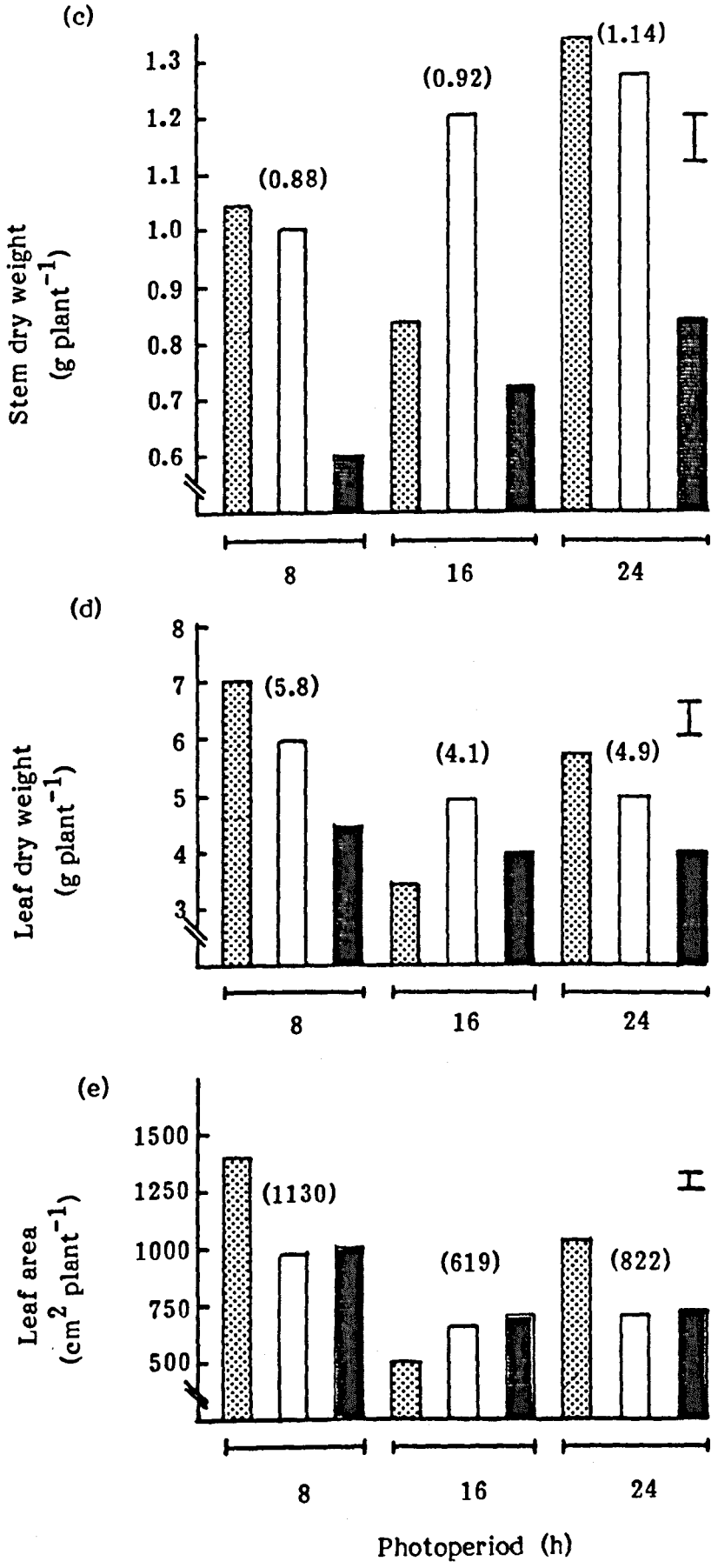
Following two or four weeks' vernalization leaf area was reduced by photoperiod exceeding 8 h (Fig 3.10e) with no significant difference between 16 and 24 h regimes.

Fig 3.10 Effect of photoperiod on leaf number and shoot components at time of curd initiation following one ▒, two □ or four ■ weeks at 5 °C



Figures in parentheses represent mean values for individual photoperiods


(a)
Leaf number (plant^{-1})
45
40
35
30
25
20
15
(22)
(25)
(27)
I
8
16
24
(b)
Stem length (cm plant^{-1})
16
15
14
13
12
11
10
9
8
(9.3)
(11.4)
(12.7)
I
8
16
24
Photoperiod (h)


(c)
Stem dry weight (g plant^{-1})
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
(0.88)
(0.92)
(1.14)
8
16
24
(d)
Leaf dry weight (g plant^{-1})
8
7
6
5
4
3
(5.8)
(4.1)
(4.9)
8
16
24
(e)
Leaf area (cm^2 plant^{-1})
1500
1250
1000
750
500
(1130)
(619)
(822)
8
16
24
Photoperiod (h)

Photoperiod had a marked effect on leaf area when plants were vernalized for one week, growth under an 8 h regime increasing leaf area approximately 2 and 3 fold over that attained under 24 and 16 h photoperiods respectively. This vernalization dependent photoperiodic effect represented a significant interaction ($p < 0.001$). As might be expected leaf area was shown to be positively correlated with leaf dry weight, $r^2 = 0.86$ ($p < 0.001$, d.f. = 7).

3.5 Light quality during chilling and its effects on curd initiation

Cold treatments applied to cauliflower plants prior to transplanting have been investigated with a view to improving cropping characteristics (Salter and Ward, 1972; Salter and James, 1974; Wurr et al., 1982). Their cold treatments generally used frame raised bare-root transplants, pulled and stored in the dark at approximately 2°C. Little attention was given to any possible requirement for light during this period, and any possible effects of light quality on curd initiation. A preliminary investigation was therefore undertaken here to examine these possibilities. This served both to clarify the effect of light quality during chilling on curd initiation and to compare the effect of light sources to be used in future experiments.

3.5.1 Materials and methods

Seeds of the cvs Perfection and White Fox were germinated, and seedlings grown, as described in section 2.1.1. Experimental treatments commenced when plants had attained maturity (Chapter 4), this was confirmed by sampling the plants and determining the leaf number as

described in section 2.6. Measurements of leaf number along with shoot components are summarised in Table 3.13.

Plants were chilled for four weeks at 5 ± 1°C under three lighting regimes. Lamps used were either of the high pressure mercury vapour (HLRG) type or warm white flourescent tubes. The third treatment comprised chilling in complete darkness. Under both lighting regimes plants received a 12 h photoperiod. Photon flux densities (PFD) of 120 ± 10 and 115 ± 5 μmol m^{-2} s^{-1} PAR (400-700 nm) were measured under warm white and HLRG sources respectively.

Plants were returned to warm (20°C) glasshouse conditions after four weeks at 5°C. Measurements of leaf number and shoot components were made in samples of plants taken after two weeks' chilling and at curd initiation as described in section 2.6.

The experiment was of a completely randomised design with nine plants per cultivar for each treatment x sampling.

3.5.2 Results

3.5.2.1 Leaf number at curd initiation Leaf number at curd initiation in chilled plants of both cvs Perfection and White Fox was not significantly affected by any light treatment (Table 3.13). Determination of leaf number at the commencement of experimental treatments (Table 3.13) showed that the cv Perfection initiated a further six leaves before initiation of the curd. This was in contrast to the cv White Fox where initiation of the curd followed the initiation of only one or two additional leaves. Leaf numbers determined after two weeks under experimental conditions were not shown to differ significantly from the final leaf number at curd initiation. This would indicate that curd evocation occurred after approximately two weeks under these conditions.

Table 3.13 Change in leaf characteristics at curd initiation following chilling at 5°C for 4 weeks under different light conditions in cvs Perfection and White Fox

Leaf characteristics	Cultivar	Light source		
		HLRG	WWF	DARK
Leaf number	Perfection	30	30	29
	24 ± 0.2+	(31)	(30)	(29)
	White Fox	28	29	28
	27 ± 0.3+	(30)	(30)	(29)
Leaf area cm^2	Perfection	3181	3104	2776
	600 ± 30+	(456)	(509)	(319)
	White Fox	1954	2080	2114
	671 ± 27+	(716)	(686)	(621)
Leaf dry weight g^{-1}	Perfection	18.6	17.6	20.0
	2.7 ± 0.15+	(3.4)	(3.9)	(1.6)
	White Fox	11.9	12.1	12.8
	3.6 ± 0.18+	(4.6)	(4.8)	(3.1)

Light sources: High pressure mercury vapour (HLRG)
Warm white fluorescent (WWF)

Figures in parenthesis represent shoot components after 2 weeks' treatment

+ Leaf characteristics at commencement of treatments ± SE

SEDs at curd initiation followed by SED after 2 weeks' treatment, in parenthesis:

Leaf number	1.1 (1.2)	d.f. = 48
Leaf area	83.0 (48.6)	d.f. = 48
Leaf dry wt	13.1 (4.2)	d.f. = 48

3.5.2.2 Leaf size at curd initiation Leaf dry weight was shown not to differ significantly with light treatment during chilling in either cv Perfection or White Fox (Table 3.13). Significant differences were apparent however, when comparing the two cvs ($p < 0.001$). Leaf dry weight of the cv Perfection was approximately 6 to 8 g greater than cv White Fox. This was consistent throughout all experimental treatments and not dependent on light source.

Leaf expansion was suppressed in the cv Perfection by two weeks' growth under conditions of total darkness when compared with the two light sources, which were shown not to differ significantly. This was in contrast to the cv White Fox where no significant difference was measured. Similarly at curd initiation leaf area was lower in plants of cv Perfection that had been chilled in darkness.

3.6 Summary

1. Low temperature promoted curd initiation in the summer cauliflower cvs Perfection, Dok, Alpha Cliro and Abundantia as marked by a reduction both in leaf number beneath the curd and in the number of days to macroscopic curd visibility. Accelerated curd initiation was associated with a reduction in leaf dry weight and leaf area at the time of macroscopic curd visibility.

2. Chilling plants at 5°C was more effective in promoting curd initiation than chilling at 2°C. Under both temperature regimes the promotory effect of chilling was increased with increasing exposure up to four weeks.

3. The extent to which curd initiation was accelerated depended on both cultivar and plant age. Greater response to chilling was observed in the early summer cultivars Perfection and Alpha Cliro than in the mid/late summer cvs Dok, Abundantia and White Fox. This may have been the result of a difference in the quantitative cold requirement for curd initiation and/or longer juvenile phases in the later season cultivars.

4. Leaf numbers marking the ends of the juvenile stages in the cvs under study were estimated as: Perfection, 12-19 leaves; Alpha Cliro, 9-18; Dok, $\geqslant 19$. In this preliminary study juvenile stages in Abundantia and White Fox were less evident.

5. In cv White Fox, linear regressions described the relationship between days to curd visibility and leaf dry weight ($r^2 = 0.67$, $p < 0.001$) and leaf area ($r^2 = 0.72$, $p < 0.001$). In other cultivars however, no significant relationship between the number of days to macroscopic curd visibility and either leaf dry weight or leaf area was established.

6. Reduced irradiance receipt in plants grown at c 20°C delayed curd initiation, marked by an increase in the number of leaves present beneath the curd. In cv Perfection 55 leaves were produced in unshaded treatments compared to 64 in the most shaded. Similar treatments applied to cv White Fox resulted in 49 and 59 leaves respectively. The reductions in light integral required to increase leaf number below the curd by one were 35.7 and 45.0 MJm^{-2} for cvs Perfection and White Fox under the conditions employed here. No attempt was made here to determine a critical time for this effect.

7. Stem dry weight at curd visibility increased linearly with increasing total irradiance in both cvs Perfection and White Fox. Light integrals required per g stem dry weight were estimated as 104 and 54 MJm^{-2} respectively. The linear relationship of leaf dry weight on light integral for cv Perfection indicated a requirement of 13.1 MJm^{-2} per g dry weight increase.

8. The rate of leaf initiation was reduced by shading in both cvs Perfection and White Fox. Light integrals of 6.64 and 7.82 MJm^{-2} incident at plant height were required for the initiation of one leaf in cvs Perfection and White Fox respectively. Leaf initiation rates in cv White Fox were slower than in cv Perfection.

9. Growth in shoot weight and leaf area increased exponentially over the irradiance range 125 to 350 MJm^{-2}. However, this rate was not maintained at irradiance integrals greater than 350 to 400 MJm^{-2}, suggesting reduced efficiency of light utilization for both relative dry weight and leaf area increase.

10. Increasing photoperiod, as distinct from light integral, applied after sub-optimal chilling (exposure to 5°C for one week), delayed curd initiation, measured as an increase in leaf number beneath the curd. In contrast, short photoperiods after sub-optimal chilling accelerated curd initiation.

11. Stem length increased with increasing photoperiod after sub-optimal chilling. Stem length was highly correlated with leaf number at the time of curd visibility.

12. Minimum stem dry weight attained under a 16 h photoperiod following sub-optimal vernalization combined with a positive correlation between leaf number and stem dry weight, may suggest an optimum photoperiod of 16 h for curd initiation following sub-optimal vernalization, compared with 8 and 24 h photoperiods.

13. Curd initiation was not influenced either by light source or by total absence of light during chilling.

Chapter 4

JUVENILITY

Introduction

Acceleration of curd initiation following chilling was shown in the previous chapter to depend on plant age indicating a juvenile phase of development as reported in previous studies (Wiebe, 1972a, 1974; Salter and James, 1974; Wurr, 1981). In those studies however the juvenile phase was not investigated thoroughly or defined closely. Accurate prediction of crop development and efficient manipulation of curd initiation can only be achieved if the duration of the juvenile phase is clearly defined. Chilling would promote curd initiation applied after phase change, but would delay it when applied during juvenile development (refer to section 3.1).

The experiments reported here determine the duration of the juvenile phase for cvs Perfection and White Fox under controlled environment conditions. Phase transition and sensitivity to vernalization were assessed by chilling both plants of different ages and germinating seeds.

The effect of growth at constant temperatures of 7, 10, 18 and 20°C during juvenility on plants' subsequent sensitivity to vernalization after phase change was also studied.

4.1 Plant age and chilling sensitivity

The first two experiments in this chapter attempted to characterise juvenility in cvs Perfection and White Fox. This involved chilling different age plants for four weeks at 5°C and then assessing sensitivity to chilling primarily by determining the reduction of leaf

number beneath the curd. The stage of phase transition was found by plotting sensitivity to chilling against the number of leaves present at the commencement of the low temperature treatments. Possible relationships between other changes in leaf development and phase transition were also examined to provide information on alternative markers for phase change.

4.1.1 Materials and methods

Cauliflower cvs Perfection and White Fox were sown and germinated as described in section 2.1.1. In both experiments sequential sowing dates provided plants with differing leaf numbers at the start of vernalization treatments (Table 4.1). This ensured that all plants were vernalized over the same four week period, and that they were returned to the glasshouse at the same time for subsequent curd initiation. Prior to commencement of chilling treatments (on 14 July 1985 and 13 November 1985 in the first and second experiments respectively) plants were grown under glasshouse conditions at a temperature of $20 \pm 4°C$. Natural glasshouse irradiance was supplemented during the second experiment using 400 W SON/T lamps providing an additional 65 to 70 Wm^{-2} at plant height for 16 h each day, commencing at dawn. The natural October photoperiod of 12 h was therefore extended to 16 h, approximating to that received by plants in the first experiment. General plant husbandry was as detailed in Chapter 2.

A standard chilling treatment used for both experiments consisted of four weeks at $5 \pm 1°C$ applied using the controlled environment rooms described previously (see section 2.2). Throughout low temperature treatments plants received a 16 h photoperiod from warm white fluorescent tubes providing an irradiance of c 55 ± 5 Wm^{-2} incident at

Table 4.1 Dates of sowing and vernalization treatments for cvs Perfection and White Fox with associated leaf numbers for experiments one and two

Exp 1

Sowing date	Vernalization starts	Leaf number ($\bar{x}$ of 9)		Vernalization completed
		Perfection	White Fox	
9.6.85	14.7.85	36	33	11.8.85
12.6.85	"	29	31	"
15.6.85	"	22	26	"
18.6.85*	"	19	-	"
21.6.85	"	16	18	"
25.6.85	"	12	17	"
29.6.85	"	9	12	"
3.7.85	"	6	8	"

Exp 2

26.9.85	13.11.85	23	19	11.12.85
29.9.85	"	22	14	"
2.10.85	"	20	14	"
4.10.85	"	17	13	"
7.10.85	"	15	12	"
9.10.85	"	13	11	"
11.10.85	"	13	10	"
13.10.85	"	10	5	"
15.10.85	"	7	5	"
17.10.85	"	6	6	"

* Perfection only

plant height. Control plants were retained under warm (c 20°C) glasshouse conditions. On completion of low temperature treatments all plants were returned to the glasshouse and randomised with unchilled control plants.

Plant development in the first experiment was measured both before and after chilling treatments to determine the effect of low temperature. Measurements of leaf number, leaf dry weight and leaf area were as described in section 2.6. Similar measurements were taken at the time of macroscopic curd visibility. The 32 and 40 treatments comprising the first and second experiments respectively (sowing dates x cultivars x chilled or unchilled controls) were arranged in a completely randomised design with nine plants per treatment at each sampling. Sampling dates were as described above.

4.1.2 Results

The results of the two experiments investigating phase transition are considered together to facilitate comparison, and enable assessment of the stability of markers for the end of the juvenile phase.

4.1.2.1 Leaf number as a marker of phase transition Phase transition was defined accurately in both cvs Perfection and White Fox (Fig 4.1a and b). In both experiments plants of cv Perfection that had either initiated fewer than 10 leaves prior to chilling or were unchilled, formed between 41 and 59 leaves beneath the curd (Fig 4.1a). This indicated an inability to perceive or express chilling as a vernalization stimulus. Plants that had initiated 12 leaves prior to chilling in the first experiment initiated a further two leaves and five large bracts before the curd. Possible inclusion of these atypical bracts in the final leaf count would indicate the presence of 17 'leaves' beneath the curd or 14 if they are omitted (Fig 4.1a). This

intermediate habit may suggest that phase transition occurred during the chilling treatment, and the lower of the two points, corresponding to 14 leaves (Fig 4.1a) may represent the earliest point of phase transition. This was confirmed when plants were chilled after initiating 13 to 15 leaves. Under these conditions a total leaf number of 23 was recorded beneath the curd in contrast to the 56 present in the unchilled controls. Competence to respond to vernalization had therefore been acquired suddenly at that stage of development. The initiation of 9 leaves after chilling and before curd initiation is consistent with a true 'indirect' effect (after-effect) of chilling on curd initiation through vernalization, as both leaf and curd initiation will have taken place on returning the plants to glasshouse conditions. Plants that had initiated 19 leaves or more prior to vernalization would have passed the period of phase transition, and subsequently initiated curds without additional leaves being produced.

Plants of cv White Fox that had either initiated fewer than 14 leaves prior to chilling or remained unchilled, formed between 36 and 47 leaves before the curd (Fig 4.1b). Plants chilled after initiating 17 to 18 leaves however proceeded to initiate curds after a maximum of an additional two leaves, suggesting rapid attainment of competence to respond to the vernalization stimulus. The dependency of competence to perceive vernalization on leaf number was highly significant ($p < 0.001$).

The stability of leaf number as a marker for phase transition was evident when comparing conditions for early plant growth in the two experiments. Plants were raised for the first study from seeds sown between late September and early November, in contrast to the June to July period used in the second investigation. Despite attempts to extend the natural daylength and supplement irradiance receipt, autumn sown

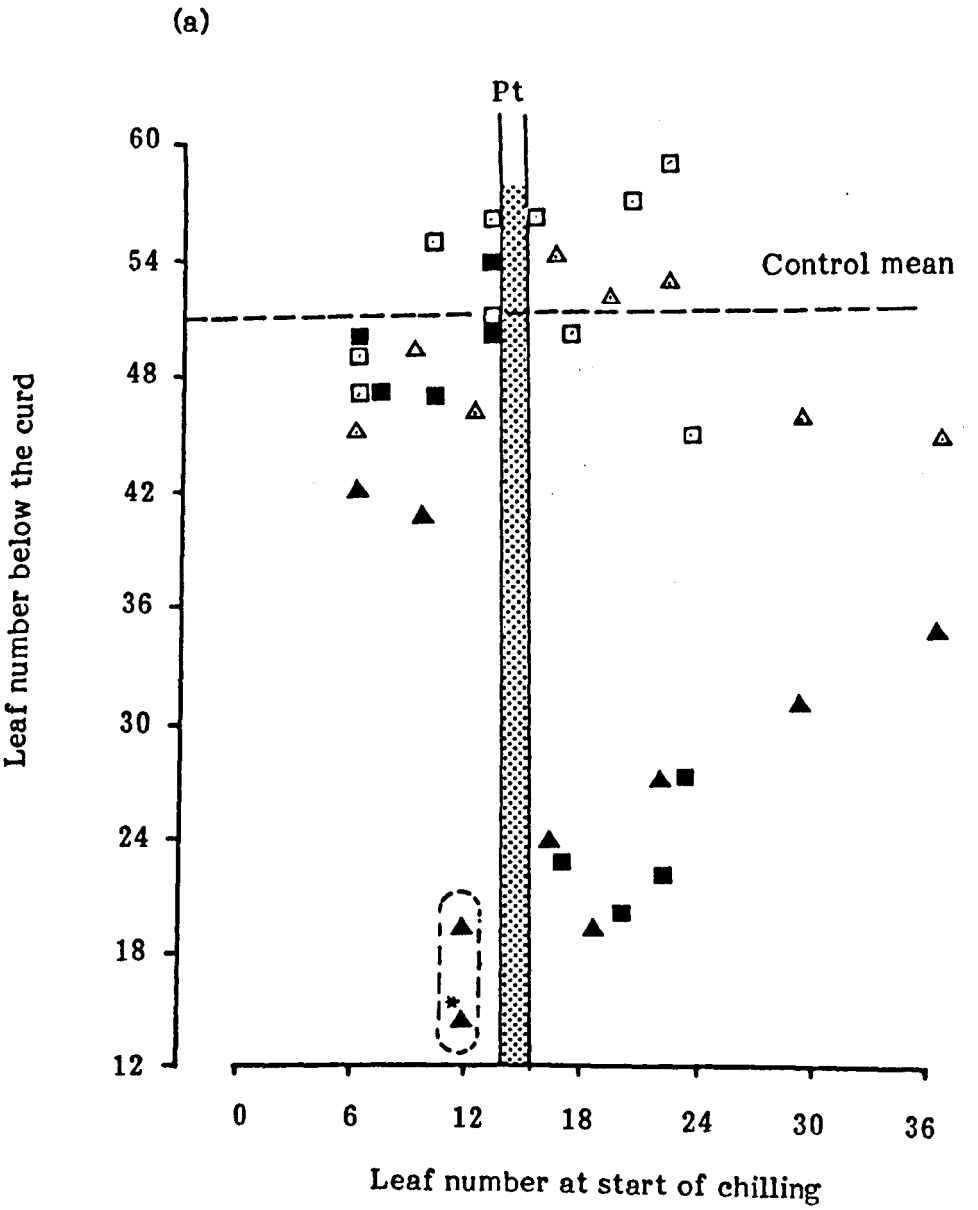
Fig 4.1 Phase transition (Pt) in cauliflower cvs Perfection (a) and White Fox (b) marked by total leaf number initiated when plants were first able to perceive chilling as a vernalization stimulus

Vernalization was measured as a decrease in leaf number below the curd in chilled plants (▲ ■) relative to control plants (△ □)

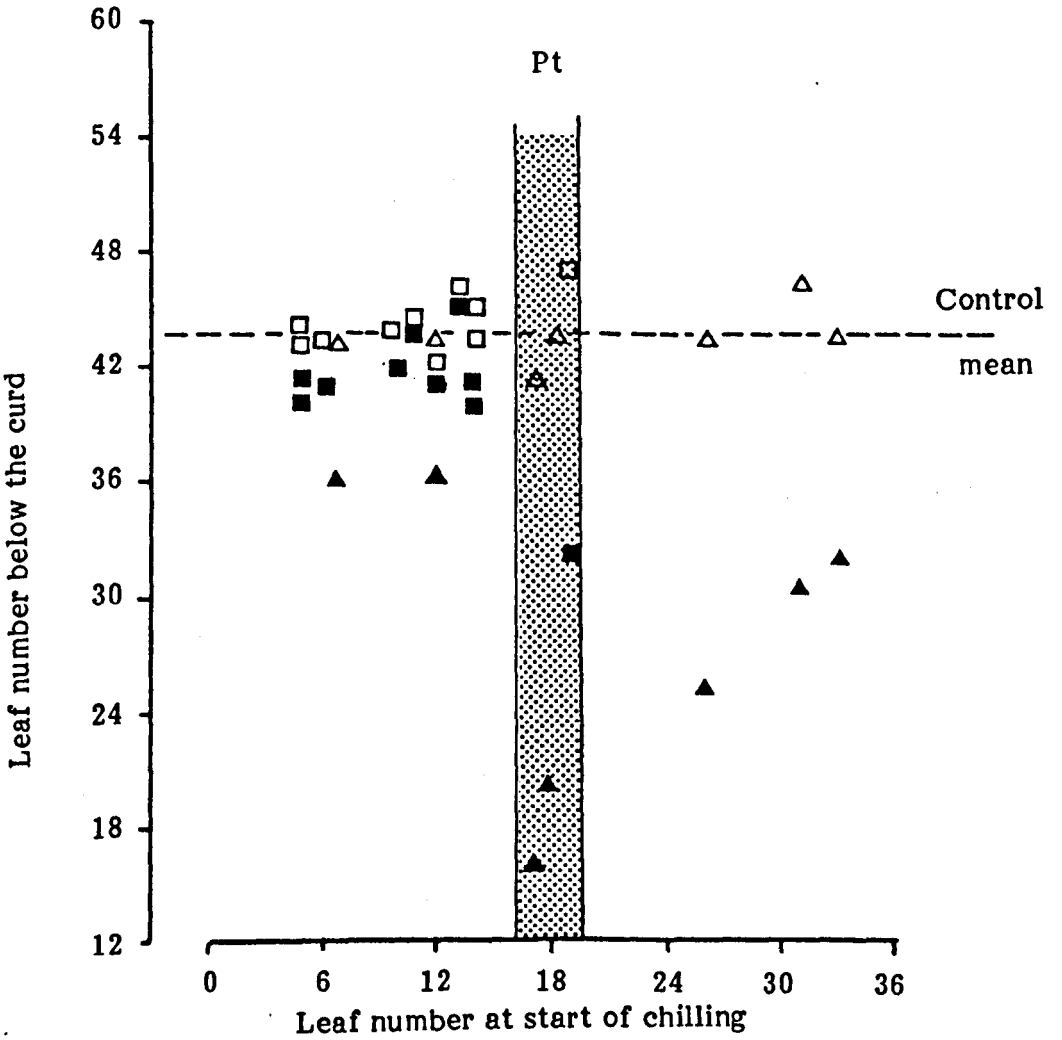
Data derived from the first (▲ △) and second (■ □) experiments respectively

Each value is a mean of nine

See text in section 4.1.2.1 for explanation


(a)
Pt
Control mean
Leaf number below the curd
60
54
48
42
36
30
24
18
12
0
6
12
18
24
30
36
Leaf number at start of chilling

(b)


60
54
48
42
36
30
24
18
12
Pt
Control
mean
Leaf number below the curd
0
6
12
18
24
30
36
Leaf number at start of chilling

plants were raised under less favourable conditions, particularly irradiance. Leaf number marking phase transition however was unchanged.

4.1.2.2 Leaf growth and phase transition Leaf dry weight was not a stable marker for phase transition under the conditions employed here. Plotting leaf number at macroscopic curd visibility against leaf dry weight ($\log_e$ scale) at the start of chilling showed a leaf dry weight of 0.18 g corresponded with the point of phase transition in cv Perfection in the second experiment (Fig 4.2b) but not in the first (Fig 4.2a). Similar inconsistencies were evident when comparing the response of cv White Fox in the two experiments.

Although not presented here, attempts to use leaf area as a stable marker of phase transition produced similarly inconsistent results. Having previously demonstrated a highly significant linear relationship between leaf area and leaf dry weight (Chapter 3, section 3.1.3.5), this observation could have been anticipated.

4.2 Effects of temperature during juvenile development on the curd initiation response to chilling

In the preceding study plants were raised prior to chilling treatments at a minimum glasshouse temperature of 16°C. This contrasts with temperatures of around 10°C or below used commercially for raising cauliflower transplants (Anon, 1985a).

It was thought possible that raising temperature may alter the response to a subsequent vernalization stimulus. In particular, pre-vernalization high temperatures (predevernalization) have been shown to reduce the response to vernalization in cabbage (Heide, 1970) and Chinese

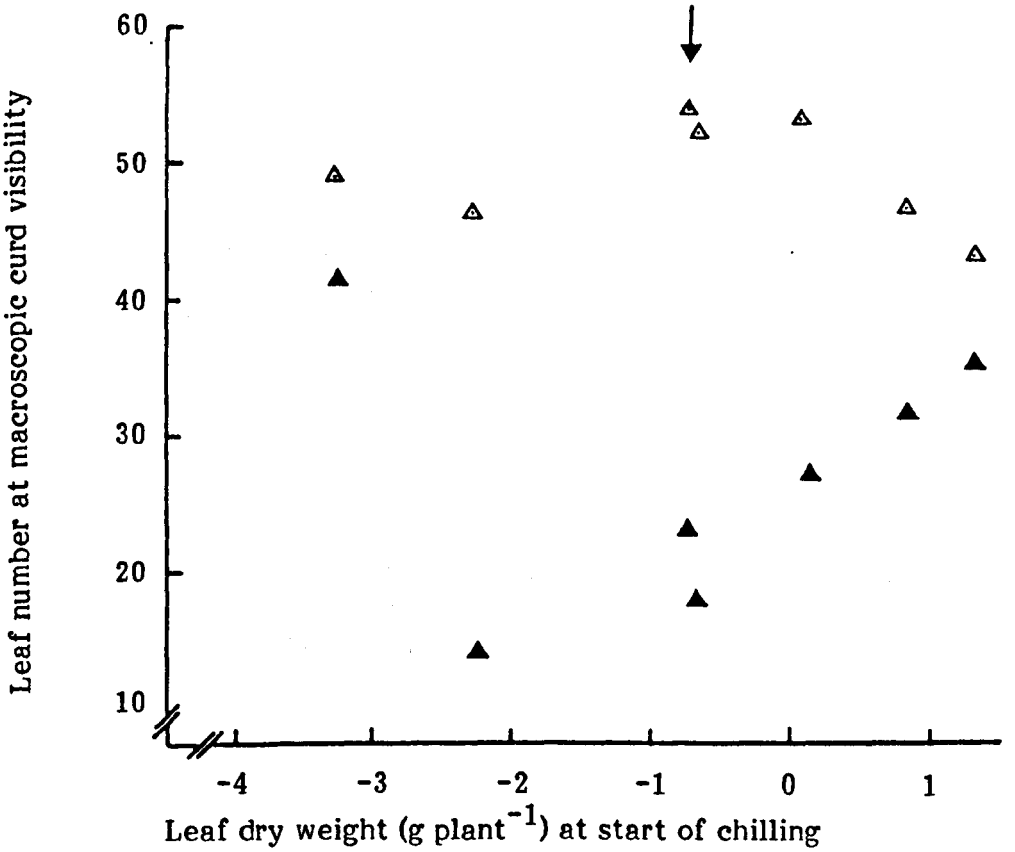
Fig 4.2 Leaf number at macroscopic curd visibility measured against leaf dry weight g (Log_e scale) at the start of chilling for chilled (▲ ■) and unchilled (△ □) control plants of cv Perfection

Data derived from the first (▲ △) and second (■ □) studies

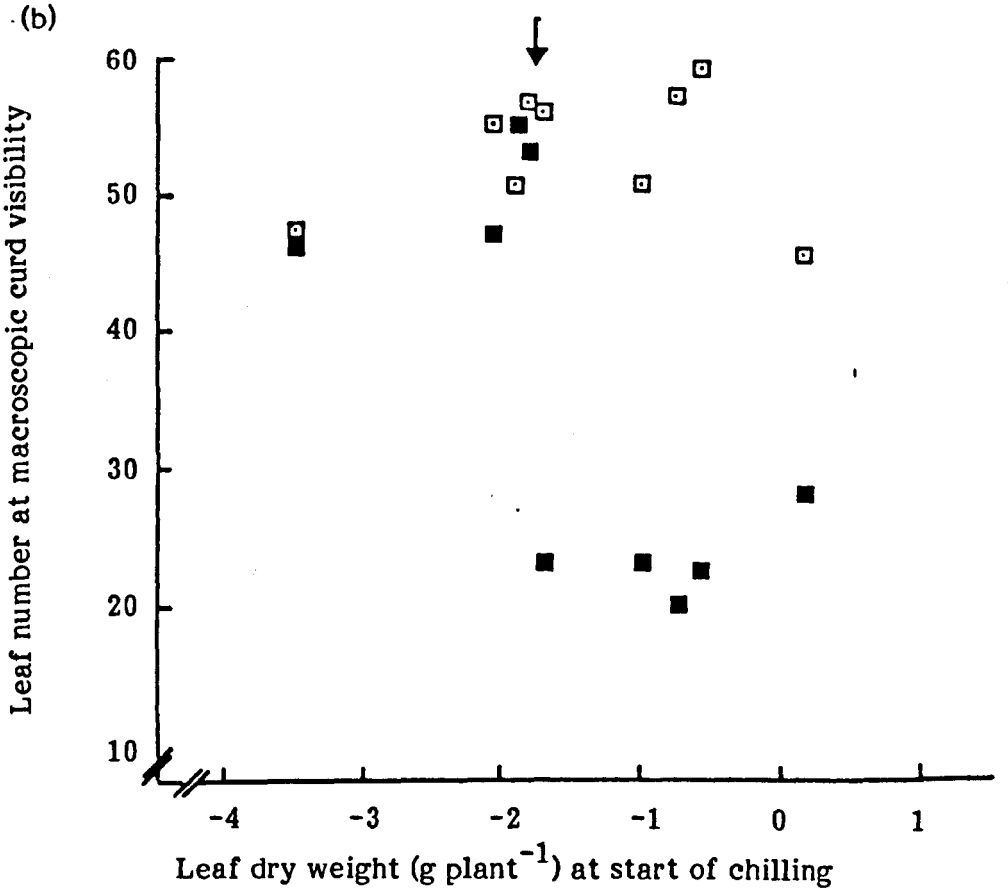
Each point is a mean of nine

(↓) denotes point of phase transition derived from Fig 4.1a in cv Perfection

(a)


Leaf number at macroscopic curd visibility
60
50
40
30
20
10
-4
-3
-2
-1
0
1
Leaf dry weight (g plant^{-1}) at start of chilling

(b)


Leaf number at macroscopic curd visibility
60
50
40
30
20
10
-4
-3
-2
-1
0
1
Leaf dry weight (g plant^{-1}) at start of chilling

cabbage (Elers and Wiebe, 1984). The following experiment was designed primarily to examine this possibility for cauliflower.

4.2.1 Materials and methods

Seeds of the cvs Perfection and White Fox were sown on 27 November 1985 and germinated under glasshouse conditions at a mean daily temperature of 20°C. Seedlings were potted-up and grown on under an extended photoperiod of 12 h in the same glasshouse until establishment. The natural November photoperiod was extended to 12 h, commencing at dawn, using 400 W SON/T lamps. This also increased irradiance incident at plant height by c 55 Wm^{-2}. On 12 December 1985 seedlings were transferred to a range of controlled environments to continue growth at a constant 7, 10, 18 or 25°C $\pm$ 1°C. Lighting during the 12 h photoperiod was provided by a bank of 80 W warm white flourescent tubes supplemented by 100 W incandescent lamps giving an irradiance of 55 $\pm$ 4 Wm^{-2} incident at plant height. Adjustments to lighting installations ensured uniform irradiance levels throughout the temperature treatments.

In those temperature treatments that allowed attainment of phase transition at 14 and 19 leaves in cvs Perfection and White Fox respectively, nine plants from each temperature treatment were transferred to a controlled environment room at 5°C. Irradiance levels and photoperiod were as described for the preceding treatments. Plants were retained under these conditions for four weeks and then returned to natural glasshouse conditions. The effect of temperature during juvenile development on the subsequent vernalization response to four weeks at 5°C was assessed as leaf number beneath the curd. The nine plants per treatment were arranged in a completely randomised design.

4.2.2 Results

4.2.2.1 Effect of temperature during juvenile development Curd initiation was observed in all chilled plants. However, the preceding plant raising temperature had little significant effect on the leaf number beneath the curd (Table 4.2).

Plants of both cvs grown at 7 and 10°C were precluded from this study as they had failed to initiate the requisite number of leaves marking phase transition, namely 14 and 18 in cvs Perfection and White Fox respectively, at the time of transfer to the low temperature treatment.

Plants of cv Perfection raised at 25°C and having 15 leaves prior to transfer to low temperature (5°C) conditions, initiated curds on return to the glasshouse environment after the initiation of approximately 7 leaves. This resembles closely results recorded in the preceding section (Fig 4.1A), suggesting that the ability of plants to initiate curds following four weeks at 5°C was not reduced by an initial growing temperature of 25°C. Similar results were evident when considering cv White Fox grown at 25°C, and both cvs Perfection and White Fox raised at 18°C during juvenility prior to chilling (Table 4.2). The duration of juvenility measured chronologically was shortened in both cvs with increasing raising temperature as indicated by the dates on which plants were transferred to the low temperature treatment (Table 4.2).

4.3 Leaf initiation rate during juvenility phase transition and mature, vegetative development

Leaf number has been shown to be a convenient and stable marker for phase transition (refer to section 4.1). However, it is of limited use in

Table 4.2 Effect of raising temperature preceding chilling on leaf number (± S.E.) beneath the curd in cvs Perfection and White Fox

Cultivar	Raising temperature (°C)	Date of transfer to 4 wks at 5°C	Leaf number at transfer	Leaf number beneath the curd
Perfection	25	9.1.86	15 ± 0.6	21 ± 0.3
Perfection	18	12.1.86	15 ± 0.4	20 ± 0.4
White Fox	25	15.1.86	20 ± 0.3	23 ± 0.3
White Fox	18	18.1.86	21 ± 0.6	24 ± 0.6

suggesting a physiological mechanism for the event. The rate of leaf initiation however would reflect possible changes in apical activity (Dale and Milthorpe, 1983) associated with phase transition.

From the preceding study and investigations undertaken by Wiebe (1972c), it may be concluded that rate of leaf initiation is likely to vary with time because of temperature fluctuations. However, rates may be analysed allowing for such fluctuations in temperature by calculating the daily temperature effective for leaf initiation, assuming a base temperature (T_b) of 2°C (Fig 4.3). Tb represents that temperature at or below which no further initiation of leaves takes place. The daily temperature effective for development could then be accumulated to give thermal time sums (Monteith, 1981). A full account of theoretical and practical considerations relating to the use of thermal time is given in Chapters 1 and 5.

A preliminary investigation of the effect of temperature on leaf initiation during juvenile and early mature vegetative growth in cv Perfection is described here. This was followed by a detailed study of the same cultivar grown both at constant 15°C and constant 20°C.

4.3.1 Materials and methods

For the preliminary investigation seeds of cv Perfection were sown on 8 May 1986 and germinated under glasshouse conditions at a mean daily temperature of 20°C. Seedlings were potted-up and grown on under a natural photoperiod of approximately 16 h in the same glasshouse allowing uniform establishment. On 19 May 1986 seedlings were transferred to a range of controlled environments to continue growth at a constant 2, 10, 15, 20, 25 or 30°C. Lighting during the 12 h photoperiod was provided by a

bank of 80 W warm white fluorescent tubes supplemented by 100 W incandescent lamps giving an irradiance of c 55 Wm^{-2} incident at plant height.

Fourteen days after the temperature treatments began on 19 May 1986, and at 5 to 10 day intervals thereafter, samples of five plants were selected at random and dissected to enable counts of total leaf number.

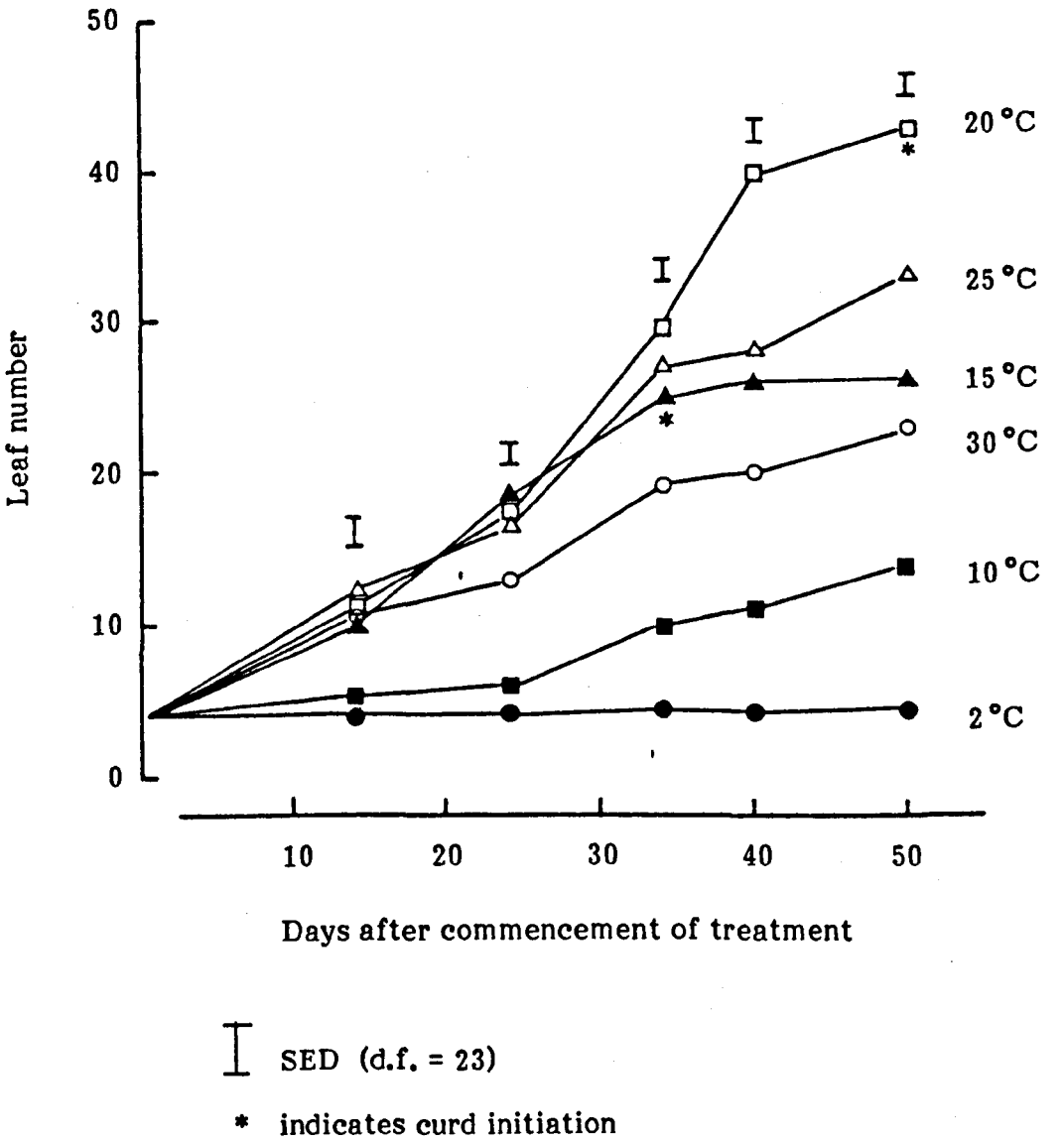
In the second study plants of cv Perfection were raised from seeds germinated directly in pots at 20°C in a growth room. This served to remove any possible check in leaf initiation associated with transplanting from seed trays. Immediately after emergence seedlings were thinned to one per pot and transferred to growth rooms at 15 and 20 $\pm$ 1°C under warm white flourescent tubes arranged to give an irradiance incident at plant height of c 60 Wm^{-2} for 12 h each day. Particular care was taken to ensure uniform lighting conditions between the rooms, as replication of temperatures was not possible. Samples of five plants were selected at random from each treatment at approximately 2 day intervals enabling total leaf number to be determined.

Plants from both studies were arranged in a completely randomised design.

4.3.2 Results

4.3.2.1 Leaf initiation at constant temperature Increasing the temperature from 2 to 20°C increased the rate of leaf initiation in cv Perfection (Fig 4.3). As further increase in temperature to 25 and 30°C caused a decline in the rate of leaf initiation, an optimum of c 20°C is suggested. T_b was indicated at 2°C.

Fig 4.3 Rate of leaf initiation in cultivar Perfection grown at constant temperatures in growth rooms



Growth at 15°C for 34 days resulted in curd initiation after the production of 25 leaves. Similarly plants grown at 20°C initiated curds within the 50 day sampling period, but at a higher leaf number of 43 (Fig 4.3).

Where sampling dates were excluded in which leaf initiation rate was confounded by initiation of the curd (refer to Fig 4.3), along with the first sampling and plants grown at 2°C for which no leaf dry weights could be recorded, a highly significant linear relationship was established when regressing leaf number on log shoot dry weight, $r^2 = 0.77$ ($p < 0.001$) (Fig 4.4). This would suggest a relationship between leaf number and shoot dry weight during juvenile and early mature vegetative growth.

4.3.2.2 Rate of leaf initiation through juvenility and phase transition Regression of leaf number from plants grown at 10, 15 and 20°C in the preceding study, on accumulated degree days above 2°C are used to show rates of leaf initiation (Fig 4.5). As plants at 25 and 30°C were above the optimum temperature (c 20°C) for leaf initiation, these data were excluded.

Regressions suggested an increase in the rate of leaf initiation coincident with phase transition to maturity at approximately 14 leaves (Fig 4.5).

Points from all temperature treatments were present on the 'juvenile' line (line 1, Fig 4.5), with the 'mature' line (line 2, Fig 4.5) comprising points from the 15 and 20°C treatments. Early or transitional stages of curd initiation were associated with plants grown at 10°C for 50 days, having 14 leaves. At 10°C curd initiation was coincident with phase transition, accounting for the absence of any mature vegetative growth (line 2, Fig 4.5). Initiation of leaves numbered acropetally 5 to 14 was slow

Fig 4.4 Regression of leaf number on Log_e shoot dry weight during juvenile and mature vegetative growth in cv Perfection

$y = 20.01 + 5.395x$

$r^2 = 0.77 \quad (p < 0.001, \text{ d.f.} = 15)$

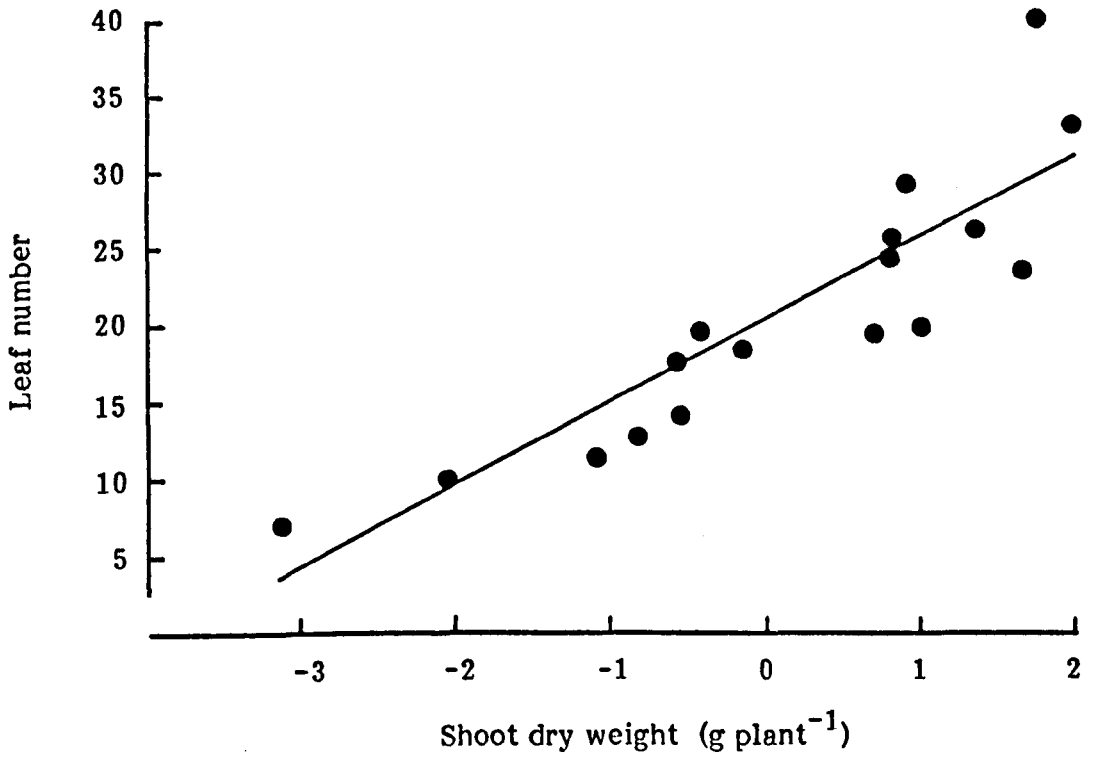

40
35
30
25
20
15
10
5
Leaf number
-3
-2
-1
0
1
2
Shoot dry weight (g plant^{-1})

Fig 4.5 Relations between leaf initiation in cv Perfection, during the predicted juvenile phase (< 14 leaves) and mature, vegetative phase (> 14 leaves), and degree days (°C > 2 °C x days) accumulated during temperature treatments at 10 (●), 15 (■) and 20 °C (▲)

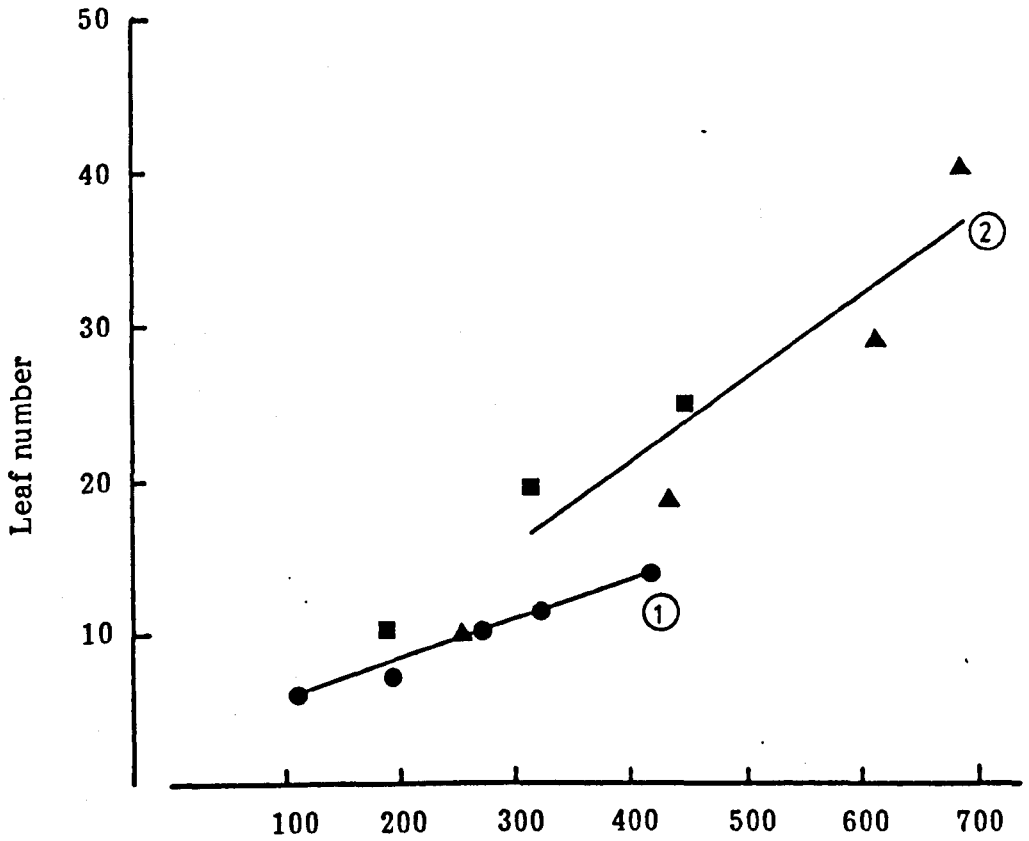
Equations for lines :

(1) $y = 3.55 + 0.02470x$

$r^2 = 0.86 \quad (p < 0.01, \text{ d.f.} = 5)$

(2) $y = -0.04 + 0.0532x$

$r^2 = 0.82 \quad (p < 0.05, \text{ d.f.} = 3)$


50
40
30
20
10
Leaf number
100
200
300
400
500
600
700
1
2
°C d > 2 °C during temperature treatments

relative to leaves 19 to 40. From the reciprocal of the slope of the regressions, 41°C d was required per leaf then, as compared with 19°C d in mature vegetative plants. The regression lines showed significant fits in each case.

Separate regression of leaf numbers in each temperature regime on accumulated degree-days also showed clear linear relationships (Fig 4.6). The slope of the regression for the 10°C plants however, was significantly less than for the 15 and 20°C regimes ($p < 0.01$), indicating a greater thermal requirement for leaf initiation in that treatment. As plants in this particular treatment were all juvenile, slower leaf initiation during juvenile development was again indicated. No significant differences in slope or intercept were apparent between regressions for 15 and 20°C plants. One line fitted to both data sets, accurately describing the linear relationship ($p < 0.01$).

Strong evidence supporting an increase in leaf initiation rate associated with phase transition was obtained from the second study, with data points close to the point of phase transition itself (Fig 4.7). Both juvenile and mature vegetative plants are represented across the accumulated temperature range (45 to 650°C d) for both treatments at 15 and 20°C.

No significant differences in thermal requirements for leaf initiation were apparent between the treatments and the change in leaf initiation rate corresponded with the stage of phase transition as shown, albeit less clearly, in Fig 4.5. Rates of leaf initiation measured in degree-days during juvenile and mature phases of vegetative growth were calculated as 50 and 18°C d per leaf respectively, giving close agreement with the figures of 41 and 19°C d derived from the preliminary study.

Fig 4.6 Leaf initiation in cv Perfection related separately to degree-days accumulated during growth at 10 (●), 15 (■) and 20 °C (▲)

Data is as described for Fig 4.5

Equations for lines :

(10 °C) $y = 2.354 + 0.02761x$

$r^2 = 0.98 \quad (p < 0.001, \text{ d.f.} = 3)$

(15 °C) $y = 0.31 + 0.05692x$

$r^2 = 0.97 \quad (p < 0.05, \text{ d.f.} = 1)$

(20 °C) $y = -8.12 + 0.0657x$

$r^2 = 0.95 \quad (p < 0.05, \text{ d.f.} = 2)$

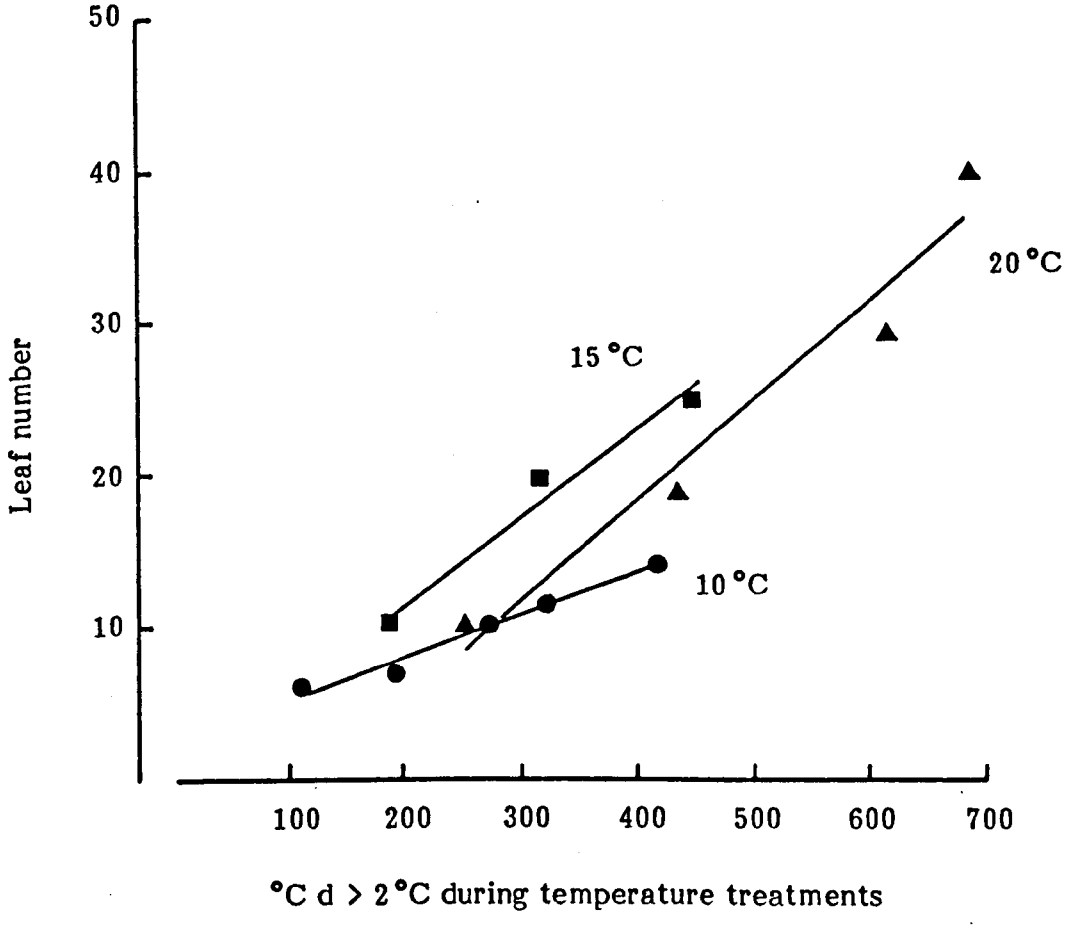

50
40
30
20
10
Leaf number
15 °C
20 °C
10 °C
100
200
300
400
500
600
700
°C d > 2 °C during temperature treatments

Fig 4.7 Relations between leaf initiation in cv Perfection and degree-days accumulated during growth at 15 (■) and 20 °C (▲)

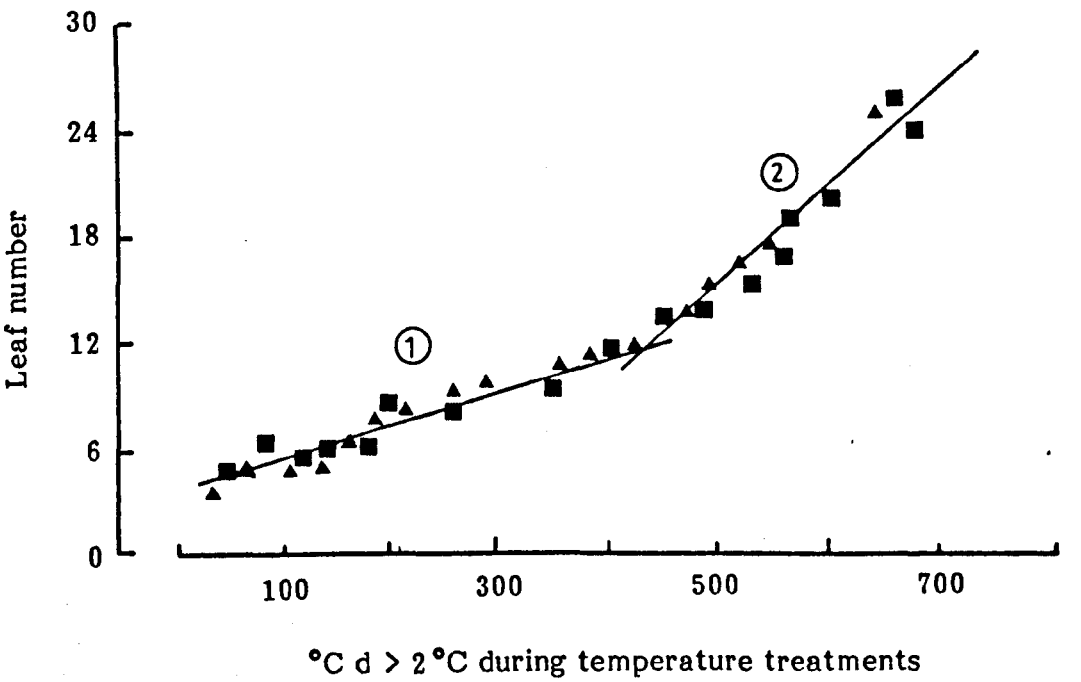
Equations for lines :

(1) $y = 3.457 + 0.019953x$

$r^2 = 0.96 \quad (p < 0.001, \text{ d.f.} = 19)$

(2) $y = -12.63 + 0.05585x$

$r^2 = 0.92 \quad (p < 0.001, \text{ d.f.} = 11)$


30
24
18
12
6
0
Leaf number
①
②
100
300
500
700
°C d > 2 °C during temperature treatments

4.4 Curd initiation in plants raised from seed chilled during germination

Distinct juvenile phases of growth in cvs Perfection and White Fox extended from cotyledon expansion to the initiation of the fourteenth and eighteenth leaves in cvs Perfection and White Fox respectively. However, chilling imbibed seeds has been reported both to accelerate curd initiation (Kato, 1964; Fujime and Hirose, 1979) or to be ineffective (Wiebe, 1972a). The response of seeds to vernalization stimuli would appear then to be dependent on cv and/or method of chilling.

The investigations described here comprised a preliminary study with cv Perfection, in which seeds were chilled at 5°C during imbibition for 2, 4 or 7 days.

Longer periods of chilling, up to a maximum of 35 days, applied both to imbibed seeds and seeds sown in compost, were incorporated into the second study which also included the cv White Fox.

The possible effects of post chilling temperatures were also considered, as warmer conditions may induce devernalization in the seedlings. Sensitivity to vernalization was assessed as leaf number beneath the curd.

4.4.1 Materials and methods

Seeds of cv Perfection comprising the first experiment were imbibed using distilled water in jars for periods of two, four or seven days. Vernalization at 5 ± 1°C was imposed using a controlled environment cabinet in which the jars were placed, in complete darkness. Distilled water used in this study had been allowed to equilibrate with the controlled

environment prior to imbibition of the seeds. The same procedure was adopted throughout with control treatments, where seeds were imbibed at 20 ± 1°C. Following imbibition for the required duration, seeds from both vernalized and control treatments were sown in compost and germinated as described in Chapter 2; germination appeared to be unaffected by the treatments. After transplanting plants were grown under standard glasshouse conditions with a mean daily temperature of 20°C. Natural glasshouse irradiance was supplemented using 400 W SON/T lamps providing an additional 65 to 70 Wm^{-2} at plant height for 16 h each day, commencing at dawn. The natural February photoperiod of approximately 11 h was therefore extended. Sensitivity to vernalization was assessed as the leaf number present at macroscopic curd visibility.

Seeds of cvs Perfection and White Fox comprising the second experiment were vernalized during imbibition, as described above, for either seven or 35 days. Control treatments comprised seven days at 20°C. In addition, seeds were vernalized having been sown directly into compost contained in polystyrene modules, with treatments as described for seeds vernalized during imbibition. Temperatures of both distilled water and compost surface were monitored periodically throughout the treatments using a digital thermometer (Digitron Instrumentation Ltd). Sequential sowings ensured that all seeds completed vernalization treatments on the same date; 13 February 1987.

On completion of temperature treatments both vernalized and control seeds from distilled water were sown individually in pots and returned to one of two glasshouses with mean daily temperatures of 16 and 21°C. Seeds vernalized in modules were similarly treated, being transplanted to pots after expansion of the cotyledons. Growth continued

under conditions of natural irradiance. Sensitivity to vernalization, as with the preliminary study, was assessed by measuring the number of leaves beneath the curd.

Plants from both studies were arranged in a completely randomised design with 12 and 9 plants per treatment, in the first and second study respectively, recorded at macroscopic curd visibility.

4.4.2 Results

4.4.2.1 Leaf number at macroscopic curd visibility No consistent effect of seed vernalization was indicated from the number of leaves beneath the curd in plants from the preliminary study. Although seeds vernalized at 5°C for seven days had significantly fewer leaves beneath the curd than control seeds imbibed at 20°C (Table 4.3) a greater difference in leaf number was evident when comparing four and seven day treatments at 20°C.

Table 4.3 Leaf number at macroscopic curd visibility in cv Perfection chilled during germination

Duration (days)	Temperature (°C)	
	5	20
2	40.1	40.3
4	39.0	36.5
7	38.5	43.6

SED = 1.52 (d.f. = 66)

Each value represents the mean of 12

Seed vernalization was shown to be equally ineffective in accelerating curd initiation when chilling treatments were imposed for up to 35 days, on seeds sown in compost (Table 4.4). Seeds vernalized during imbibition for the same duration failed to germinate. Plants grown under warmer (21°C) post-vernalization conditions initiated curds at consistently higher leaf numbers.

Table 4.4 Leaf number at macroscopic curd visibility in cvs Perfection and White Fox chilled during germination

	Method of vernalization:	Compost			Imbibition		
	Duration at 5°C (days):	0+	7	35	0+	7	35
Cultivar	Post-vernalization growing temp °C (daily mean)						
Perfection	16	25.5	27.0	29.0	26.6	28.1	—
Perfection	21	38.3	32.6	32.5	40.8	44.2	
White Fox	16	24.9	27.2	25.0	29.6	27.9	
White Fox	21	34.7	38.5	38.3	38.2	35.9	—

SED = 1.37 (d.f. = 152)

\+ = Control plants (7 days at 20°C)

4.5 Summary

1. Leaf number was shown to be a stable and accurate marker for phase transition. Competence to respond to vernalization stimuli was associated with the initiation of 14 and 18 leaves in cvs Perfection and White Fox respectively, marking the earliest point of phase transition.

2. The duration of phase change itself appeared short, lasting approximately two plastochrons.

3. Both leaf dry weight and leaf area gave inconsistent results when used as markers for phase transition under the conditions employed here. As log shoot dry weight was linearly related to leaf number however, it was anticipated that this would be a stable marker for phase transition.

4. Growth at 18 or 25°C during juvenile development had little significant effect on the subsequent curd initiation response to chilling. Pre-vernalization high temperatures (predevernalization) did not therefore appear to reduce the response to vernalization in cauliflower cvs Perfection and White Fox.

5. Rate of leaf initiation in cv Perfection increased with increasing temperature from 2 to 20°C. As further increase in temperature to 25 and 30°C caused a decline in the rate of leaf initiation, an optimum of approximately 20°C is indicated. The base temperature (T_b), at or below which no leaf initiation occurred was indicated from plants grown at 2°C. Duration of the juvenile phase, measured chronologically, was therefore shorter at higher temperatures.

6. During juvenile and early vegetative growth of cv Perfection a highly significant linear relationship was established when regressing leaf number on log shoot, dry weight, $r^2 = 0.77$ ($p < 0.001$, d.f. = 15). A relationship between leaf number and shoot dry weight during juvenile and early mature vegetative growth was therefore suggested.

7. Increase in leaf initiation rate was associated with phase transition. Leaves numbered acropetally 5 to 14 were initiated more slowly than leaves 19 to 40. No significant differences in thermal requirements for leaf initiation were apparent when comparing 15 and 20°C treatments. Rates of leaf initiation measured in degree-days (°C d > 2°C) during juvenile and mature phases were calculated as 50 and 18°C d per leaf respectively. These figures are in close agreement with those of 41 and 19°C d derived from the preliminary study.

8. Chilling imbibed seed and seed sown in compost proved to be ineffective in reducing the number of leaves initiated before the curd in both cvs Perfection and White Fox. Seeds imbibed for 35 days failed to germinate.

Chapter 5

PREDICTION OF CURD INITIATION

Introduction

Following completion of the juvenile phase, the time of curd initiation shows a quantitative response to low temperature (Chapters 3 and 4; Haine, 1959; Austin, 1968; Wiebe, 1972b, 1974, 1979; Fujime and Hirose, 1980). With the exception of Wiebe's studies (1972b, 1974 and 1975) little effort has been directed towards establishing either the range of temperatures or the duration of low temperature effective in curd induction. The spread of curd initiation time within a crop, rather than the spread of curd growth rates is thought to determine the spread of curd maturity (Salter, 1969). Temperatures experienced after completion of the juvenile phase will therefore be critical in influencing the maturity characteristics of the crop.

The purposes of the experiments described in this chapter are:

To determine the range of temperatures over which curd initiation will take place and establish the three cardinal temperatures for this process. These are the base (T_b) and maximum (T_m) temperatures below and above which the rate of progress to curd initiation is zero and the optimum temperature (T_o) at which this rate is at its maximum.

To use these cardinal temperatures in a predictive model that gives a thermal time for curd initiation (refer to Chapter 1).

To examine possible devernalizing effects of high temperature following chilling. This has previously been reported (Sadik and Ozbun, 1968; Fujime and Hirose, 1980, 1981).

To measure effects of temperature on early curd growth.

5.1 Determination of the cardinal temperatures and thermal requirements for curd initiation

The first experiment described in this chapter was designed to derive the cardinal temperatures for curd initiation and thus facilitate the calculation of a theoretical thermal time for curd initiation.

5.1.1 Materials and methods

Seeds of the cvs Perfection and White Fox were sown on 22 October 1985. Germination and general husbandry followed the methods described in section 2.1.1. Prior to experimental treatments commencing on 13 December, plants were grown under glasshouse conditions at a mean daily temperature of 20°C. Natural irradiance was supplemented with 400 W SON/T lamps, giving an additional irradiance of 60 $\pm$ 5 Wm^{-2} at plant height for 12 h each day starting at dawn. The natural October photoperiod of c. 10 h was therefore extended to 12 h.

At the end of juvenile development plants were transferred to constant temperatures of 0, 5, 7, 10, 13, 18, 20 or 25°C $\pm$ 1°C for a period of four weeks before being returned to the 20°C glasshouse. During temperature treatments plants were retained under a 12 h photoperiod at an irradiance of 50 Wm^{-2} provided by a bank of 80 W warm white fluorescent tubes supplemented by 100 W incandescent lamps. Care was

taken to ensure uniform lighting throughout the controlled environments as replication of temperature treatments was not possible. Nine plants from each cv were sampled prior to temperature treatments with a further nine from each temperature regime sampled on completion of the treatments. Effects of temperature treatments on curd induction was assessed both as the number of days to macroscopic curd visibility and the number of leaves initiated before the curd. The experiment was a completely randomised design with nine plants per cv x temperature treatment sampled on completion of temperature treatments and at macroscopic curd visibility. Regression analysis was used to describe the relationship of rate of progress towards curd initiation, measured as the reciprocal of days to macroscopic curd visibility and as reciprocals of leaf number subtending the curd.

5.1.1.1 Cardinal temperatures for curd initiation A procedure for calculating thermal time, developed by Garcia-Huidobro, Monteith and Squire (1982a) for calculating the thermal time requirements of seed germination in Pearl millet Pennisetum typhoides, is adapted here to investigate the effects of temperature on the rate of curd initiation in the summer cauliflower. The three cardinal temperatures were established as follows:

The rate of curd initiation expressed either as the reciprocal of time, $\frac{1}{t}$, days to macroscopic curd visibility or process acceleration measured as the reciprocal of leaf number subtending the curd, $\frac{1}{n}$, were regressed on controlled environment temperature (°C) as two lines. The first describing a rate increase and the second a rate decrease. The rate increasing between T_b and T_o by the same increment for each degree rise in temperature. The rate declining in a linear fashion between T_o and T_m.

T_b and T_m can be determined by extrapolation, T_o being the intercept of the regressions.

5.1.1.2 Thermal time and curd initiation The response to temperature in the range T_b to T_o can be expressed as:

$$\frac{1}{t} = \text{constant} \times (\bar{T} - T_b) \qquad \text{eqn 5.1}$$

The constant is the slope of the line and the intercept is zero if $(\bar{T} - T_b)$ is the x component, similarly at supra-optimal temperatures rate of progress can be expressed by the equation:

$$\frac{1}{t} = \text{constant} \times (T_m - \bar{T}) \qquad \text{eqn 5.2}$$

Thermal time, Θ, is the multiple of time and effective temperature. Therefore thermal time at both sub (Θ_1), and supra-optimal temperatures (Θ_2), can be represented by the equations:

$$\Theta_1 = (\bar{T} - T_b)\, t \qquad \text{eqn 5.3}$$

$$\Theta_2 = (T_m - \bar{T})\, t \qquad \text{eqn 5.4}$$

Therefore thermal time is equal to the reciprocal of the slope of the straight lines. For ease of calculation where $T > T_o$ an 'equivalent' temperature below T_o was derived mathematically for substitution into equation 5.3 (Appendix 1).

5.1.2 Results

5.1.2.1 Cardinal temperatures for macroscopic curd appearance The number of days to macroscopic curd visibility was shown to differ following four weeks at different constant temperatures in both cvs Perfection and

White Fox (Table 5.1). The rates of curd appearance at the different temperatures were given by the reciprocal of the number of days to macroscopic curd visibility. Regressing the reciprocals against temperature enabled two lines to be fitted as described in section 5.1.1.1. Points were assigned to either of the two regressions based on minimising residual variation about the fitted line. Results in Figure 5.1 a and b show T_b and T_m as the intercepts of the temperature axis when the rate is zero. T_o was estimated from the point of intersection of the two regressions.

In both cvs Perfection and White Fox the rates increased linearly with temperatures above T_b to a defined optimum T_o, then decreased linearly with temperatures above T_o reaching zero at T_m. The cardinal temperatures for curd appearance are summarised in Table 5.2.

Results from Figures 5.1a and b would suggest that curd appearance takes place over a similar range of temperatures in both cvs Perfection and White Fox. However, cv White Fox would appear to have a higher optimum temperature of 15.8°C by comparison with 12°C observed for cv Perfection. With cv White Fox representing later season cvs this result may have been anticipated. Whilst rate of attainment of macroscopic curd visibility is clearly influenced by temperature the linearity of this process is questionable, with a parabolic relationship indicated for cv Perfection (Fig 5.1a). Clearly the process of curd appearance comprises two components; curd initiation and early curd growth. Assuming a higher T_b for curd growth (refer to section 5.2) the relationship described in Fig 5.1 may be considered as incorporating two bilinear, rate temperature responses, curd growth being displaced to the right of curd initiation (Fig 5.2).

Table 5.1 Days to macroscopic curd appearance following four weeks at differing constant temperatures under controlled environment conditions in cvs Perfection and White Fox

Controlled environment temperature (°C)	Cultivar	
	Perfection	White Fox
0	110	112
5	89	105
7	87	98
10	87	94
13	85	92
18	87	89
20	93	100
25	112	108

Each figure is a mean of nine
SED = 1.8 (d.f. = 119)

Table 5.2 Cardinal temperatures for curd appearance derived from regressing rate of macroscopic curd visibility on controlled environment temperature

Cardinal temperature (°C)	Cultivar	
	Perfection	White Fox
T_b	- 4.5	- 3.5
T_o	12.0	15.8
T_m	29.5	28.3

Fig 5.1 The relationship between rate of macroscopic curd appearance and temperature following four weeks at different constant temperatures in cvs Perfection (a) and White Fox (b)

(a)

(1) $y = 0.009415 + 0.00025x$

$r^2 = 0.85 \quad (p < 0.05, \text{ d.f.} = 2)$

(2) $y = 0.01524 + -0.0002387x$

$r^2 = 0.87 \quad (p < 0.05, \text{ d.f.} = 2)$

(b)

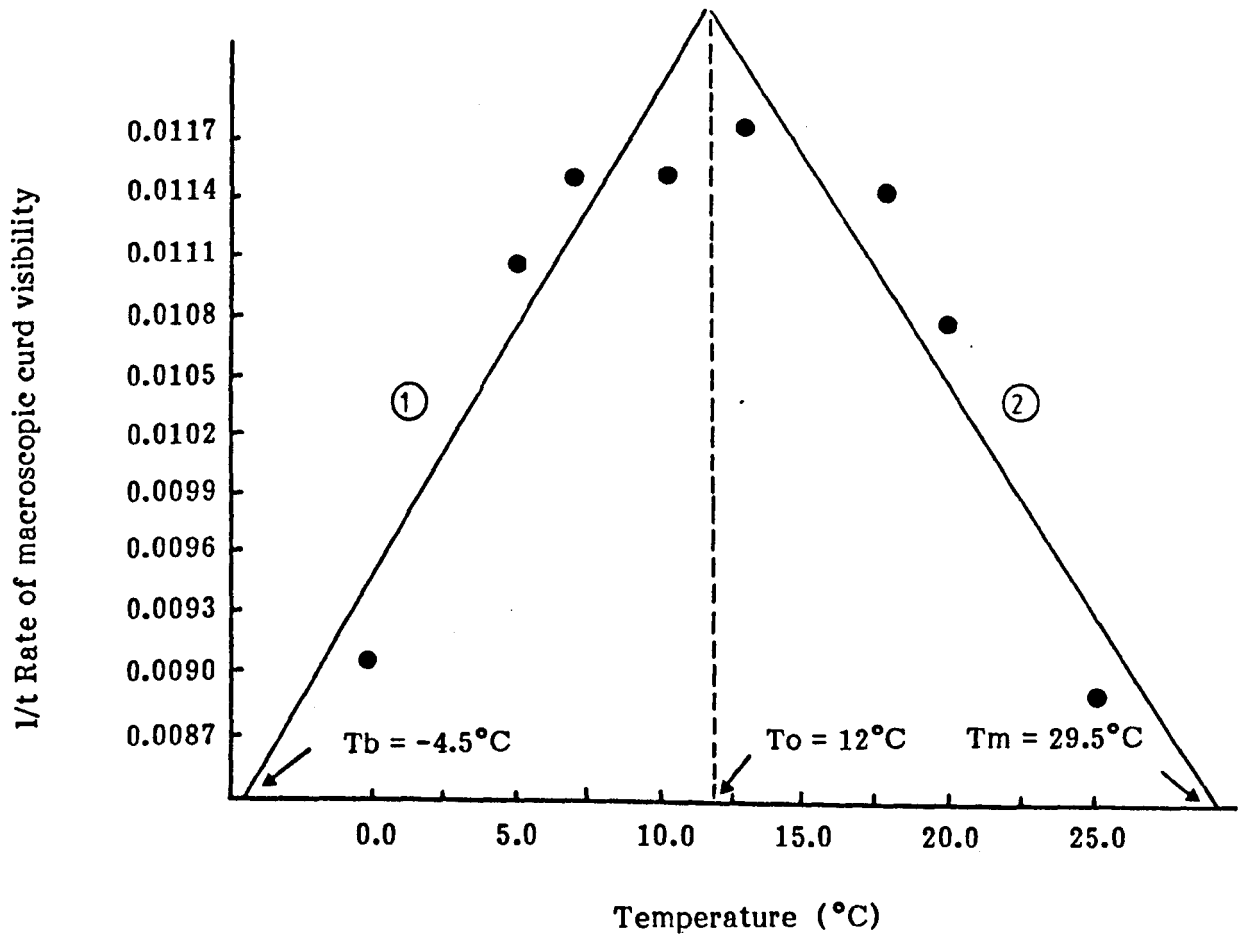
(1) $y = 0.008897 + 0.0001572x$

$r^2 = 0.97 \quad (p < 0.01, \text{ d.f.} = 3)$

(2) $y = 0.01526 + -0.000244x$

$r^2 = 0.84 \quad (p < 0.05, \text{ d.f.} = 1)$

(a)


1/t Rate of macroscopic curd visibility
0.0117
0.0114
0.0111
0.0108
0.0105
0.0102
0.0099
0.0096
0.0093
0.0090
0.0087
①
②
Tb = -4.5°C
To = 12°C
Tm = 29.5°C
0.0
5.0
10.0
15.0
20.0
25.0
Temperature (°C)

(b)

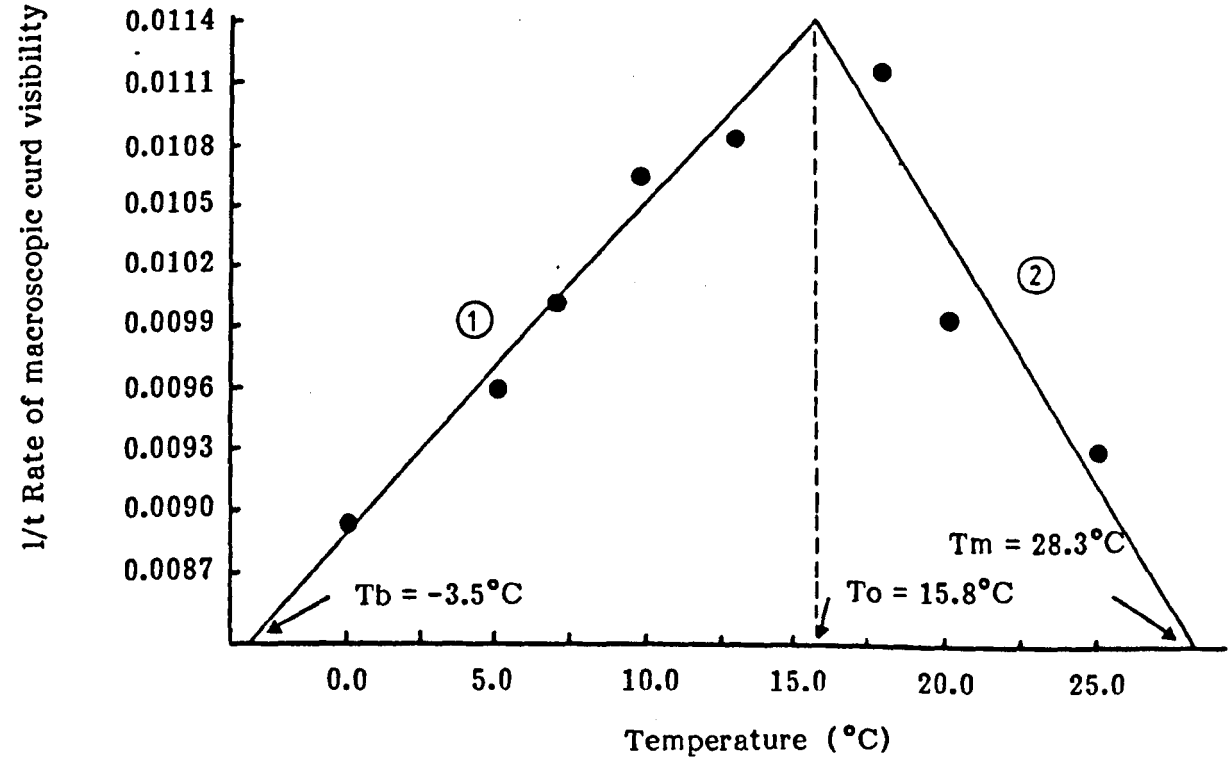
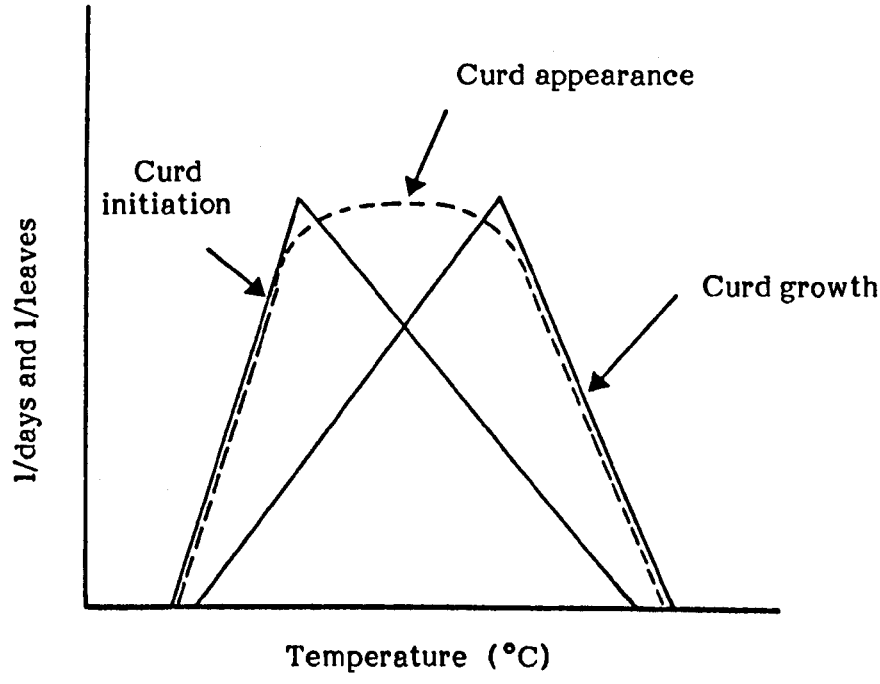

1/t Rate of macroscopic curd visibility
0.0114
0.0111
0.0108
0.0105
0.0102
0.0099
0.0096
0.0093
0.0090
0.0087
①
②
Tb = -3.5°C
To = 15.8°C
Tm = 28.3°C
0.0
5.0
10.0
15.0
20.0
25.0
Temperature (°C)

Fig 5.2 Hypothetical relationship between the thermal responses of curd appearance, curd initiation and curd growth



5.1.2.2 Cardinal temperatures for curd initiation Leaf number below the curd was shown to differ between controlled environment temperature treatments (Table 5.3). Four weeks at 0°C or 25°C resulted in leaf numbers of 35 and 54 respectively, initiated before the curd in cv Perfection. This compared with leaf numbers of 48 and 41 for plants of the cv White Fox under the same treatments. Minimum leaf numbers of 15.5 and 19.6 were recorded in cvs Perfection and White Fox respectively following four weeks' treatment at 5 and 7°C. Reciprocal of leaf number ($\frac{1}{n}$) initiated before the curd indicated the degree to which curd initiation was accelerated by the different temperatures. Regression of $\frac{1}{n}$ on temperature enabled an estimate of the cardinal temperatures for vernalization and curd initiation in cvs Perfection and White Fox (Fig 5.3a and b), summarised in Table 5.4.

5.1.2.3 Thermal time for curd initiation The relationship between leaf number subtending the curd and thermal time accumulated during controlled environment treatments gives an indication of the thermal requirement for curd initiation. Regression of final leaf number for cv Perfection on thermal time accumulated over a T_b of -1.25 (Fig 5.2a and Table 5.4) was accurately described by a quadratic curve, $r^2 = 0.97$; $p < 0.001$ (Fig 5.4a). Reduction in leaf number below the curd was therefore seen to require a longer thermal time of vernalization for leaves 21 to 16 (numbered acropetally) than for leaves 42 to 29. Figures of 13.0°C d and 2.2°C d were estimated as the thermal requirement to accelerate curd initiation by one leaf over the ranges 21 to 16 and 42 to 29 leaves respectively. Estimates were based on fitted lines one and two in Figure 5.4a. This observation is consistent with cv Perfection having a

Table 5.3 Leaf number below the curd following four weeks at constant temperatures under controlled environment conditions in cvs Perfection and White Fox

Controlled environment temperature (°C)	Cultivar	
	Perfection 15 ± 0.24*	White Fox 19 ± 0.22*
0	35.0	48.1
5	15.5	26.3
7	15.9	20.8
10	17.6	19.6
13	20.8	22.0
18	29.2	29.6
20	42.6	40.4
25	53.9	40.4

SED = 1.71 (d.f. = 119)

* Figures represent leaf numbers at the start of constant temperature treatments ± S.E.

Table 5.4 Cardinal temperatures for curd initiation derived from regressing reciprocal of leaf number before the curd on controlled environment temperature

Cardinal temperature (°C)	Cultivar	
	Perfection	White Fox
T_b	- 1.25	- 3.0
T_o	5.5	8.6
T_m	23.5	31.5

Fig 5.3 The relationship between reciprocal of leaf number and temperature following four weeks at different constant temperatures in cvs Perfection (a) and White Fox (b)

(a)

(1) $y = 0.02857 + 0.0071889x$

$r^2 = 1.0$ (d.f. = 0)

(2) $y = 0.08196 + -0.002664x$

$r^2 = 0.98$ ($p < 0.001$, d.f. = 4)

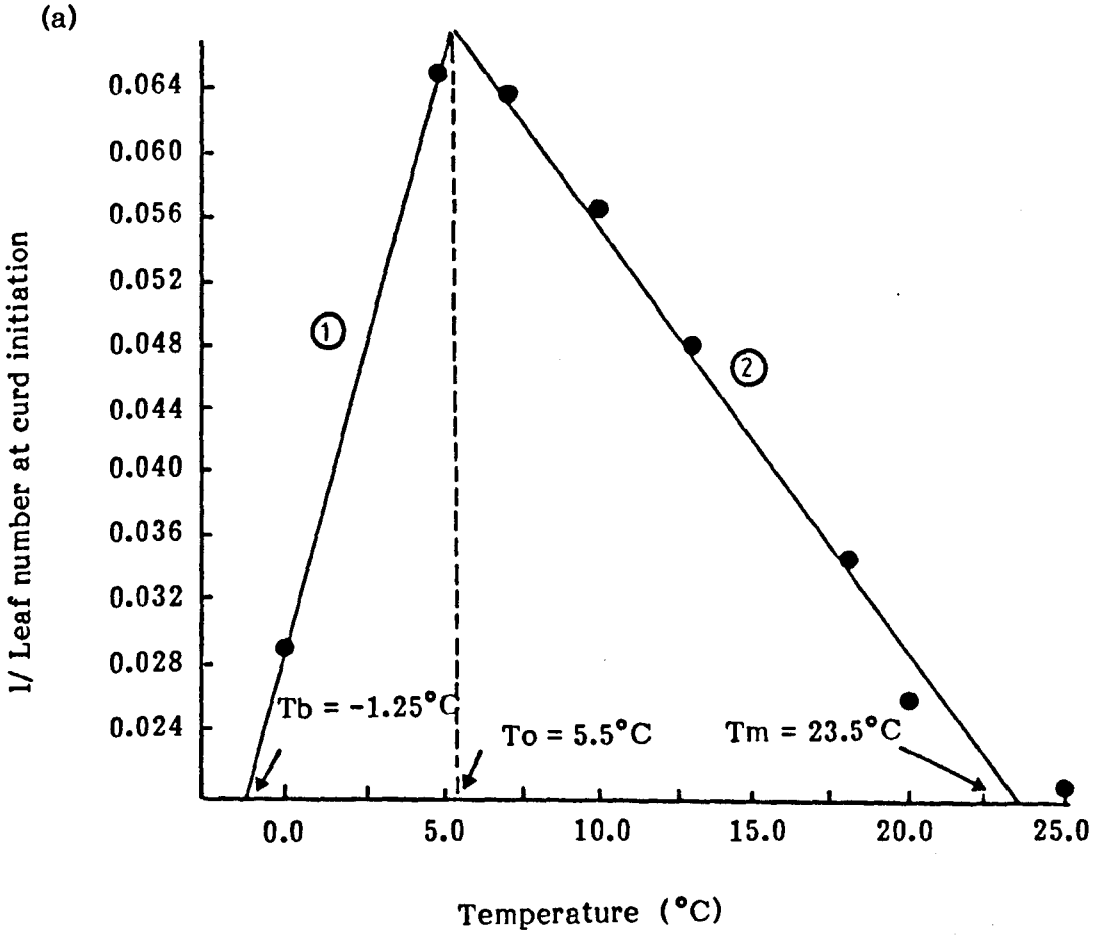
(b)

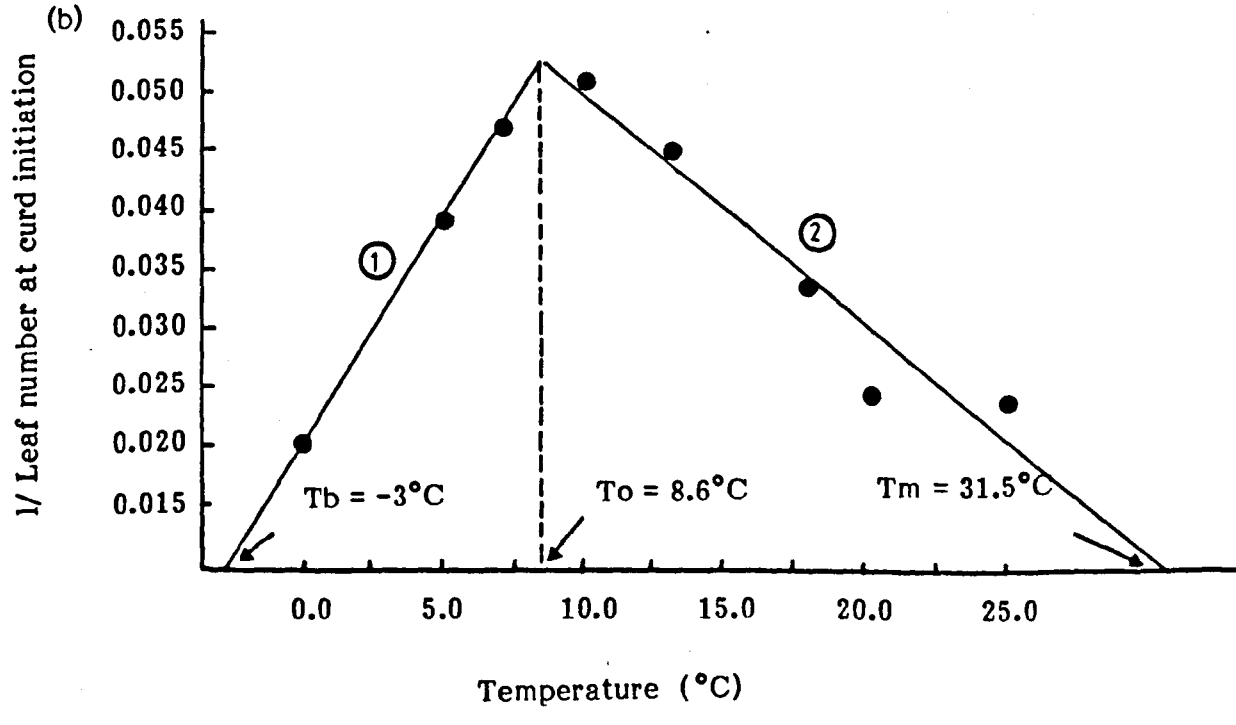
(1) $y = 0.02036 + 0.003821x$

$r^2 = 0.99$ ($p < 0.05$, d.f. = 1)

(2) $y = 0.06943 + -0.001945x$

$r^2 = 0.91$ ($p < 0.05$, d.f. = 3)


(a)
1/ Leaf number at curd initiation
0.064
0.060
0.056
0.052
0.048
0.044
0.040
0.036
0.032
0.028
0.024
①
②
Tb = -1.25°C
To = 5.5°C
Tm = 23.5°C
0.0
5.0
10.0
15.0
20.0
25.0
Temperature (°C)


(b)
1/ Leaf number at curd initiation
0.055
0.050
0.045
0.040
0.035
0.030
0.025
0.020
0.015
①
②
Tb = -3°C
To = 8.6°C
Tm = 31.5°C
0.0
5.0
10.0
15.0
20.0
25.0
Temperature (°C)

quantitative requirement for low temperature whereby older plants are able to initiate curds either without or with little cold stimulus. In contrast to cv Perfection, the relationship in cv White Fox between leaf number subtending the curd and thermal time of vernalization was shown to be linear, $r^2 = 0.92$, $p < 0.001$ (Fig 5.4b). Thermal time required in this case for decreasing the number of leaves initiated before the curd was therefore constant over the range of 19 to 48 leaves measured here, with 8.1°C d required per leaf, determined from the reciprocal of the slope (Fig 5.4b).

Regression of the number of days to macroscopic curd appearance on thermal time for cvs Perfection and White Fox (Fig 5.5a and b), showed a thermal time of 17.3°C d required to reduce the number of days to macroscopic curd appearance by one in cv White Fox, under the conditions employed here. In the case of the cv Perfection it was considered that the distribution of data points on the curve (Fig 5.5a) made approximation of the response, by fitting linear regressions unjustified. A precise measure of the thermal time requirement for reducing the time to macroscopic curd appearance in cv Perfection was therefore not made. However, the same trend was displayed as observed when regressing leaf number on thermal time (Fig 5.4a); the thermal requirement increasing with successive reductions in the number of days to curd appearance.

A thermal sum could be calculated from the end of juvenility (commencement of temperature treatments) to curd initiation using equation 5.3

$$\Theta_1 = (\overline{T} - T_b)\, t \qquad \text{eqn 5.3}$$

Fig 5.4 The relationship between leaf number subtending the curd and thermal time (°C d) accumulated during controlled environment conditions for cvs Perfection (a) and White Fox (b)

Equation of curve :

(a) $y = 51.52 + -0.430x + 0.001298x^2$

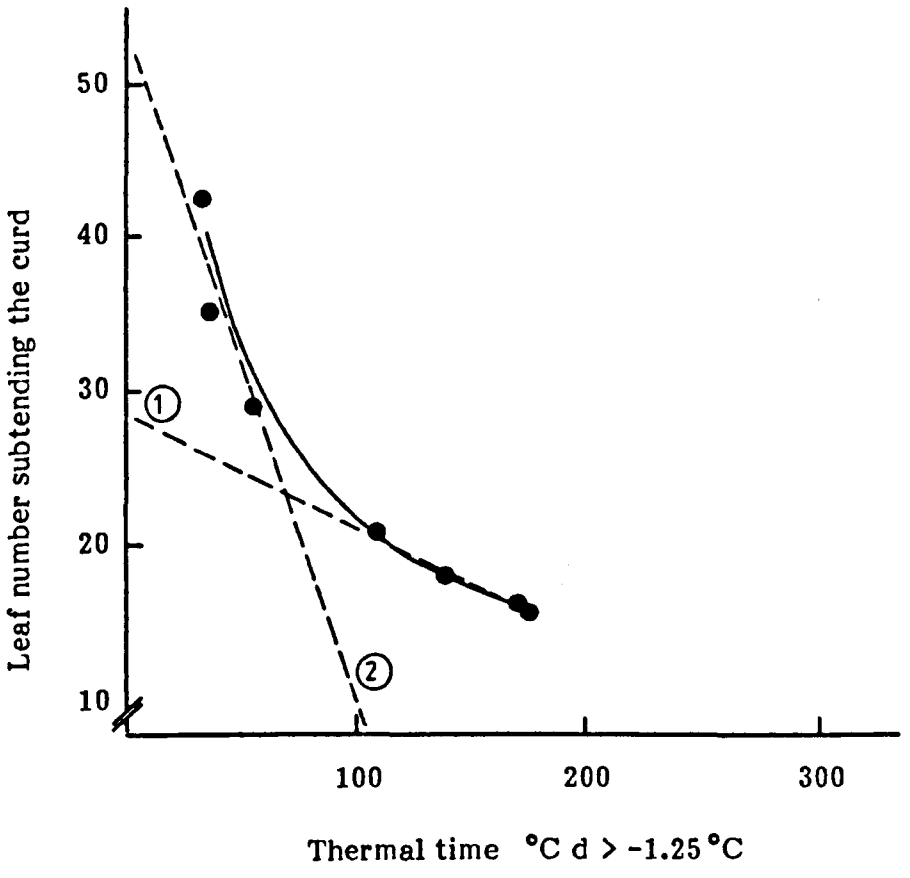
$r^2 = 0.97 \quad (p < 0.001, \text{ d.f.} = 5)$

(b) $y = 55.35 + -0.1239x$

$r^2 = 0.92 \quad (p < 0.001, \text{ d.f.} = 6)$

Refer to text for explanation of hatched lines

(a)


Leaf number subtending the curd
50
40
30
20
10
1
2
100
200
300
Thermal time °C d > -1.25 °C

(b)

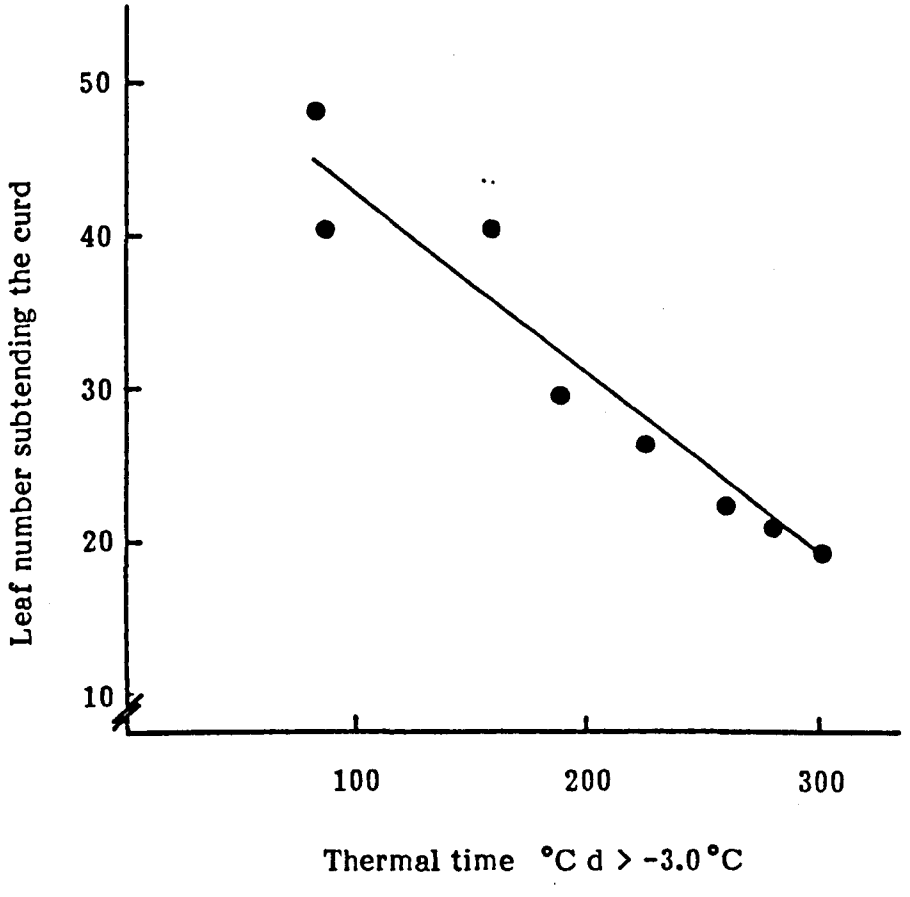

Leaf number subtending the curd
50
40
30
20
10
100
200
300
Thermal time °C d > -3.0 °C

Fig 5.5 The relationship between number of days to macroscopic curd visibility and thermal time (°C d) accumulated during controlled environment conditions for cvs Perfection (a) and White Fox (b)

(a)

$$y = 147 + -0.3299x + 0.0004389x^2$$

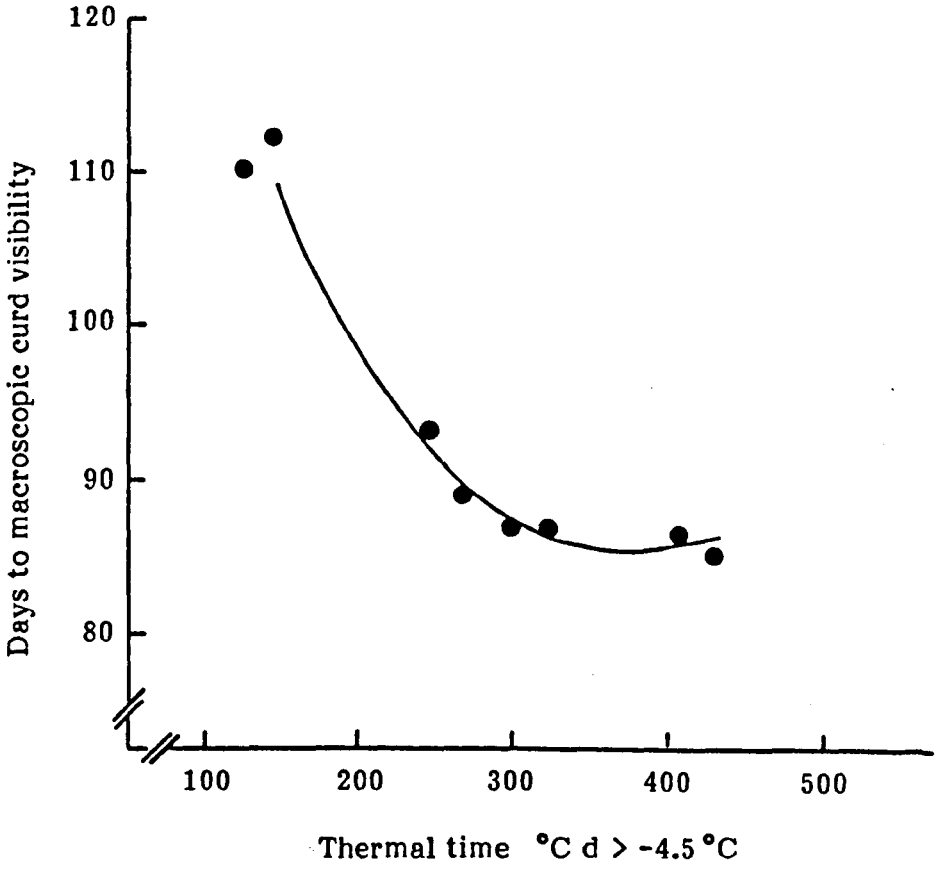
$$r^2 = 0.97 \quad (p < 0.01, \text{ d.f.} = 5)$$

(b)

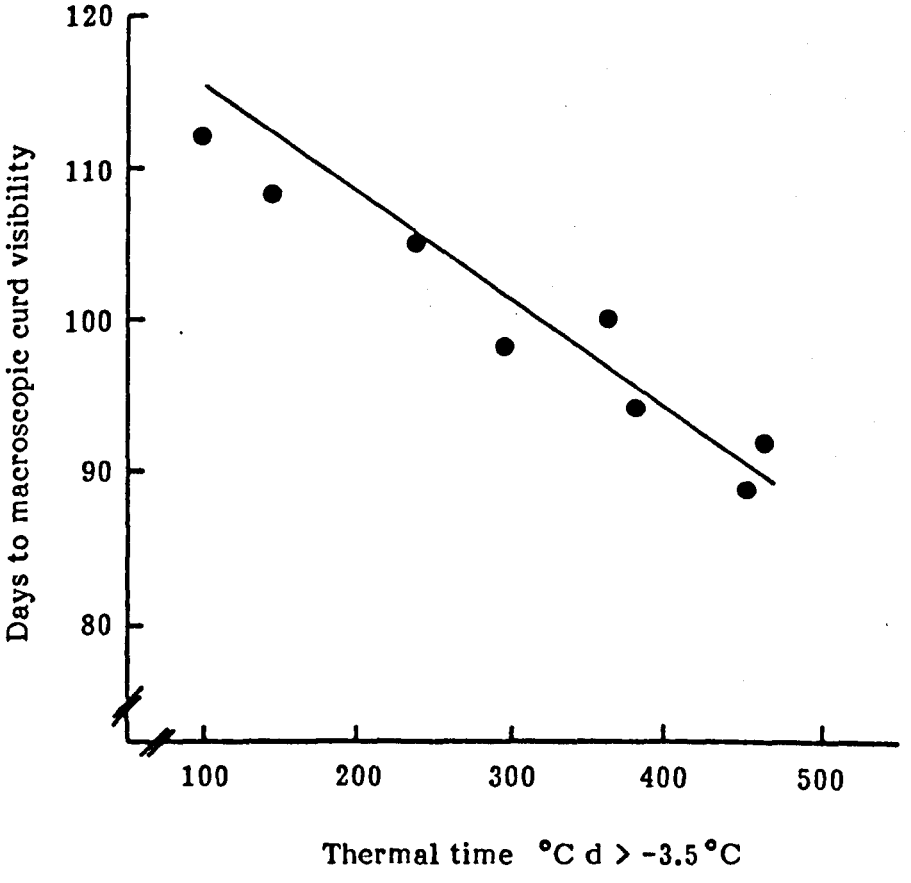
$$y = 117.29 + -0.05786x$$

$$r^2 = 0.92 \quad (p < 0.001, \text{ d.f.} = 6)$$

(a)


120
110
100
90
80
Days to macroscopic curd visibility
100
200
300
400
500
Thermal time °C d > -4.5 °C

(b)


120
110
100
90
80
Days to macroscopic curd visibility
100
200
300
400
500
Thermal time °C d > -3.5 °C

This will give:

for cv White Fox: Θ_{WF} = 280 to 310°C d

for cv Perfection: Θ_{p} = 170 to 175°C d

In both cvs White Fox and Perfection additional leaves were initiated before the curd in sub-optimal and supra-optimal temperature treatments (Tables 5.5 and 5.6). The relationship between leaf number below the curd and thermal time (Fig 5.4a and b) was used to estimate the thermal time of vernalization that had elapsed during the initiation of those further leaves. This procedure is described first for cv White Fox.

Plants of cv White Fox grown at 10°C for four weeks produced the minimum 19 leaves before the curd (Table 5.5); this was taken as the base from which to calculate elapsed thermal time. At 18°C, curd initiation occurred after the production of 29 leaves, showing a delay of 10 leaves. Using the figure of 8.1°C d required per leaf to increase or decrease leaf number below the curd, an additional 81.0°C d was added to the 187°C d already accumulated during the 4 weeks treatment (Table 5.5). This resulted in a total thermal time of vernalization of 268°C d for curd initiation at 18°C. The mean total thermal time of vernalization derived in this way from the four individual temperature regimes was 283 $\pm$ 7.4°C d in cv White Fox under controlled environment conditions.

A similar procedure was adopted for cv Perfection. The linear regressions, represented by hatched lines (Fig 5.4a) described earlier, gave an approximation of thermal time of vernalization required per leaf over the ranges 21 to 16 leaves and 42 to 29 leaves of 13.0°C d and 2.2°C d respectively.

Table 5.5 Calculation of a theoretical thermal time for curd initiation in cv White Fox using degree-days (°C d) accumulated under controlled environment conditions

Controlled environment temperature (°C)	Equivalent temp when $\bar{T} > T_o$ (T_o = 8.6°C)	Thermal time (°C d) during 4 wks t'ment (T_b = -3°C)	Leaf number after 4 wks treatment	Apical status*	Corrected thermal time (°C d)
0	0	84	22	9V	-
5	5	224	23	9V	-
7	7	280	20	2V7T	288
10	7.75	301	19	9R	301
13	6.22	258	22	9R	274
18	3.67	187	29	9R	268
20	2.66	158	41	9V	-
25	0.12	87	41	9V	-

* Number of plants from sample of nine, Vegetative (V), Transitional (T) or Reproductive (R)

Table 5.6 Calculation of a theoretical thermal time for curd initiation in cv Perfection using degree-days (°C d) accumulated under controlled environment conditions

Controlled environment temperature (°C)	Equivalent temp when $\bar{T} > T_o$ (T_o = 5.5°C)	Thermal time (°C d) during 4 wks t'ment (T_b = -1.25°C)	Leaf number after 4 wks treatment	Apical status*	Corrected thermal time (°C d)
0	0	35	16	9V	-
5	5	175	16	9R	175
7	4.83	170	16	9R	170
10	3.72	139	17	9R	152
13	2.60	108	21	9R	173
18	0.75	56	27	9R	164
20	0.014	35	37	9R	191
25	$-1.8 > T_b$	-	51	9V	-

* Number of plants from sample of nine, Vegetative (V), Transitional (T) or Reproductive (R)

Considerable scatter of data points for cv Perfection was accounted for by the fitting of these lines, with $r^2 = 0.97$ ($p < 0.05$) for line one and $r^2 = 0.68$ ($p < 0.05$) for line two. Although the probability of attaining line two by chance was high ($p < 0.05$), owing to the presence of only three points (d.f. = 1), it was considered to represent a good approximation. Where the leaf number subtending the curd was greater than the minimum of 16 recorded for cv Perfection (Table 5.6), the thermal time of vernalization was calculated as described for White Fox. The mean of these six figures indicated a thermal time from the end of juvenility to curd initiation of 171 ± 5.3°C d for cv Perfection under controlled environment conditions.

5.1.3 Thermal time for curd initiation under field conditions

Using thermal time of vernalization derived from the controlled environment studies the predicted thermal time for curd initiation at a specific leaf number was compared with the actual figure measured in field grown plants. This was restricted to cv White Fox only, as sufficient field data for cv Perfection were not available.

5.1.3.1 Materials and methods Plants of cv White Fox were transplanted at two sites; Kirton Experimental Horticulture Station, Lincolnshire (latitude 52.8° N) and the Institute of Horticultural Research, Wellesbourne, Warwickshire (52.2° N) on four dates at known numbers of leaves initiated (Table 5.7). Trial sites were located on silty soil and sandy loam at Kirton and Wellesbourne respectively. At approximately 10 day intervals 10 plants were sampled at random, dissected and both leaf number and time of curd initiation (apical diameter reaching 0.6 mm) determined using a binocular microscope (Chapter 2).

Table 5.7 Thermal time of vernalization and leaf number at curd initiation in cv White Fox under field conditions

Site	Transplanting date	Leaf number at transplanting	Leaf number at curd initiation	Thermal time to curd initiation
Kirton	(1) 27.2.85	11	28	263
	(2) 3.5.85	11	23	71
	(3) 7.6.85	12	28	82
	(4) 18.7.85	17	30	124
Wellesbourne	(1) 20.3.85	13	28	262
	(2) 7.5.85	9	22	51
	(3) 10.6.85	8	26	72
	(4) 16.7.85	11	24	93

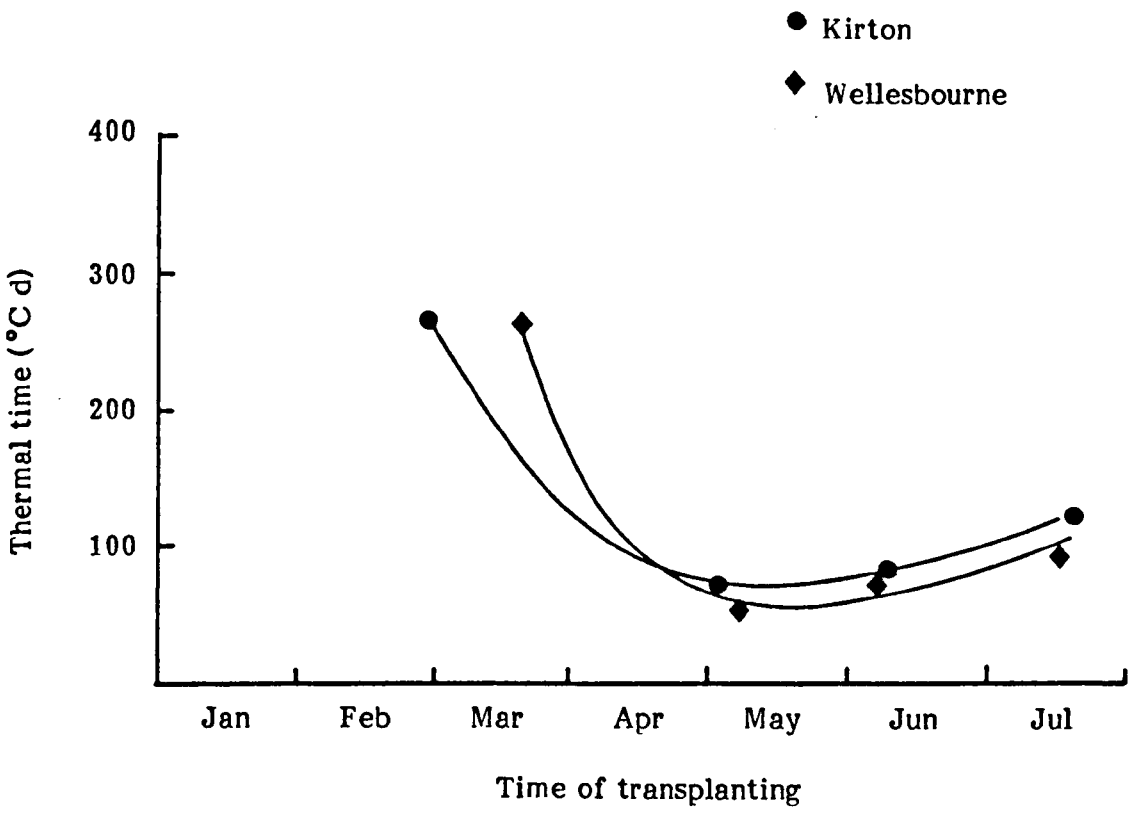
Thermal time of vernalization accumulated from the end of the juvenile phase (18 leaves) to the time of curd initiation (apical diameter of 0.6 mm) was calculated for cv White Fox using the response described in Figure 5.3b. Thermal time measured in the field could then be compared with the thermal time for curd initiation at the same leaf number estimated previously under controlled environment regimes.

5.1.3.2 Results Thermal times for curd initiation measured under field conditions from the first transplantings at both field sites were very close to those predicted from controlled environment studies. Curds were initiated after 28 leaves and a thermal time of 262°C d and 263°C d at Wellesbourne and Kirton respectively (Table 5.7), with 268°C d predicted for 29 leaves from controlled environment studies (Table 5.5).

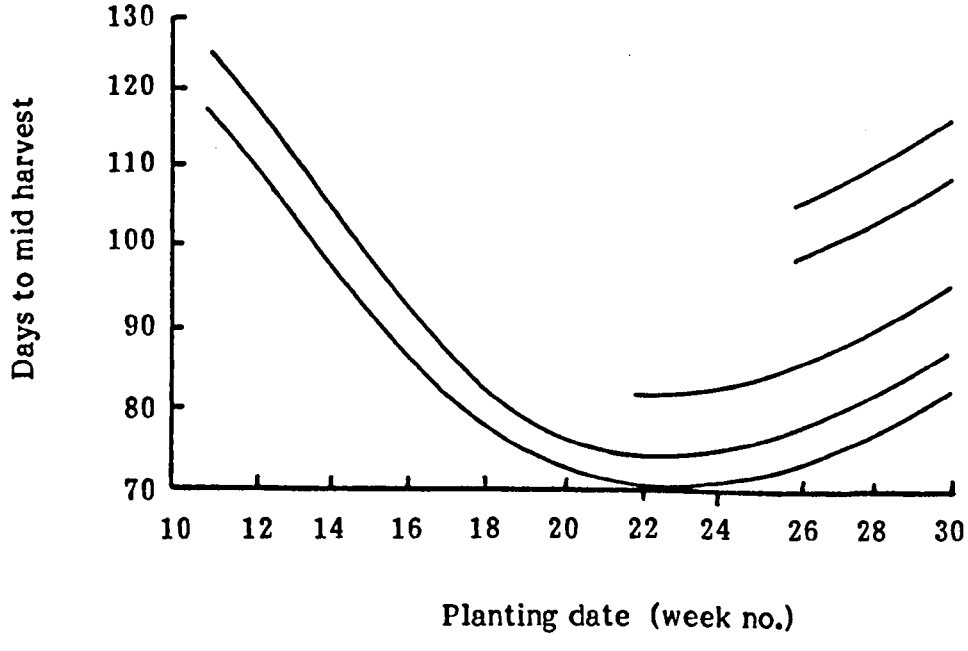
The thermal time of vernalization required for curd initiation at later transplanting dates however was much less than predicted (Table 5.7), with the same trend exhibited at both field sites (Fig 5.6a). The trend was for a sharp decline in thermal time from March to May and then a slight increase from May to July. This may indicate an interaction between the 'cold' requirement and other climatic variables, particularly light. Increased irradiance has in a preceding experiment (section 3.2) been shown to accelerate curd initiation. Light levels employed in the controlled environment rooms during the thermal time determinations were approximately 66% of those in the field for early transplantings but only 27 to 35% of those for later dates.

The curves relating thermal time to time of transplanting at both sites (Fig 5.6a) display the same trend as curves describing cauliflower maturity characteristics (Fig 5.6b) derived from the number of days to mid-

Fig 5.6 (a) Thermal time accumulated from the end of juvenility to curd initiation in cv White Fox grown under field conditions at two sites



(b) Cauliflower maturity characteristics (after Martin, 1985)



harvest plotted against planting date (Martin, 1985). Possible explanations for these trends are discussed later in Chapter 8.

5.2 Post-chilling effects of temperature on curd initiation and early curd growth

The objectives of the experiment described here were twofold, the first being the establishment of a relationship between curd growth and temperature. Characterisation of this relationship should enable both the time of curd initiation to be determined by extrapolation back from macroscopic curd appearance, and allow the time of curd maturity to be predicted. These possibilities are considered here.

A second consideration was that sustained periods of high temperature, c. 25°C, may reduce the effectiveness of preceding inductive conditions. When attempting to develop a predictive model for the effect of low temperature on curd initiation such responses may be important. Partial devernalization has previously been reported for cauliflowers grown under conditions of alternating low and high temperature days (Fujime and Hirose, 1980 and 1981).

However, despite the intercalation of high temperature the inductive effect of low temperature was considered to be additive (Fujime and Hirose, 1980).

5.2.1 Materials and methods

Seeds of the cv Perfection were sown on 8 October 1985. Germination and general husbandry followed the methods described in section 2.1.1. Prior to experimental treatments commencing on 28 November, plants were grown under glasshouse conditions at a mean daily

temperature of 20°C. Natural glasshouse irradiance was supplemented with 400 W SON/T lamps, providing an additional irradiance of 60 ± 5 Wm^{-2} at plant height for 12 h each day commencing at dawn. The natural October photoperiod of c. 10 h was therefore extended to 12 h. On 28 November, having completed juvenile development (Chapter 4) plants were transferred to vernalizing conditions in a growth room, comprising four weeks at a constant 5°C. On completion of vernalization plants were distributed between seven post chilling temperatures, 5, 7, 10, 13, 18, 20 or 25°C.

During vernalization and post vernalization temperature treatments plants were retained under a 12 h photoperiod at an irradiance of 50 Wm^{-2} provided by a bank of 80 W warm white fluorescent tubes supplemented by 100 W incandescent lamps. As with the preceding study (section 5.1) care was taken to ensure uniform lighting throughout the controlled environments as replication of temperature treatments was not possible. Nine plants were sampled following chilling to determine both leaf number and apical status. A further 5 plants were sampled from each post chilling temperature treatment after four and six weeks had elapsed. Leaf number was again determined. Curd growth was measured by recording both curd diameter (taken as the mean of two measurements of diameter at 90° to each other) and curd fresh weight. The experiment was a completely randomised design with 9 plants sampled following chilling, an additional 10 plants being sampled from post chilling temperature treatments as described above.

5.2.2 Results

Post-chilling temperatures of 20°C and 25°C significantly increased the leaf number before the curd when compared with effects of

temperatures over the range 5°C to 18°C which were shown not to differ significantly (Table 5.8). This suggested that partial devernalization had occurred and is therefore consistent with the theoretical maximum temperature (T_m) for vernalization in cv Perfection of 23.5°C, derived in the preceding section (Fig 5.3, Table 5.4).

Curd morphology was clearly influenced by post-chilling temperature conditions. Highly bracteate curds were formed after four weeks' growth at 20°C (curd B, Plate 2). With further increase in temperature to 25°C the development of vegetative characteristics was more pronounced, the number of green bracts increasing markedly.

Curd size measured both as curd diameter and curd fresh weight increased significantly ($p < 0.001$) with temperature in the range 5 to 13°C (Table 5.8). A particularly marked increase in growth was associated with plants at 13°C, with the maximum curd diameter of 70.0 mm and curd fresh weight of 51.38 g attained after six weeks' growth. Further increase in post-chilling temperature to 20 and 25°C resulted in a decrease in both curd diameter and curd fresh weight (Table 5.8).

Relative changes in both curd diameter and fresh weight (Log_e), were adequately described by quadratic functions when regressed on thermal time over a base temperature (T_b) of 2°C (Fig 5.7a and b). Similar curves would be expected as curd diameter and curd fresh weight were highly correlated ($r^2 = 0.92$) under the conditions employed here. The decline in relative growth rate above c. 500°C d was probably associated with these pot-grown plants reaching the limit of their potential for curd growth.

Prolonged exposure to temperatures in the range 18 to 25°C is unlikely under field conditions owing to diurnal fluctuations in temper-

Table 5.8 Effect of post-chilling temperature on curd growth and leaf number before the curd

Temperature (°C)	Curd diameter mm		Curd fresh weight g		Leaf number (23 ± 1.2)*	
Duration:	4 wks	6 wks	4 wks	6 wks	4 wks	6 wks
5	1.4	12.2	0.004	0.53	24	25
7	3.7	12.0	0.02	0.84	25	27
10	7.7	11.8	0.09	0.89	27	26
13	55.2	70.0	15.32	51.38	27	26
18	50.9	65.4	28.29	47.63	27	26
20	44.4	62.6	13.47	31.98	32	34
25	42.1	57.6	15.42	27.92	31	30

SED curd diameter = 1.29 (d.f. = 55)
SED curd fresh weight = 1.156 (d.f. = 55)
SED leaf number = 1.6 (d.f. = 55)

* Figure in parenthesis represents leaf number at commencement of chilling

Plate 2 Curd morphology as influenced by four weeks' growth at different post-chilling temperatures

Four weeks at :

(A) 25°C (B) 20°C

(C) 10°C (D) 13°C

 = 1 cm

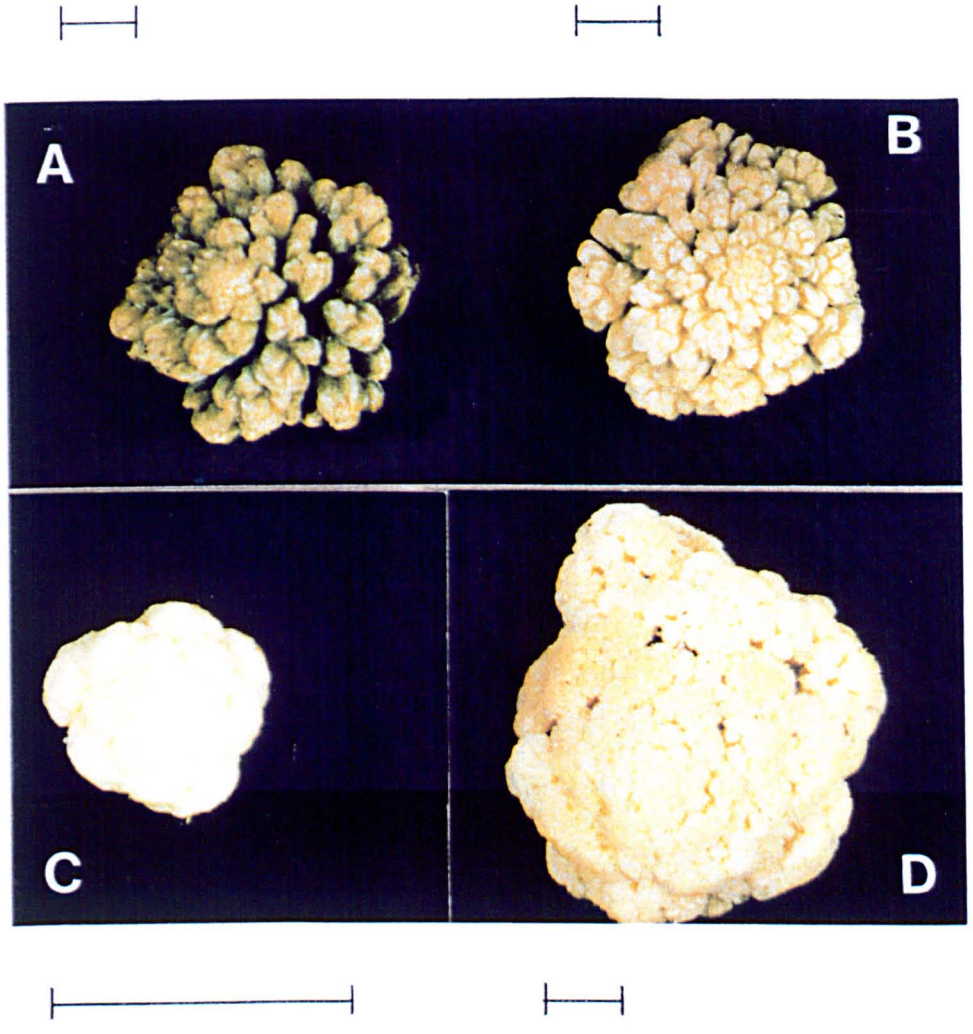

A
B
C
D

Fig 5.7 Regression of Log_e curd diameter (a) and Log_e curd fresh weight (b) on thermal time °C d > 2 °C for cv Perfection grown at a constant 5 °C to 25 °C under controlled environment conditions

(a)

$$y = 0.236 + 0.01139x + -0.00000798x^2$$

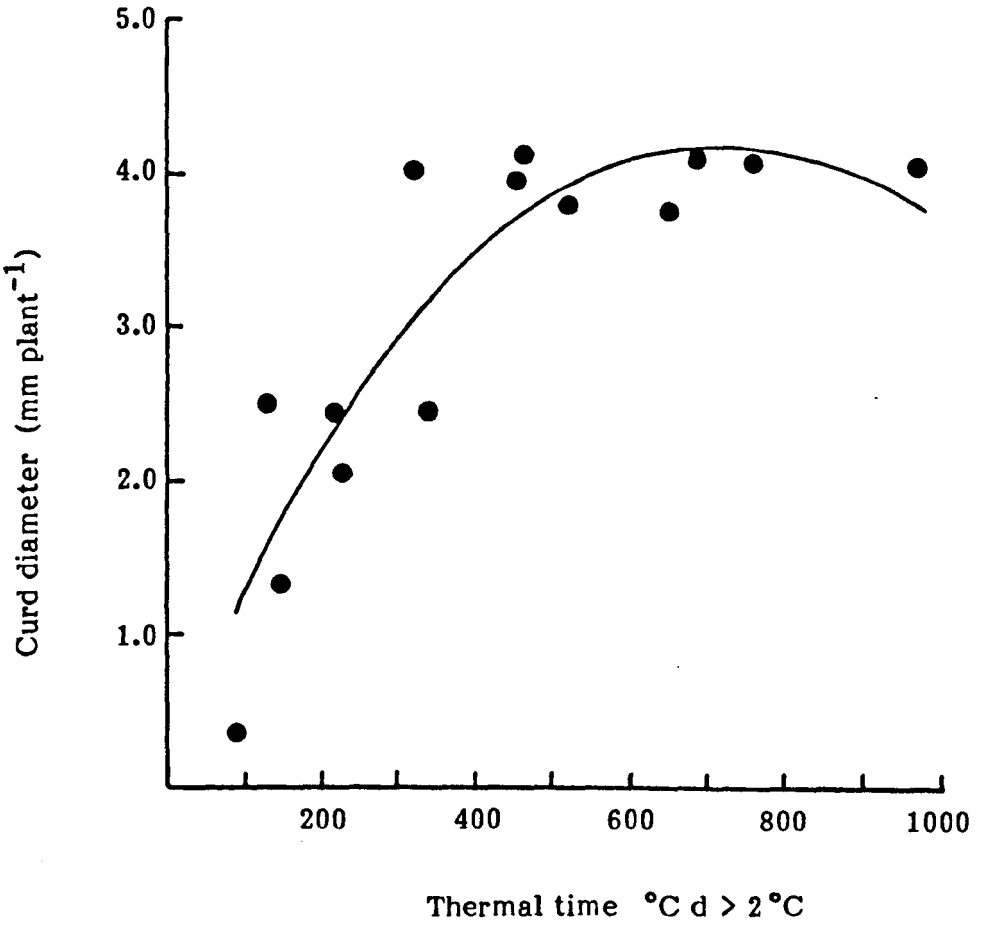
$$r^2 = 0.80 \quad (p < 0.001, \text{ d.f.} = 11)$$

(b)

$$y = -6.37 + 0.02926x + -0.00002056x^2$$

$$r^2 = 0.82 \quad (p < 0.001, \text{ d.f.} = 1)$$

(a)


5.0
4.0
3.0
2.0
1.0
Curd diameter (mm plant^{-1})
200
400
600
800
1000
Thermal time °C d > 2°C

(b)

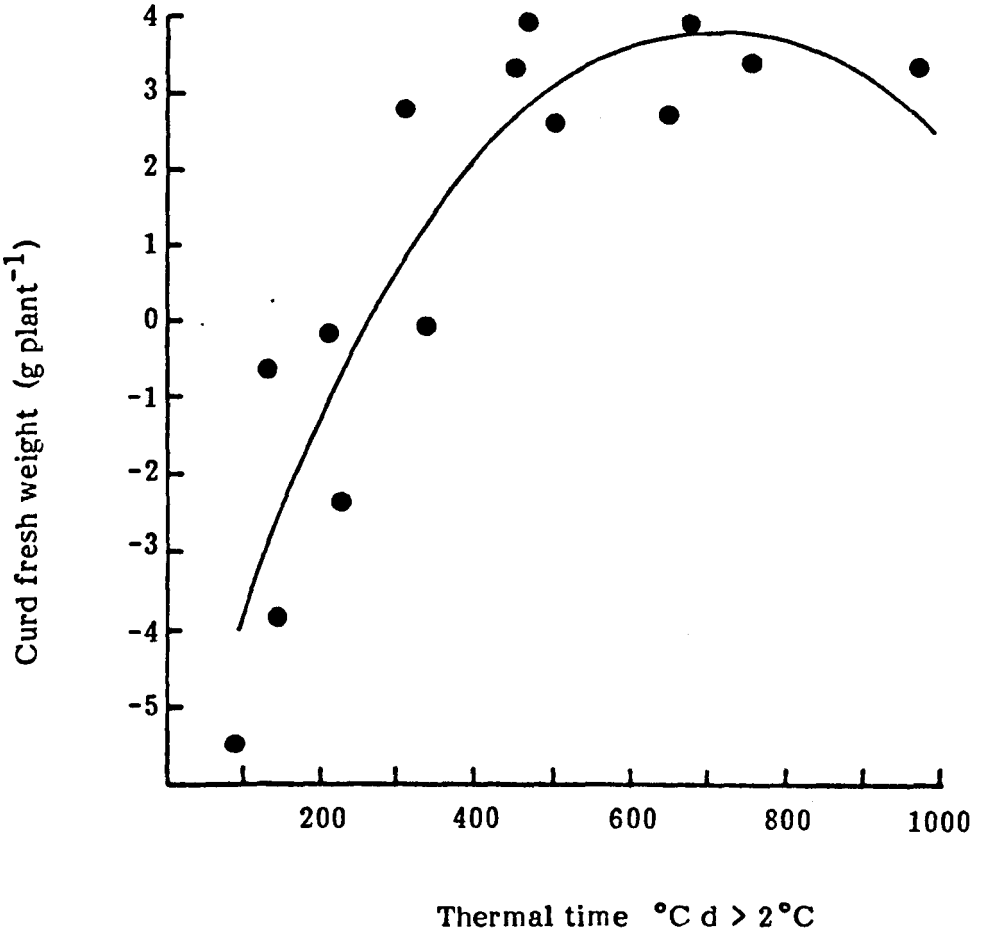

4
3
2
1
0
-1
-2
-3
-4
-5
Curd fresh weight (g plant^{-1})
200
400
600
800
1000
Thermal time °C d > 2°C

Fig 5.8 Regression of Log_e curd diameter (a) and Log_e curd fresh weight (b) on thermal time °C d > 2 °C for cv Perfection grown at a constant 5 °C to 13 °C under controlled environment conditions

(a)

$$y = 0.433 + 0.00846x$$

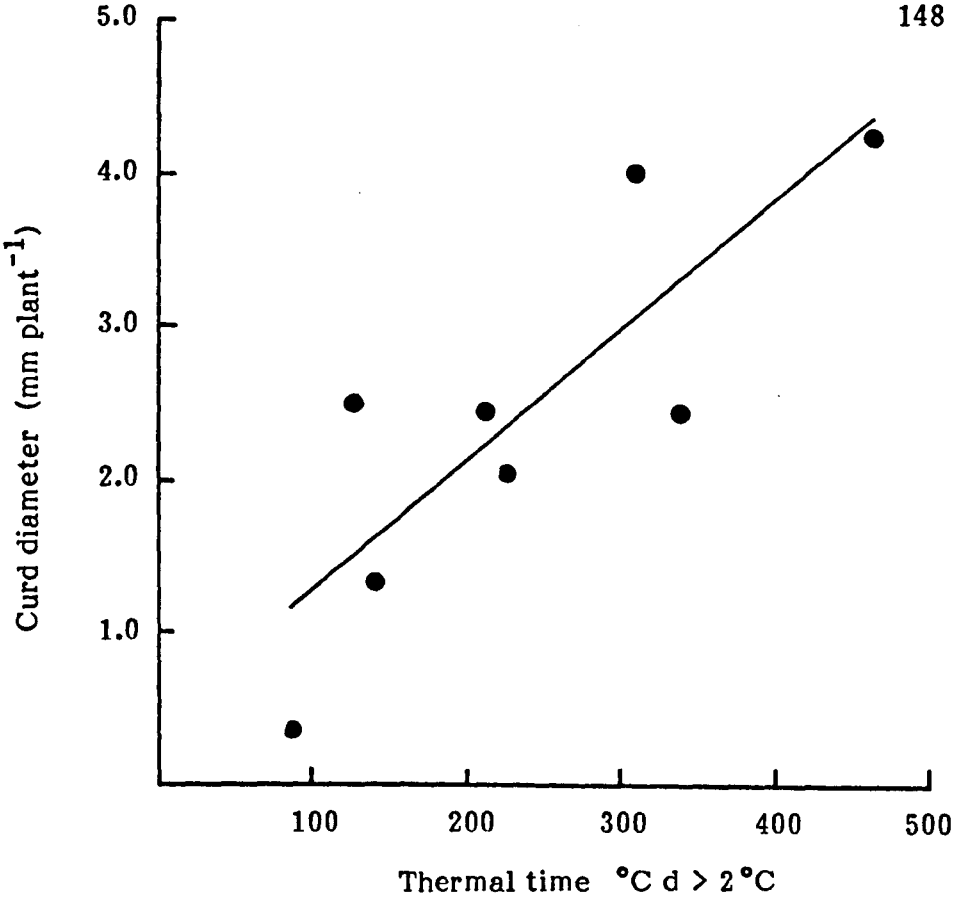
$$r^2 = 0.70 \quad (p < 0.01, \text{ d.f.} = 6)$$

(b)

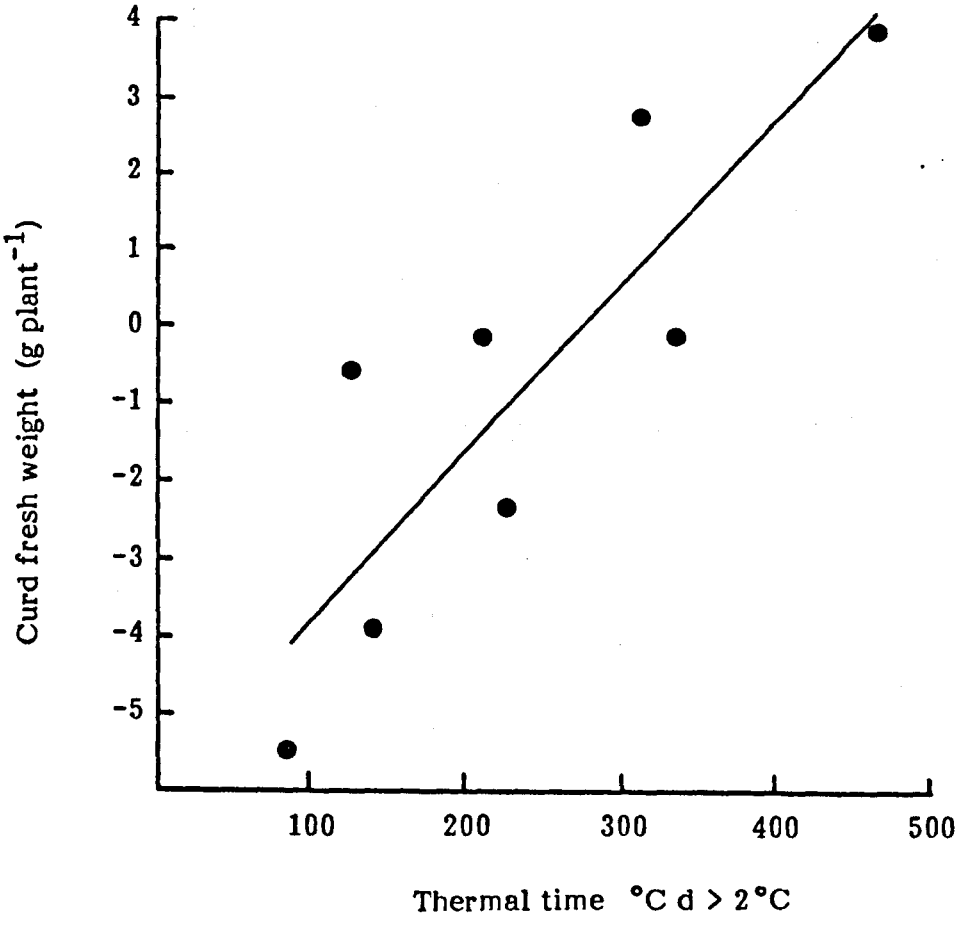
$$y = -5.84 + 0.02148x$$

$$r^2 = 0.73 \quad (p < 0.01, \text{ d.f.} = 6)$$

(a)


5.0
4.0
3.0
2.0
1.0
Curd diameter (mm plant^{-1})
100
200
300
400
500
Thermal time °C d > 2°C

(b)


4
3
2
1
0
-1
-2
-3
-4
-5
Curd fresh weight (g plant^{-1})
100
200
300
400
500
Thermal time °C d > 2°C

ature. However, daily mean temperatures in the field of approximately 13°C are known to occur during the phase of curd growth for this cultivar.

Relative increase in both curd diameter and fresh weight were shown to be linear functions of thermal time (°C d > 2°C) when calculated over the temperature range 5 to 13°C (Fig 5.8a and b). As an example, the relationship between Log_e curd diameter (ln D) and thermal time (Θ) (Fig 5.8a) can be represented by the equation

$$\ln D = a + b\Theta \qquad \text{eqn 5.5}$$

where a is the intercept and b the slope of the line. Curd diameter, D can therefore be expressed as follows:

$$D = e^{a + b\Theta} \qquad \text{eqn 5.6}$$

with change in curd diameter as a function of thermal time equivalent to

$$\frac{dD}{d\Theta} = b.e^{a + b\Theta} \qquad \text{eqn 5.7}$$

the change in thermal time requirement with respect to curd diameter being the reciprocal of equation 5.7

$$\frac{d\Theta}{dD} = \frac{1}{b.e^{a + b\Theta}} \qquad \text{eqn 5.8}$$

From equation 5.5 the thermal time required to attain a curd diameter of say 15 cm (150 mm) under the conditions employed here is equivalent to

$$\Theta = \frac{\ln D - a}{b} \qquad \text{eqn 5.9}$$

where ln D = 5.01, a = 0.433 and b = 0.00846

$$\Theta = \frac{5.01 - 0.433}{0.00846} = 541°C\,d$$

The same procedure may be adopted for curd weight gain. The possibility that such a relationship could be used both to predict curd maturity and the precise time of curd initiation (taken to be an apex diameter of 0.6 mm) under field conditions using meteorological records is discussed in Chapter 8.

5.3 Summary

1. Reciprocal of leaf number subtending the curd, denoting process acceleration, was linearly related to temperature under controlled environment conditions. Fitting regressions allowed derivation by extrapolation of both base (T_b) and maximum (T_m) temperatures for curd initiation. The intersect of the two regressions defined the optimum temperature (T_o). These cardinal temperatures T_b, T_o and T_m were -1.25°C, 5.5°C and 23.5°C respectively for cv Perfection. Corresponding values for White Fox of -3°C, 8.6°C and 31.5°C were established.

2. Cardinal temperatures for the rate of curd appearance derived from regressing reciprocal of days to macroscopic curd visibility on temperature were -4.5°C, 12.0°C and 29.5°C for T_b, T_o and T_m respectively in cv Perfection. The corresponding cardinal temperatures for cv White Fox were -3.5°C, 15.8°C and 28.3°C. Although linear regressions adequately described the relationship of rate of curd appearance on temperature a parabolic curve could describe the response in cv Perfection. Combination of curd initiation and early curd growth processes measured as curd appearance may account for this observation in association with the higher values of T_o.

3. The range of temperatures over which curd initiation occurred was wider in the later season cv White Fox, with a higher optimum for vernalization of 8.6°C as compared to 5.5°C defined for cv Perfection.

4. The relationship between leaf number subtending the curd and thermal time accumulated during controlled environment conditions was accurately described by fitting quadratic ($r^2 = 0.97$, $p < 0.001$) and linear ($r^2 = 0.92$, $p < 0.001$) functions for cvs Perfection and White Fox respectively. Thermal time required to reduce the leaf number subtending the curd by one was estimated as 8.1°C d over the range 19 to 48 leaves in cv White Fox. This compared with 13.0°C d and 2.2°C d required per leaf over the ranges 16 to 21 and 28 to 43 leaves respectively in cv Perfection.

5. Where temperature treatments resulted in greater leaf numbers below the curd than the minima of 16 and 19 for cvs Perfection and White Fox respectively, additional thermal time was added to that accumulated during the four weeks temperature treatment. This additional thermal time was that which elapsed during the initiation of the additional leaves. In the case of White Fox an additional 8.1°C d was added per leaf over the base of 19.

6. Comparison of thermal times of vernalization for plants grown in the field and in controlled environments in which curd initiation had taken place at the same leaf number showed close agreement for the earliest transplantings at two separate sites.

7. The degree to which thermal times of vernalization departed from the predicted figure in later transplantings was consistent between different

held sites. This suggested a possible interaction with other climatic or field variables.

8. Partial devernalization associated with high temperatures experienced after chilling was suggested by an increase in leaf number of three to ten before the curd in plants grown at temperatures of 20 or 25°C, compared with plants grown at between 5 to 13°C.

9. Curd morphology was clearly influenced by post-chilling temperature conditions. Bracteate curds were recorded following four weeks' growth at 20 and 25°C. The presence of green bracts was particularly evident at the higher of the two temperatures.

10. Curd growth rate measured both as curd diameter and curd fresh weight was significantly ($p < 0.001$) increased as temperatures increased over the range 5 to 13°C. Further increase in post-chilling temperature to 20 and 25°C resulted in a decline in curd size after four and six weeks' treatment.

11. Relative changes in both curd diameter and fresh weight were adequately described by quadratic functions when regressed on thermal time (°C d > 2°C) calculated over the temperature range 5 to 25°C. Squared correlation coefficients (r^2) of 0.80 and 0.82 were calculated for regressions of Log_e curd diameter and Log_e curd weight respectively. Similarity in the curves was shown to be due to a strong association of curd diameter with curd weight, $r^2 = 0.92$.

12. Linear functions adequately described regression of Log_e curd diameter ($r^2 = 0.70$) and Log_e curd weight ($r^2 = 0.73$) on thermal time (°C d > 2°C) calculated over the temperature range 5 to 13°C. From equation 5.9

$$\Theta = \frac{\ln D - a}{b}$$

the thermal requirement for a specified curd diameter could be calculated. The thermal time required to produce a curd of 15 cm diameter was calculated as 541°C d from the relationship described here under controlled environment conditions.

Chapter 6

ROOT ENVIRONMENT

Introduction

Time to curd initiation measured on both chronological and developmental time scales is influenced by the aerial environment, being reduced by both high irradiance receipt and 'low' temperature. This chapter will consider how conditions in the root environment influence curd initiation. Nitrogen nutrition and water availability particularly were examined in this context.

Nitrogen availability is known to influence curd growth and yield (Cutcliffe and Munro, 1976; Dufault and Waters Jnr, 1985) and has been strongly implicated in the phenomenon of 'buttoning'. Whilst nitrogen nutrition has been shown to regulate floral initiation and development in a wide range of species (Blake and Harris, 1960; and references cited therein), whether nitrogen availability is able to influence curd initiation remains unclear.

Similarly investigations into effects of different soil moisture conditions on the growth and yield of early summer cauliflowers did not consider possible effects on curd initiation (Salter, 1960b). The last section of this chapter describes a preliminary study into the role of water stress in curd initiation.

6.1 Interaction of nitrogen nutrition and chilling on curd initiation

The first experiment described in this chapter was designed to examine the effects of nitrogen applied at different levels during juvenile growth on curd initiation in the cauliflower cv Perfection. On attainment of

maturity, plants were transferred to controlled environment conditions and either chilled for four weeks at 5°C or retained under warm, 20°C, conditions for the same period. The possibility that the level of nitrogen could modify the response to low temperature was therefore investigated.

6.1.1 Materials and methods

Seeds of Perfection were sown on 27 March 1985 and germinated as described in section 2.1.1. When the cotyledons were fully expanded, seedlings were potted on into compost from which nitrogen based fertiliser was omitted (section 2.5). Nitrogen treatments commenced on expansion of the first true leaf.

Nitrogen, in the form of ammonium nitrate (NH_4NO_3; 34.5% N) dissolved in water was supplied as a liquid feed at concentrations of 0, 50, 100 and 400 ppm. Rates of application were also varied being one, three or seven times per week. Potassium concentration was maintained at a constant 200 ppm throughout the course of the experiment. However, whilst potassium levels were equal between nitrogen treatments at a given rate, they were different between rates (Table 6.1). Ammonium nitrate solutions were applied using an automatic dispenser (Rudolph Brand, W. Germany), each plant receiving 50 ml per application. Plants not treated on a particular date received water only. Additional water was given to plants to maintain adequate moisture in the compost when necessary. Application of a predetermined volume of ammonium nitrate solution enabled the amount of nitrogen (mg) received by each plant to be calculated (Table 6.1).

On 22 April when plants had completed juvenile development, estimated here as occurring on initiation of the 19th leaf, half were

Table 6.1 Nitrogen and potassium levels (mg) applied weekly

Nitrogen concentration (ppm)	Application rate (No. per week)		
	1	3	7
0	0	0	0
50	2.5	7.0	17.5
100	5.0	15.0	35.0
400	20.0	60.0	140.0
Potassium concentration (ppm)			
200	10.0	30.0	70.0

transferred to chilling for four weeks at 5°C, and half were retained in a growth room at 20°C for the same period as controls. Lighting during growth in controlled environments was provided by a bank of 80 W warm white fluorescent tubes giving an irradiance of 50 ± 5 Wm^{-2} incident at plant height for 12 h each day. On completion of growth room treatments all plants were returned to warm (c. 20°C) glasshouse conditions. Natural glasshouse irradiance was supplemented using 400 W SON/T lamps providing an additional 65 to 70 Wm^{-2} at plant height for 16 h each day commencing at dawn.

The experiment ended at macroscopic curd appearance. The number of days taken to reach this stage from seed sowing was recorded, as was the number of leaves initiated before the curd. Measurements of leaf dry weight and leaf area were also taken as described previously (section 2.6).

Experimental treatments were arranged in randomised complete blocks with each treatment replicated three times. A total of nine plants, three from each replicate, were recorded at the time of macroscopic curd appearance.

An unbalanced experimental design resulted from the confounding effect of potassium (Table 6.1). The application of a given nitrogen level at only one of the three potassium levels prohibited a full analysis of variance. The technique of analysis of deviance (Snedecor and Cochran, 1967) was therefore applied to the results. This analysis uses a multiple regression model to measure the variance accounted for by adding further elements to an initial regression. Using leaf number subtending the curd the following example is given. The initial model comprises a simple regression of leaf number on nitrogen concentration, the amount of

variance not accounted for being indicated by the residual sum of squares. Potassium level is then introduced into the model by the fitting of three parallel lines (common slope with different intercepts), one for each of the three potassium groups (Fig 6.1). The additional variance accounted for, if any, is expressed as a change in the residual sum of squares. The final step in the multiple regression model again fits three lines; however, these are permitted to differ in both slope and intercept indicating possible interactions between nitrogen and potassium in determining leaf number, the change in the residual sum of squares again being measured. The change in residual sum of squares divided by the number of degrees of freedom represents the mean change which, when divided by the residual mean change, provides the variance ratio and hence the level of significance that may be attached to each modification of the initial model.

6.1.2 Results

In chilled plants, nitrogen applied over the range 0 to 140 mg wk^{-1} had no significant effect on the number of leaves initiated before the curd (Fig 6.1a). These plants initiated curds at an average of 30 leaves compared to the 20 leaves present on commencement of the chilling treatment. This was in marked contrast to unchilled plants in which curd initiation was accelerated when nitrogen was applied. This was evident in all three of the potassium treatments, the minimum reduction in leaf number of five recorded at a potassium level of 30.0 mg wk^{-1} and a maximum reduction of 15 at 10 mg K wk^{-1} (Fig 6.1b). Increasing the level of nitrogen above 30 mg wk^{-1} had no further accelerating effect on curd initiation.

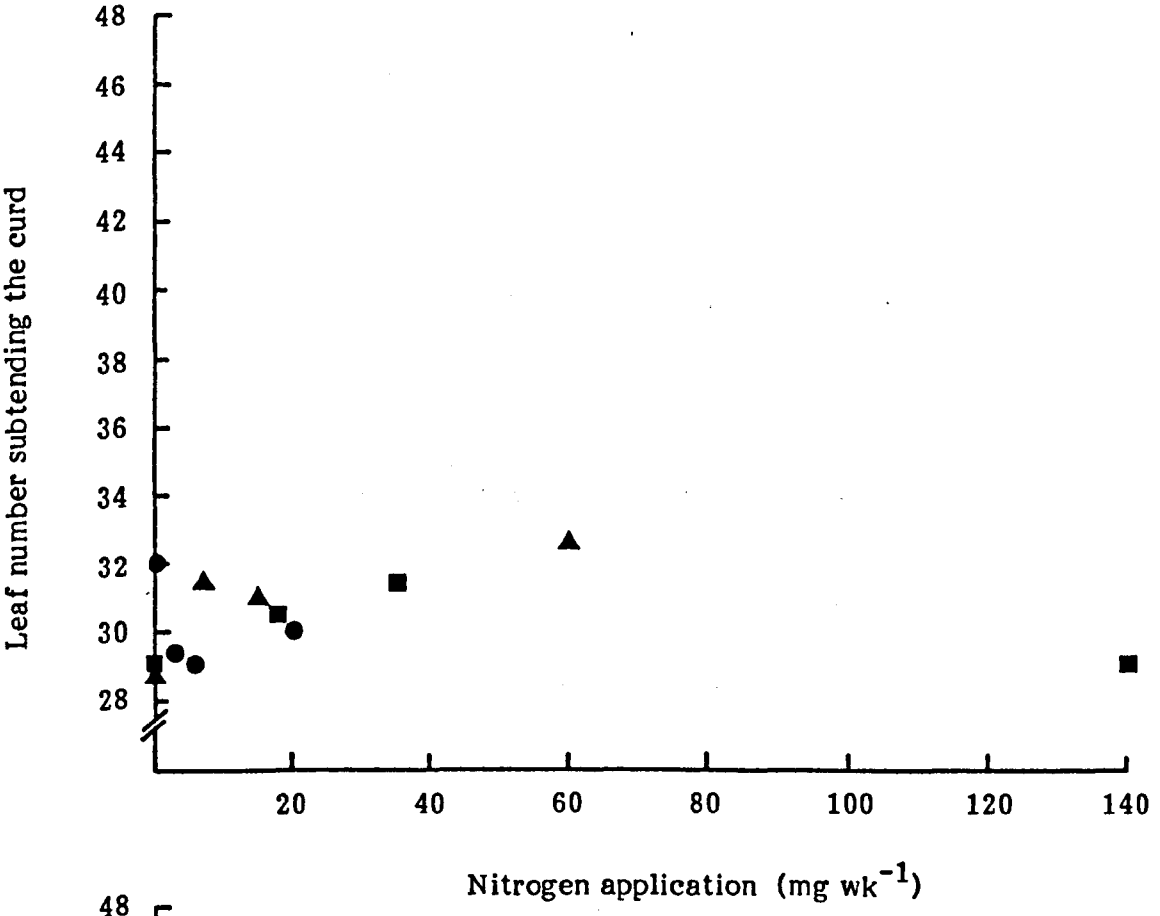
Fig 6.1 Number of leaves initiated before the curd in plants of the cv Perfection receiving different levels of nitrogen during juvenile development

(a) Plants chilled for four weeks at 5 °C

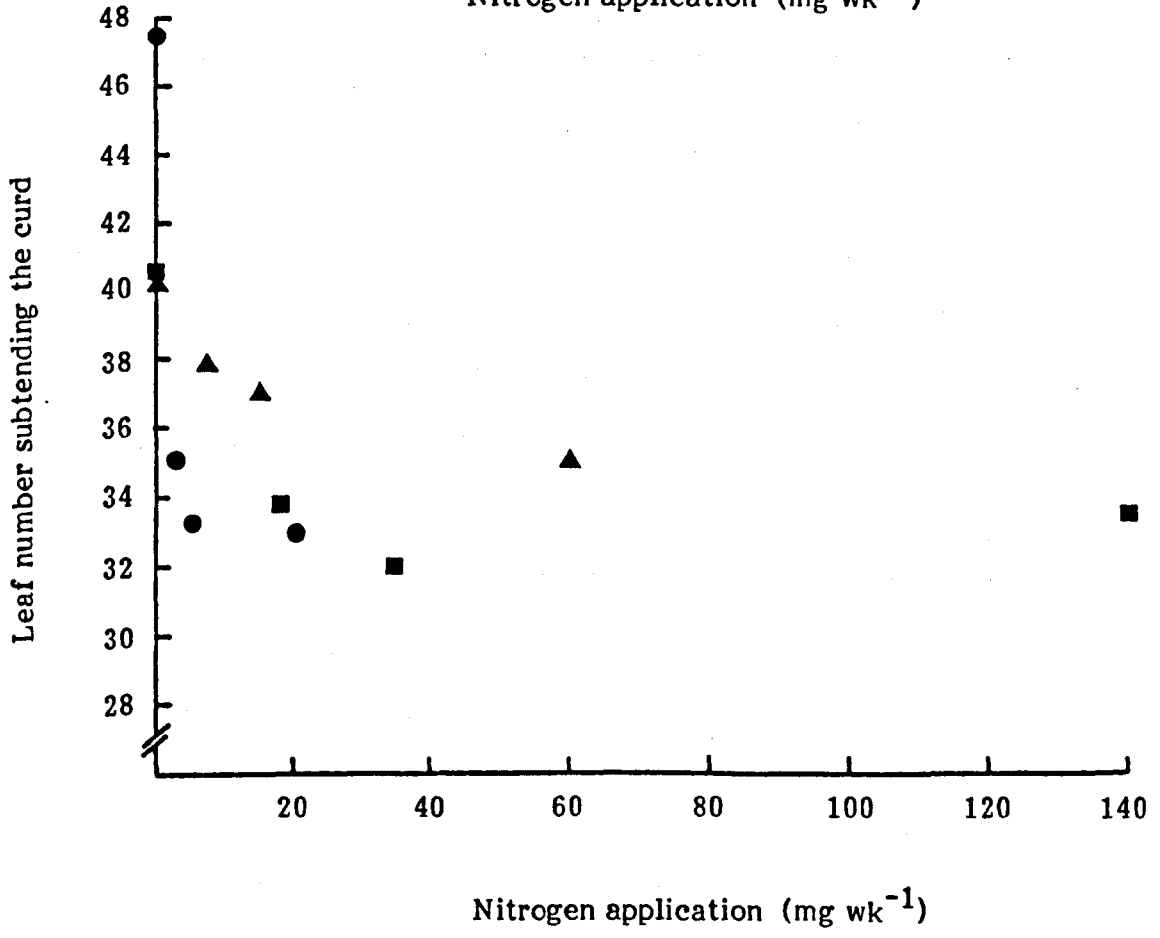
(b) Control plants retained at 20 °C for four weeks

From Table 6.1 treatments comprising 10.0, 30.0 or 70.0 mg potassium per week are represented by the symbols ● , ▲ , ■ respectively

(a)


Leaf number subtending the curd
48
46
44
42
40
38
36
34
32
30
28
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

(b)


Leaf number subtending the curd
48
46
44
42
40
38
36
34
32
30
28
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

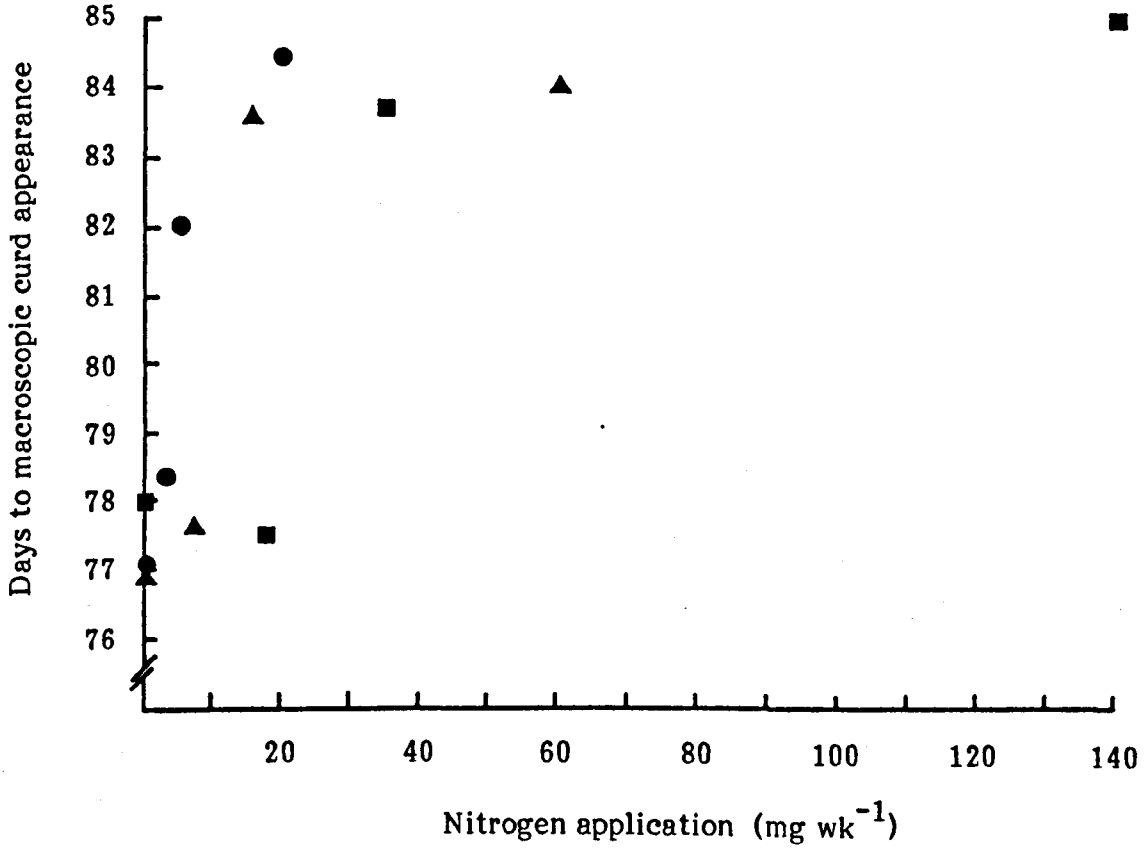
When nitrogen fertiliser was completely withheld from unchilled plants, potassium applied at a level of 10 mg wk^{-1} resulted in a marked increase in the number of leaves initiated before the curd. An average of 48 was initiated compared to c. 41 leaves when potassium was applied at levels of 30.0 and 70.0 mg wk^{-1}. With the possible exception of low nitrogen levels present in the 'nitrogen-free' compost this would suggest an effect of potassium on leaf number independent of nitrogen. The absence of any interaction between nitrogen and potassium when plants were chilled would suggest a secondary role for nitrogen in determining the point of curd initiation.

The number of days to macroscopic curd appearance increased with the level of applied nitrogen reaching a maximum of 85 days at a nitrogen level of 20.0 mg wk^{-1}. Further increase in nitrogen, although assessed by only three points did not appear to increase the number of days to curd appearance (Fig 6.2). Despite a highly significant interaction ($p < 0.001$) between nitrogen and potassium levels, the increase in the number of days to macroscopic curd appearance with increasing nitrogen application was common to all three potassium groups. Possible effects of nitrogen and potassium on curd appearance at 20°C was not assessed.

The number of days to curd appearance was poorly correlated with leaf number ($r = 0.063$) indicating that curd appearance was not dependent on the stage of development at which the curd was initiated. Further evidence in support of this view is provided by the high correlations between curd appearance and both leaf area ($r = 0.85$) and leaf dry weight ($r = 0.84$). Clearly, curd appearance in this instance is simply governed by the 'size' of the surrounding leaves. A more significant correlation between curd appearance and leaf number may have been made

Fig 6.2 The number of days to macroscopic curd appearance in plants of the cv Perfection receiving different levels of nitrogen during juvenile development. Plants were chilled for four weeks at 5 °C

From Table 6.1 treatments comprising 10.0, 30.0 or 70.0 mg potassium per week are represented by the symbols ●, ▲, ■ respectively


Days to macroscopic curd appearance
85
84
83
82
81
80
79
78
77
76
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

under warm conditions where leaf number changed in response to nitrogen and potassium levels.

Leaf dry weight measured at curd appearance increased with the level of applied nitrogen in both chilled and unchilled plants (Figs 6.3a and b). This was consistent throughout the individual potassium treatments. A highly significant interaction ($p < 0.001$) between nitrogen and potassium was shown to exist when independent regressions of leaf dry weight on the level of applied nitrogen fitted to the three potassium groups accounted for 82% and 90% of the variance in chilled and unchilled plants respectively.

Suppression of leaf dry weight by chilling, recorded previously (section 3.1.2.3), would appear to be less marked when nitrogen was withheld. This may suggest that a minimum plant dry weight is required for curd initiation to proceed. In contrast, nitrogen applied at a level of 140 mg wk^{-1} resulted in leaf dry weights of 16 g and 11 g in unchilled and chilled plants respectively; a reduction in weight of approximately one third.

Under non-inductive (c. 20°C) conditions curds were initiated after about 33 leaves had formed provided that leaf dry weight had exceeded about 5 g (Fig 6.4a). Where plants had accumulated less dry matter than this, many more leaves were initiated before the curd. Curd initiation was never observed in plants with a leaf dry weight below 1.2 g. In chilled plants curd initiation occurred at about 33 leaves irrespective of their dry weight (Fig 6.4b), a minimum of approximately 1.3 g was again suggested.

As leaf area and leaf dry weight were shown to be highly correlated ($r = 0.94$) the observation that increasing the level of applied nitrogen increased leaf area in both chilled and unchilled plants (Fig 6.5a

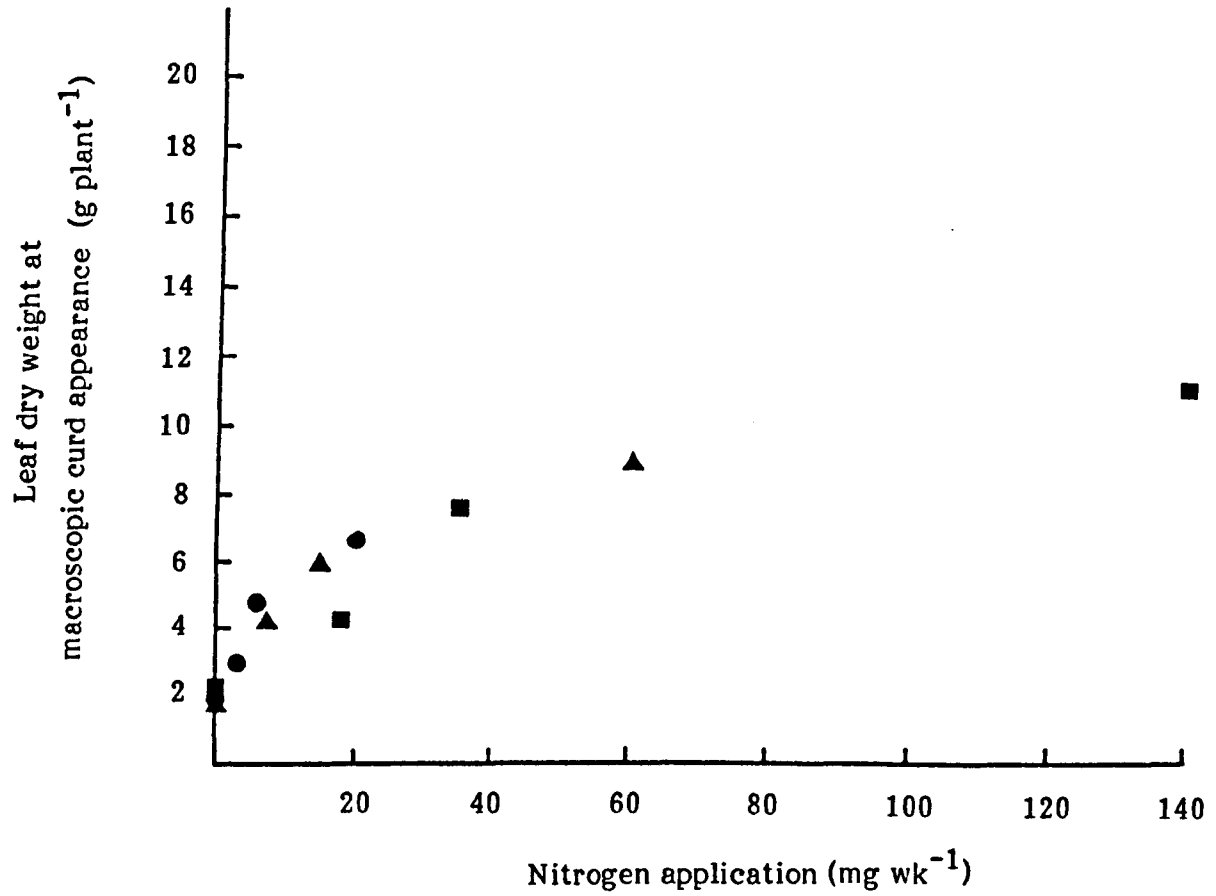
Fig 6.3 Leaf dry weight at macroscopic curd appearance in plants of the cv Perfection receiving different levels of nitrogen during juvenile development

(a) Plants chilled for four weeks at 5 °C

(b) Control plants retained at 20 °C for four weeks

From Table 6.1 treatments comprising 10.0, 30.0 or 70.0 mg potassium per week are represented by the symbols ● , ▲ , ■ respectively

(a)


Leaf dry weight at
macroscopic curd appearance (g plant^{-1})
20
18
16
14
12
10
8
6
4
2
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

(b)

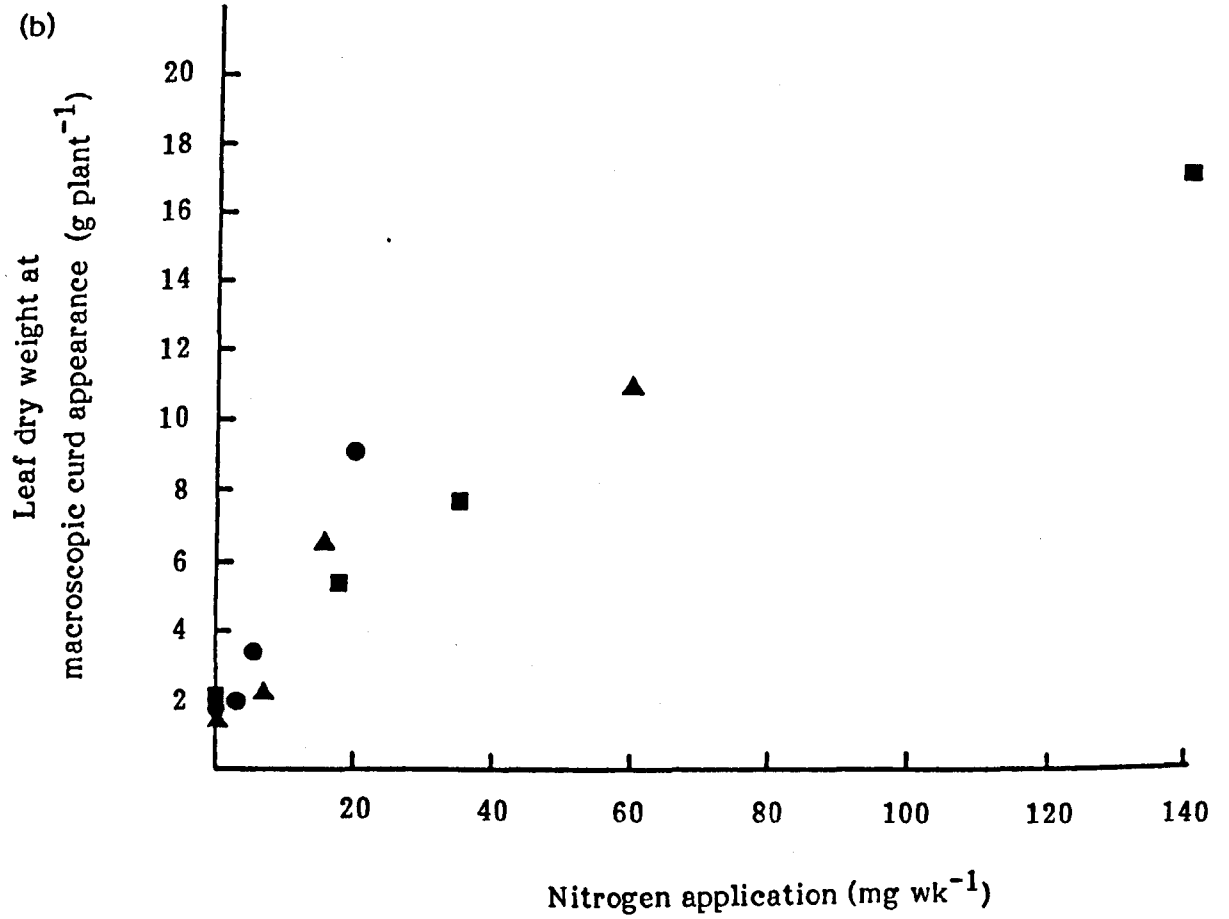
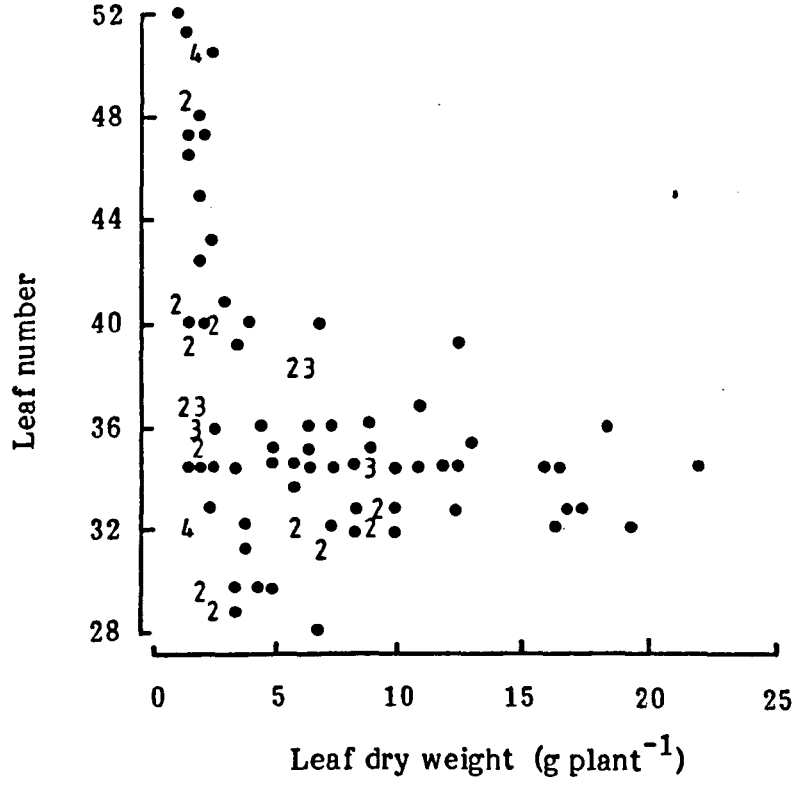

Leaf dry weight at
macroscopic curd appearance (g plant^{-1})
20
18
16
14
12
10
8
6
4
2
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

Fig 6.4 Scatter plot of leaf number and leaf dry weight at curd initiation for individual plants grown under warm (c. 20 °C) conditions (a) or chilled for four weeks at 5 °C (b)

Numerals indicate location and number of coincident points

(a)


Leaf number
52
48
44
40
36
32
28
0
5
10
15
20
25
Leaf dry weight (g plant^{-1})

(b)

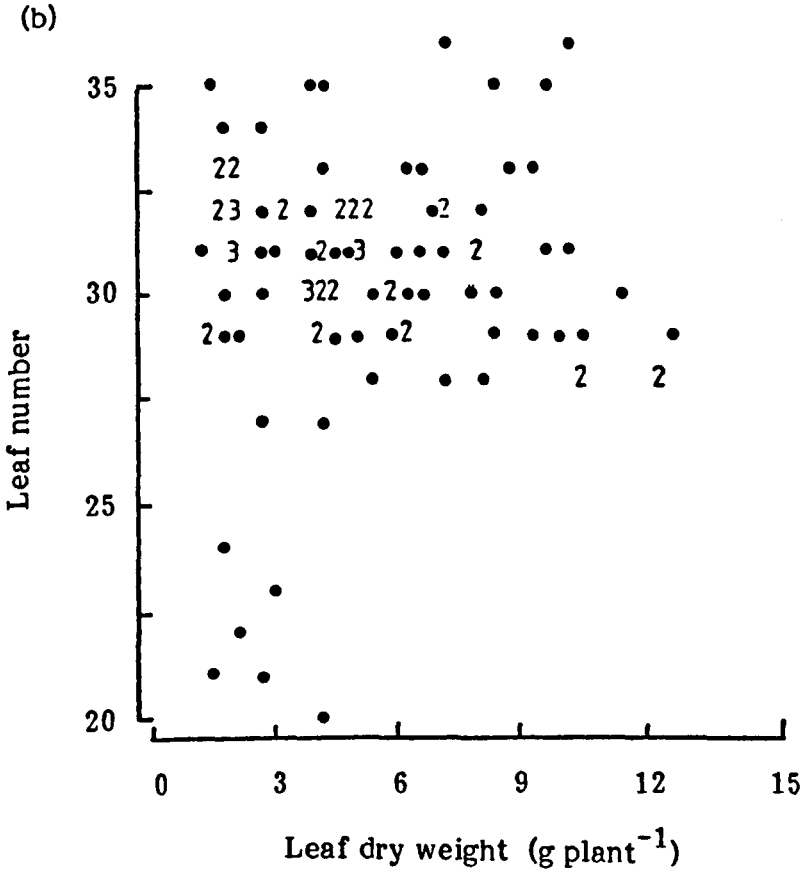

Leaf number
35
30
25
20
0
3
6
9
12
15
Leaf dry weight (g plant^{-1})

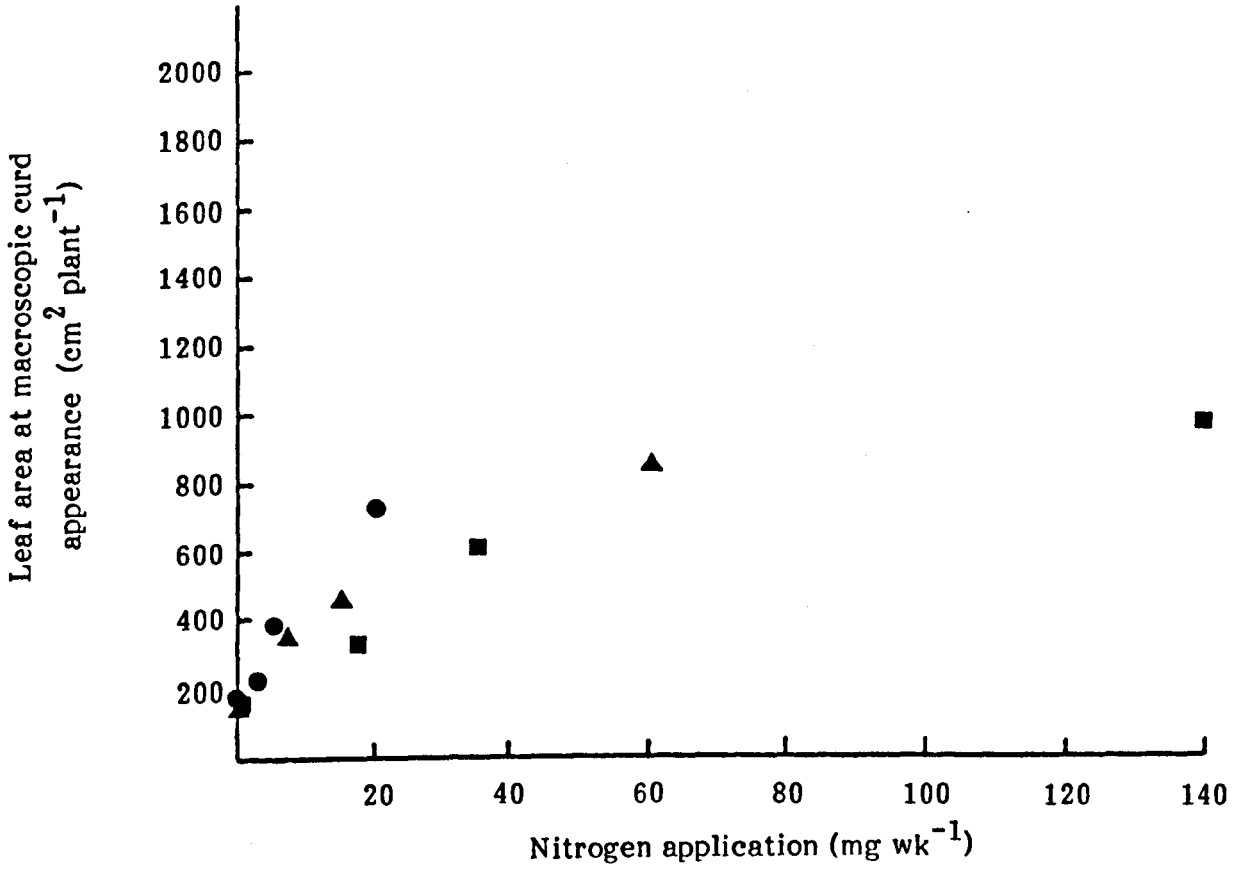
Fig 6.5 Leaf area at macroscopic curd appearance in plants of the cv Perfection receiving different levels of nitrogen during juvenile development

(a) Plants chilled for four weeks at 5 °C

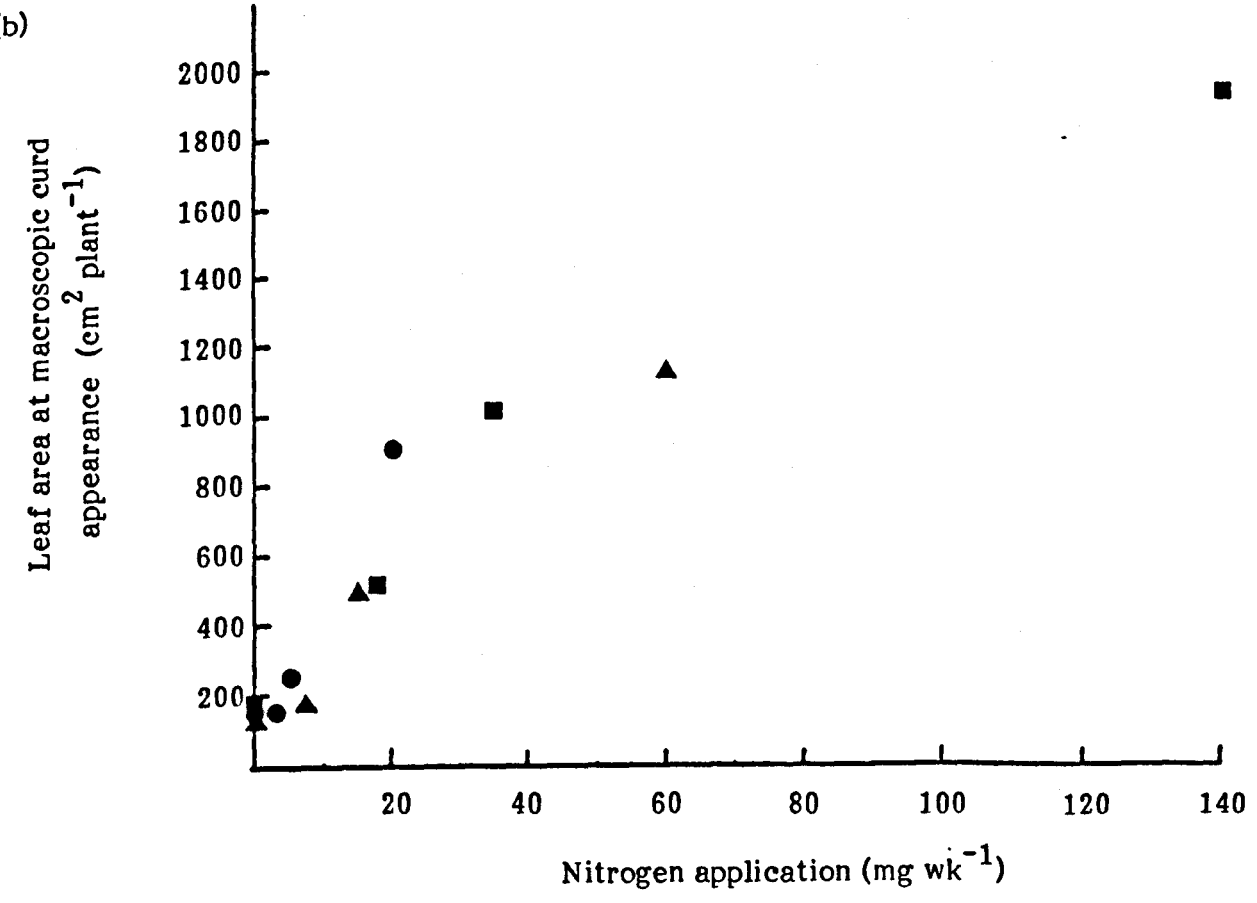
(b) Control plants retained at 20 °C for four weeks

From Table 6.1 treatments comprising 10.0, 30.0 or 70.0 mg potassium per week are represented by the symbols ●, ▲, ■ respectively

(a)


Leaf area at macroscopic curd appearance (cm^2 plant^{-1})
2000
1800
1600
1400
1200
1000
800
600
400
200
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

(b)


Leaf area at macroscopic curd appearance (cm^2 plant^{-1})
2000
1800
1600
1400
1200
1000
800
600
400
200
20
40
60
80
100
120
140
Nitrogen application (mg wk^{-1})

and b) may have been anticipated. The same trend was evident within potassium groups. The strong interaction ($p < 0.001$) between nitrogen and potassium in determining leaf area was accurately described by independent regressions which accounted for 90% and 92% of the variance in chilled and unchilled control plants repectively.

6.2 Curd initiation in response to the level of nitrogen applied to mature plants

The objective of this second experiment was to consider how the level of nitrogen influenced curd initiation when applied to mature plants.

6.2.1 Materials and methods

Sowing date and potting on procedures were exactly as detailed in section 6.1.1, whilst normal juvenile growth was ensured by following the nutritional guidelines in section 2.1.1. On attainment of maturity pots were repeatedly flushed with deionised water to remove any residual nitrogen. Ammonium nitrate solutions of the same concentrations as those used in the preceding experiment were then applied in an identical manner, with the exception that a single rate of seven applications wk^{-1} was used throughout. Treatments were applied under the same warm (20°C) glasshouse conditions described previously.

The number of days to curd appearance was again taken to indicate completion of the experiment with leaf number and shoot components measured for the different nitrogen treatments.

The use of one application rate throughout (7 times wk^{-1}) ensured that the nitrogen treatments of 0, 17.5, 35.0 and 140.0 mg wk^{-1} were not confounded by differing potassium levels, all plants receiving 70 mg wk^{-1}

(Table 6.1); results were therefore analysed using a standard analysis of variance technique.

Experimental treatments were arranged in randomised complete blocks with each treatment replicated three times. A total of 12 plants, four from each replicate, were recorded at the time of macroscopic curd appearance.

6.2.2 Results

The number of days to macroscopic curd appearance, although just significantly different ($p < 0.05$) between treatments, showed no consistent pattern (Table 6.2). Plants from which nitrogen was totally withheld took, on average, 55 days to curd appearance with treatments of 17.5 and 140.0 mg wk^{-1} taking two days less at 53.

Leaf number initiated before the curd was not affected here by applied nitrogen (Table 6.2). This may have been due to the relatively late stage of development (c. 29 leaves initiated) at which nitrogen treatments were first applied. Clearly, even under the warm (c. 20°C) conditions used here plants were close to the point of initiation as indicated by the average of 32 leaves present at curd appearance. In addition the levels of nitrogen applied during juvenile development would probably have increased the overall plant nitrogen status, acting as a buffer against subsequent withholding of nitrogen. Furthermore, despite flushing the compost some residual nitrogen may have remained.

Leaf dry weight at macroscopic curd appearance displayed a highly significant response ($p < 0.001$) to the level of applied nitrogen (Table 6.2). The maximum dry weight of 9.5 g was achieved by those plants receiving 140 mg N wk^{-1}. Whilst dry weights resulting from applications

Table 6.2 Time to macroscopic curd appearance and associated shoot characteristics in plants subjected to different levels of applied nitrogen during mature growth and development

	Applied nitrogen (mg per wk)			
	0	17.5	35.0	140.0
Days to macroscopic curd appearance	55	53	54	53
Leaf number	33	32	32	32
Leaf dwt g	7.7	8.6	7.6	9.5
Leaf area cm^2	666	778	771	1039

Each figure represents the mean of 12

Days to macroscopic curd appearance	SED = 0.7 (d.f. = 44)
Leaf number	SED = 0.6 (d.f. = 44)
Leaf dry weight	SED = 0.45 (d.f. = 44)
Leaf area	SED = 35.8 (d.f. = 44)

of 0 and 35 mg N wk^{-1} were shown not to differ significantly, an increased dry weight of 8.6 g was however attained by plants receiving 17.5 mg N wk^{-1}.

Leaf area at curd appearance showed a highly significant response to the level of applied nitrogen ($p < 0.001$) (Table 6.2). A maximum leaf area of 1039 cm^2 was achieved by those plants receiving 140.0 mg N wk^{-1} while withholding nitrogen resulted in a leaf area of 666 cm^2. Intermediate levels of 17.5 and 35.0 mg N wk^{-1} corresponded to leaf areas of 778 and 771 cm^2 respectively. Whilst not differing significantly from each other, a significant difference was evident when comparisons were made with lower and higher levels of nitrogen application.

6.3 Macro-Kjeldahl determination of total plant nitrogen

Whilst it was possible to calculate the amount of nitrogen received by plants in the two preceding experiments, this may not reflect the level of nitrogen present in the plant. Samples were therefore taken from plants in which nitrogen treatments were applied during mature vegetative growth (section 6.2.1), and total nitrogen content of the plant material was determined using Macro-Kjeldahl digestion modified from the Kjeldahl-Gunning method (section 2.5.1).

6.3.1 Results

As plant nitrogen was expressed as a percentage of total plant dry weight the square root transformation of the data was used for further analysis to normalise the data.

Nitrogen content of the plant tissue increased significantly ($p < 0.001$) with the level of applied nitrogen (Table 6.3). Application of

Table 6.3 Nitrogen content of plant material expressed as a percentage of total dry weight in plants receiving four levels of applied nitrogen during mature growth and development.

Sample number	Applied nitrogen (mg per week)			
	0	17.5	35.0	140.0
1	2.3	2.0	4.2	6.4
	(1.5)	(1.4)	(2.0)	(2.5)
2	2.4	2.3	3.9	5.8
	(1.5)	(1.5)	(1.9)	(2.4)
3	2.1	2.3	4.1	5.6
	(1.4)	(1.5)	(2.0)	(2.4)
Treatment mean (%N):	2.3	2.2	4.1	5.9
	(1.5)*	(1.4)*	(2.0)*	(2.4)*

Figures in parentheses represent transformed data;
for transformed treatment mean,* SED = 0.052 (d.f. = 6)

nitrogen at rates of 0 and 17.5 mg per week resulted in nitrogen contents of 2.29% and 2.17% respectively, which were shown not to differ significantly. However, increasing the rate of application to 35.0 or 140 mg N per week had a marked effect on nitrogen content with levels recorded at 4.1% and 6.0% of total plant dry weight respectively.

Samples across treatments (Table 6.3) did not differ significantly.

6.4 Effect of applied potassium on curd initiation

In the absence of nitrogen potassium applied to juvenile plants grown under warm conditions (c. 20°C) had at a rate of 10 mg per week significantly increased leaf number initiated below the curd (section 6.1.2). This effect was further investigated here.

6.4.1 Materials and methods

Seeds of cv Perfection were sown in 28 August 1985 and germinated as described in section 2.1.1. When the cotyledons were fully expanded, seedlings were potted on into minus-nitrogen compost as described in section 2.5.

Potassium treatments applied to juvenile plants commenced on expansion of the first true leaf when plants were considered to be equally established.

Potassium fertiliser in the form of potassium sulphate (K_2SO_4; 22% K) was prepared and applied at concentrations of 50 and 200 ppm in an identical manner to that described for nitrogen treatments in section 6.1.1. Potassium sulphate was also incorporated into the compost (27 g per 0.04 m^3; Table 2.1) enabling comparisons to be made with the earlier experiment (section 6.1.2). As applied nitrogen was absent from this

experiment treatments were not confounded as a result of the two application rates of one and three times per week. Potassium application rates expressed as mg per week are summarised in Table 6.4.

Throughout the experiment plants were grown under warm glasshouse conditions at a mean daily temperature of 20°C. Natural glasshouse irradiance was supplemented using 400 W SON/T lamps providing an additional 65 to 70 Wm^{-2} at plant height for 16 h each day, commencing at dawn. The natural September photoperiod of c.13 h was therefore extended.

Table 6.4 Potassium levels (mg) applied weekly

Potassium concentration (ppm)	Application rate (No. per week)	
	1	3
50	2.5	7.0
200	10.0	30.0

Curd initiation was, as with preceding experiments, measured both as the number of days to macroscopic curd appearance and the number of leaves initiated before the curd. Measurement of vegetative development enabled possible correlations between shoot components to be assessed.

A randomised complete block design was used throughout with each treatment replicated three times, and three plants recorded per replicate.

6.4.2 Results

Leaf number before the curd was affected significantly ($p < 0.05$) by the level of applied potassium (Table 6.5). Applications at a rate of 30 mg K wk^{-1} increased the number of leaves initiated before the curd by four to 51; treatments comprising 2.5, 7.0 and 10.0 mg wk^{-1} failed to differ significantly with an average leaf number of 47. This observation was inconsistent with earlier results (section 6.1.2; Fig 6.1b) where increasing leaf number was associated with the lowest potassium level. The reason for this is not immediately apparent. Clearly further experiments are required in order to clarify the role of potassium in curd initiation, particularly where plants are starved of nitrogen. Determination of the potassium content of plant tissue may also be of value.

Table 6.5 Number of leaves initiated before the curd in plants subjected to different levels of applied potassium during juvenile development

Potassium level (mg per week)	Leaf number
2.5	47
7.0	46
10.0	48
30.0	51

Leaf number SED = 1.2 (d.f. = 31)

The number of days to macroscopic curd appearance was shown not to differ significantly between potassium treatments. Absence of any significant effect was also evident when measuring individual shoot components; these results are therefore not presented.

6.5 Nitrogen nutrition and curd initiation in modular raised transplants grown under field conditions

The objective of this experiment was to investigate possible influences of nitrogen nutrition and root restriction on subsequent curd initiation in commercially used modular transplants. This study employed propagation facilities and field sites at Kirton Experimental Horticultural Station, Lincolnshire.

6.5.1 Materials and methods

Cauliflower cv White Fox was used throughout this experiment. Individual seeds were sown into modules made from a proprietary compost (Fisons, Ipswich) on 7 April 1986.

Two sizes of modules were used for propagation, the Hassy 104 and Hassy 308 (Hassy-Planter Systems Ltd). These trays have individual module volumes of 44.0 cm^3 and 14.0 cm^3 with 434 and 1284 modules per m^2 respectively. Germination and general husbandry were as described elsewhere (Anon, 1985a). Germination and plant growth in the glasshouse were at a mean temperature of 16°C.

Nitrogen in the form of ammonium nitrate was provided as a liquid feed at one of three concentrations, 50 ppm (rate 1 x wk^{-1}), 100 ppm (rate 2 x wk^{-1}) and 200 ppm (rate 3 x wk^{-1}). Each nitrogen treatment comprised nine trays of each of the two types. Potassium sulphate was applied at a constant 200 ppm K_2O. As a result of the small size and large number of modules in use, individual application was impractical and therefore the precise amount of nitrogen received per plant could not be accurately determined. Within nitrogen treatments GA_{4+7} was applied to

plants at three levels. A full description of these treatments is given in Chapter 7.

The combination of two module sizes, three levels of nitrogen application and three levels of GA_{4+7} applied within the nitrogen treatments resulted in a total of 18 treatments. However, due to the size of the available site only plants raised in Hassy 308 modules were transplanted; these were considered to best reflect commercially raised plants.

Transplanting of the 9 treatments was carried out by hand with plant spacings of 61 x 46 cm. As each treatment was replicated three times a total of 27 plots were set out following a randomised complete block design as was used during propagation. The positioning of the three blocks, each containing one replicate of the 9 treatments, is indicated in Plate 3. Additional treatments incorporated into the three blocks failed to give significant results and are therefore not considered further.

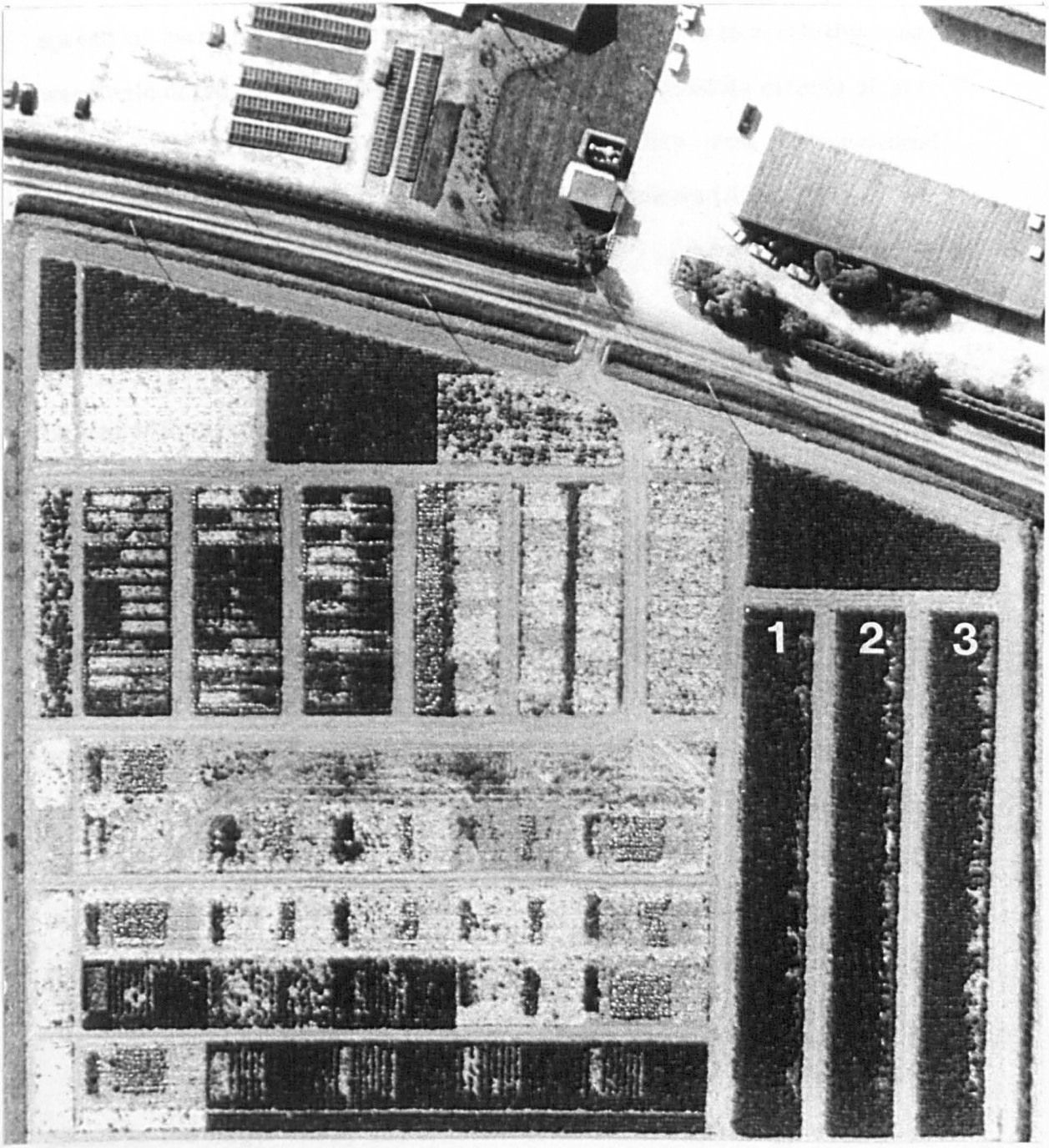
Preparation of the field site and operations carried out during growth of the crop are detailed in Table 6.6. Individual plots/replicates contained a total of 57 plants, three rows of six plants were used for sampling purposes during crop growth, an additional 30 plants (3 rows x 10 plants) were taken at final harvest to assess treatment effects on curd size/quality and the spread of curd maturity.

Dissection of plants pre- and post- transplanting was carried out on nine plants per treatment, three plants being selected at random from each replicate. Where dissection was delayed plants were stored in polythene bags at 2°C in complete darkness. All dissections were, however, completed on the same day. During propagation samples were taken weekly, while growth in the field was measured at intervals of

Table 6.6 Operations performed on trial site (field code 10 Acres 3)

Date	Remarks
	(Soil type : coarse, silty, marine alluvium of the Wisbech series)
–.12.85	10 acres 3 ploughed.
8.7.86	150 kg/ha Kaynitro applied to trial area and worked with a Lely cultivator. Trial transplanted, 61 x 46 cm. Plants treated with Birlane (Chlorfenvinphos) for control of cabbage root fly.
9.7.86	Trial sprayed with Ramrod (propachlor) and Dacthal (Chlorthal dimethyl) to control germinating annual weeds and broad leaved weeds rspectively.
23.7.86	Ambush (Cypermethrin) applied to trial to control caterpillar of the large white.
25.7.86	Trial top dressed at 100 kg/ha Nitram.
19.8.86	Trial sprayed with Hostaquick (Heptenophos) for the control of aphids.
6.10.86	Start cutting trial; first mature curds.
20.10.86	Finish cutting trial.

Plate 3 Aerial photograph showing design of field trials at Kirton EHS, replicate blocks 1 to 3 shown


1
2
3

approximately fourteen days. Leaf number and parameters of shoot growth were determined as described in section 2.6.

Visual assessment based on 90 plants per treatment, 30 from each of the replicates, determined the point at which curds were harvested. The spread of maturity and time taken for 50% of the curds to reach this stage were calculated for the different treatments. The possible effects of pre-transplanting treatments on curd size and quality were also assessed following the guidelines laid down for fresh cauliflowers (Anon, 1981).

6.5.2 Results

6.5.2.1 Leaf growth during propagation The number of leaves initiated immediately prior to transplanting on 8 July (Table 6.6) was significantly increased ($p < 0.001$) by raising plants in the larger Hassy 104 modules compared to the Hassy 308s (Table 6.7). Leaf number was, on average, increased by three in these plants.

Increasing the level of applied nitrogen from 50 to 200 ppm also significantly increased ($p < 0.001$) the number of leaves initiated. Nitrogen applied at the higher rate of 200 ppm, 3 x wk^{-1}, increased the number of leaves initiated by five when compared with treatments of 50 ppm applied once wk^{-1}. The greatest number of leaves, in this instance 22, were initiated in plants raised in Hassy 104 modules receiving 200 ppm N 3 x wk^{-1}, in contrast to plants grown in Hassy 308s receiving 50 ppm N 1 x wk^{-1} which initiated an average of fourteen leaves.

Leaf area was also significantly increased ($p < 0.001$) by growing plants in the larger Hassy 104 modules (Table 6.7). However, module size showed a highly significant interaction ($p < 0.001$) with the level of applied nitrogen on leaf area. Although plants raised in Hassy 308s displayed a

Table 6.7 Shoot characteristics in response to module size and nitrogen nutrition during propagation

	MODULE SYSTEM					
	Hassy 104			Hassy 308		
Nitrogen (ppm) :	50(1)	100(2)	200(3)	50(1)	100(2)	200(3)
Leaf number	16	20	22	14	16	19
Leaf area cm^2	33	100	169	15	42	59
Leaf dry weight g	0.85	1.85	1.97	0.33	0.63	0.68

Figures in parentheses represent application rates wk^{-1}

Leaf number	SED = 0.9	(d.f. = 34)
Leaf area	SED = 6.3	(d.f. = 34)
Leaf dry weight	SED = 0.193	(d.f. = 34)

four fold increase in leaf area from 15 to 59 cm^2 at nitrogen levels 50 ppm 1 x wk^{-1} and 200 ppm 3 x wk^{-1} respectively. This was lower than the five fold increase from 33 to 169 cm^2 when plants in Hassy 104s received the 'same' range of nitrogen treatments. As nitrogen solutions were applied by hand it was probable that plants raised in Hassy 104s received more nitrogen as a result of the larger surface area and volume of individual cells. Maximal leaf expansion to 169 cm^2 was therefore recorded for plants grown in Hassy 104 modules receiving 200 ppm N 3 x wk^{-1} in contrast to the leaf area of 15 cm^2 measured in plants grown in the smaller module and receiving 50 ppm N wk^{-1}.

Increasing module size resulted in an increased leaf dry weight, although the influence of module size on leaf dry weight was shown to interact ($p < 0.05$) with the level of applied nitrogen (Table 6.7). In both Hassy 308 and Hassy 104 modules the increase in dry weight from 0.33 g and 0.85 g to 0.63 g and 1.85 g respectively as a result of increasing the nitrogen from 50 ppm to 100 ppm was far greater than that achieved with a further increase in nitrogen level to 200 ppm where leaf dry weights of 0.68 g and 1.97 g were recorded in smaller and larger modules respectively. This may indicate a maximum leaf dry weight that can be achieved in a given module.

6.5.2.2 Curd initiation under field conditions Increasing the level of nitrogen applied during propagation resulted in an increase in the number of leaves initiated before the curd (Table 6.8).

The additional four leaves initiated before the curd when comparing extreme nitrogen treatments were shown to be highly significant ($p < 0.001$). This increase, however, may simply reflect the difference in leaf number at the time of transplanting (Table 6.7). Plants

Table 6.8

Nitrogen applied during propagation (ppm)	Leaf number initiated before the curd
50	31
100	34
200	35

Leaf number SED = 0.5 (d.f. = 107)

transplanted with fourteen and nineteen leaves may have been juvenile and mature respectively; the difference in leaf number at initiation may therefore have been expected to be greater. The possibility exists that smaller fourteen leaf plants establish faster under field conditions, making up for reduced growth during propagation. This is further supported by the observation that despite large differences in both leaf area and leaf weight immediately prior to transplanting (Table 6.7; Plate 4a) and during early field growth (Plate 4b) no consistent differences in these were recorded at the time of curd initiation. These results may possibly be explained by the levels of residual nitrogen in the field, in addition to nitrogen applied to the site immediately prior to transplanting and as a top dressing 17 days later (Table 6.6).

Similarly the spread of maturity, curd size and quality were not influenced by pre-transplanting treatments. In many cases individual plots were harvested with only two cuts, and only three buttoned curds were recorded from a total of 810 plants. Detailed analysis of the data is therefore not presented here.

Plate 4a Plants immediately prior to transplanting on 8 July 1986

Plate 4b Early field growth

6.6 Water stress and curd initiation

Low soil moisture status has previously been shown to accelerate curd initiation in the summer cauliflower, measured as a reduction in the number of leaves initiated before the curd (Salter, 1960b). However, this effect was variable and on at least one other occasion not observed (Aamlid, 1952).

A preliminary study was therefore undertaken to determine the effect of different levels of water stress, applied under controlled environment conditions, on curd initiation. The results of this study are reported here.

6.6.1 Materials and methods

Seeds of the cv Perfection were sown on 23 February 1985. Germination and general husbandry were as described in section 2.1.1.

Throughout the course of the experiment plants were grown under glasshouse conditions at a temperature of 20°C $\pm$ 3°C. Natural glasshouse irradiance was supplemented by 400 W SON/T lamps providing an additional 60 $\pm$ 5 Wm^{-2} incident at plant height for 12 h each day commencing at dawn.

On attainment of maturity, estimated here as occurring on initiation of the 19th leaf, the imposition of water stress treatments commenced. Water stress was imposed on plants in two ways. The first comprised differing levels of drought achieved by totally withholding water followed by periods of rehydration, returning plants to pot capacity. Within this 'cyclic' wet/dry regime two levels of stress were applied: intermediate stress (IS) and severe stress (SS). The degree of stress was

determined by measuring leaf water potential (Ψleaf) using the pressure bomb technique (section 2.4.2). Intermediate stress was at a Ψleaf of between -0.9 and -1.0 MPa and severe stress a Ψleaf of -1.5 MPa. These Ψleaf levels were attained typically within 24 to 48 hours as determined by periodic sampling. After achieving the desired level of stress in a sample of five plants, the plants were rewatered to pot capacity and normal watering resumed as with the controls. This cycle of drought followed by re-wetting to pot capacity was repeated on five occasions, individual cycles taking approximately 36 h.

A second, more 'constant' stress was imposed by supplying plants with known volumes of water each day. 'Constant' stress was imposed at two levels: half and quarter of full pot capacity, the latter being the control. The amount of water required daily had previously been established from a pilot experiment as 50 ml, 25 ml and 10 ml required to maintain full, half and quarter pot capacity respectively. However, as a result of variable climatic conditions careful monitoring and modification of these levels was required. Periodic measurements with the pressure bomb were also taken.

On completion of stress treatments plants were fed and watered as normal, feeding having been withheld during imposition of stress treatments. The number of days to curd appearance and leaf number subtending the curd were recorded as were measurements of vegetative shoot components as described earlier (section 2.6).

The five stress treatments were arranged in a randomised complete block design, and each treatment was replicated three times with fifteen plants per replicate. Four plants per replicate were recorded at curd appearance, the remainder being used to assess Ψleaf.

In addition to measurements of Ψleaf an attempt was made to measure the level of endogenous abscisic acid (ABA) within wilted and unwilted tissue. The accumulation of endogenous ABA in response to water stress has been well documented in a wide range of higher plants (Wright and Hiron, 1969; Wright, 1978). The procedure adopted for the extraction and analysis of ABA is described in detail in sections 2.8.1 and 2.8.2 respectively.

6.6.2 Results

Plants retained at a constant pot water capacity took on average 76 days to reach curd appearance (Table 6.9), while curd appearance in plants retained at one half pot capacity occurred five days earlier. Increasing the severity of imposed stress to one quarter pot water capacity advanced curd appearance by three days. The imposition of cyclic as opposed to the more constant stress again served to advance curd appearance with intermediate and severe stress treatments taking on average 72 and 73 days respectively compared to the 76 days recorded for control plants. When compared with each other the two levels of cyclic stress were shown not to differ significantly in their ability to accelerate curd appearance. Overall the promotory effect of water stress was shown to be highly significant.

The number of leaves initiated before the curd was significantly reduced ($p < 0.05$) by water stress (Table 6.9). The 35 leaves recorded for plants subjected to constant stresses of one half and one quarter pot capacity and a severe cyclic stress were significntly lower than the 38 leaves recorded in control plants. Intermediate cyclic stress resulted in 37 leaves being initiated before the curd which was shown not to differ significantly from the control treatment.

Table 6.9 Time to macroscopic curd appearance and associated shoot characteristics in plants subjected to different levels of imposed water stress during mature growth and development

	TYPE AND LEVEL OF IMPOSED WATER STRESS				
	CONSTANT			CYCLIC	
	Pot capacity (control)	Half pot capacity	Quarter pot capacity	Intermediate stress (-0.9 to -1.0 MPa)	Severe stress (-1.5 MPa)
Days to macroscopic curd appearance	76	71	73	72	73
Leaf number	38	35	35	37	35
Leaf dwt g	19.2	8.3	8.7	8.6	7.4
Leaf area cm^2	2035	1315	956	1024	763

Each figure represents the mean of 12

Days to macroscopic curd appearance	SED = 0.6	(d.f. = 55)
Leaf number	SED = 1.0	(d.f. = 55)
Leaf dry weight	SED = 1.05	(d.f. = 55)
Leaf area	SED = 61.0	(d.f. = 55)

A highly significant reduction in leaf dry weight ($p < 0.001$) at curd appearance was evident in all stress treatments independent of their severity (Table 6.9). Although all treatments resulted in a leaf dry weight significantly lower than the 19.2 g recorded for control plants, comparison of individual treatments showed them not to differ significantly from each other, with an average dry weight across treatments of 8.25 g.

The highly significant ($p < 0.001$) reduction in leaf area associated with stress treatments was in marked contrast to that observed for leaf dry weight measurements. Here, the reduction in leaf area was strongly influenced by the level of imposed stress (Table 6.9). All treatments were shown to differ significantly both from the leaf area of 2035 cm^2 recorded in control plants and from other stress treatments. Maximal reduction in leaf area to 763 cm^2 was associated with the imposition of a severe cyclic stress. The results here would suggest that the type of stress in addition to the level of stress is important in determining leaf area.

Despite repeated attempts, no clear increase in endogenous ABA associated with water stress was seen.

6.7 Summary

1. Nitrogen fertiliser applied to unchilled plants accelerated curd initiation as marked by a reduction in the number of leaves initiated before the curd. Curd initiation in chilled plants, however, was not affected by nitrogen applications.

2. At potassium levels of 30 mg wk^{-1}, nitrogen application to unchilled plants reduced the number of leaves initiated before the curd by five. At potassium levels of 10 mg a reduction of 15 leaves from c. 48 to 33 leaves before the curd was recorded in plants supplied with nitrogen.

3. Nitrogen applied at levels above 30 mg wk^{-1} had no further accelerating effect on curd initiation.

4. Increasing the level of applied nitrogen to chilled plants increased the number of days to macroscopic curd appearance. This effect of nitrogen was common to all three potassium levels.

5. Nitrogen applied at increased levels increased both leaf area and leaf dry weight in chilled and unchilled plants. Leaf area and leaf dry weight were shown to be highly correlated ($r = 0.94$). Independent regressions of both leaf area and leaf dry weight on applied nitrogen for the three potassium groups accounted for 82% and 90% of the variance in chilled and unchilled plants respectively when considering leaf dry weight and 90% and 92% for leaf area.

6. Curd initiation in chilled and unchilled plants appeared to require a minium leaf dry weight of c. 1.2 g. In unchilled plants curd initiation at low leaf numbers, c. 33 leaves, was associated with a higher leaf dry weight of approximately 5 g.

7. Nitrogen applied to mature plants at increasing levels significantly increased leaf area and leaf dry weight ($p < 0.001$) measured at curd appearance. The maximum leaf dry weight of 9.5 g and leaf area of 1039 cm^2 were recorded for plants receiving 140 mg N wk^{-1}.

8. Nitrogen content of plant tissue expressed as a percentage of total dry weight increased with the level of applied nitrogen. Plants receiving 140 mg N wk^{-1} had a nitrogen content of 6%.

9. Potassium applied at 30 mg wk^{-1} significantly increased ($p < 0.05$) the number of leaves initiated before the curd by four to a total of 51. The number of days to curd appearance and measurements of leaf growth were shown not to differ significantly in response to potassium treatments.

10. Larger modules (Hassy 104) used during propagation increased the number of leaves initiated prior to transplanting by three. Increasing the level of applied nitrogen from 50 to 200 ppm also increased the number of leaves initiated. Plants grown in Hassy 104 modules at a nitrogen level of 200 ppm 3 x wk^{-1} initiated 22 leaves during the propagation period by comparison with the fourteen leaves recorded for plants grown in Hassy 308s at 50 ppm N 1 x wk^{-1}.

11. Increasing module size increased the leaf area and leaf dry weight attained during propagation. Module size, however, showed a significant interaction with the level of applied nitrogen on both leaf area ($p < 0.001$) and leaf dry weight ($p < 0.05$). Maximal leaf growth was recorded for plants grown in Hassy 104 modules at 200 ppm N 3 x wk^{-1}.

12. Nitrogen applied during propagation at the highest level of 200 ppm 3 x wk^{-1} significantly increased ($p < 0.001$) the number of leaves initiated before the curd under field conditions by four, to 35, as compared with plants receiving 50 ppm 1 x wk^{-1} which had initiated 31 leaves. Both leaf development at curd maturity and the curds themselves were unaffected by pre-transplanting nitrogen and potassium treatments.

13. Water stress advanced curd appearance in unchilled plants by between three to five days, from the 76 days recorded in control plants retained at pot capacity. Severe water stress accelerated curd initiation by three leaves in unchilled plants. In all cases imposition of water stress resulted in a significant reduction ($p < 0.001$) in leaf dry weight at curd appearance. The highly significant reduction in leaf area ($p < 0.001$) displayed by plants under water stress was greatest at the highest level of stress imposed.

Chapter 7

GIBBERELLINS AS REGULATORS OF CURD INITIATION

Introduction

A role for gibberellins in mediating the acceleration of curd initiation by low temperature has been proposed by Wurr et al. (1981). This possible role is examined in preliminary studies here. These involved measuring effects of exogenous applications of gibberellins on curd initiation in cauliflower plants that were chilled for different periods. Gibberellin effects on curd initiation in modular raised transplants were also considered.

7.1 Comparison of the effects of GA_3 and GA_{4+7} on curd initiation

In many species floral initiation resulting from the application of exogenous gibberellins is known to be dependent on the specific GA applied (Michniewicz and Lang, 1962). Gibberellins A_3 and the combination of GA_{4+7} have been widely implicated in the floral initiation of cold requiring plants (Zeevaart, 1983).

The possibility that curd initiation could be accelerated by the application of a specific GA was considered in a preliminary study during which GA_3 and GA_{4+7} were applied to plants grown under warm (c. 20°C) conditions. The results of this study are reported here.

7.1.1 Materials and methods

Seeds of the cvs Perfection and White Fox were sown on 4 November 1985. Germination and general plant husbandry was as described

in section 2.1.1. On attainment of maturity (refer to Chapter 4) plants were treated with aqueous solutions of GA_3 or GA_{4+7} at concentrations of 100 ppm in each case. Preparation and application of the GAs followed the procedure described in section 2.7. A total of three applications were made over a fourteen day period, plants being sprayed until runoff. Application of a known volume enabled the weight of GA (µg) received by each plant to be calculated. However, plant growth during the treatment period meant that larger volumes were applied to the plants with subsequent applications; 4, 4.5 and 5 ml being applied to each plant on the first, second and third treatments respectively. A total of 1.35 mg was therefore applied to the leaves of each plant. Molecular weights of 346 g for GA_3 and 331 g for GA_{4+7} (m.w. GA_4 332; m.w. GA_7 = 330) enabled the molarity of the solutions to be calculated at 2.89×10^{-4}M and 3.02×10^{-4}M for GA_3 and GA_{4+7} respectively.

Throughout the course of the experiment plants were grown under warm glasshouse conditions at a mean daily temperature of 20°C. Natural irradiance was supplemented using 400 W SON/T lamps poviding an additional 60 ± 5 Wm^{-2} incident at plant height for 16 h each day commencing at dawn. The natural January photoperiod of c. 10 h was therefore extended.

Experimental treatments were considered complete at macroscopic curd appearance, and the effect of treatments on curd initiation were assessed as the number of leaves initiated before the curd. Attempts were also made to correlate changes in shoot development with time of curd initiation. Treatments were arranged using a completely randomised design with nine plants per treatment sampled at curd appearance.

7.1.2 Results

Curd initiation marked by the number of leaves initiated before the curd was promoted by the application of GA_{4+7} when compared with those plants which received application of GA_3 (Table 7.1). The number of leaves initiated before the curd was reduced by six and five to 39 and 33 leaves in cvs Perfection and White Fox respectively; a highly significant response to applied GA_{4+7} ($p < 0.001$).

Leaf dry weight at curd appearance was lowest in plants treated with GA_{4+7} (Table 7.1), and dry weights of 23.3 g and 22.6 g were recorded for cvs Perfection and White Fox respectively. However, despite an effect ($p < 0.01$) of gibberellin type, the difference was only significant when considering cv Perfection where application of GA_3 increased leaf dry weight by an average of 6.6 g to 26.9 g.

A highly significant increase ($p < 0.001$) in stem dry weight was measured in response to the application of GA_{4+7} in both cvs Perfection and White Fox (Table 7.1). Stem dry weights were increased from 7.9 g and 12.9 g in plants receiving GA_3, to 12.3 g and 19.4 g following treatment with GA_{4+7} in cvs Perfection and White Fox respectively. Stem dry weights at curd appearance were also shown to differ significantly when comparing cvs ($p < 0.001$). A reasonable negative correlation ($r = -0.76$; d.f. = 26) was evident between the number of leaves initiated, and stem dry weight at curd appearance. This correlation is consistent with the time of curd initiation being controlled by stem dry matter content, which in turn is increased by the application of GA_{4+7}.

Stem length was also significantly increased by the application of GA_{4+7} ($p < 0.001$) (Table 7.1) in both cvs studied. White Fox, however,

Table 7.1 Leaf number below the curd and associated shoot characteristics in cvs Perfection and White Fox treated with gibberellins under warm (c. 20°C) conditions

	CULTIVAR			
	PERFECTION		WHITE FOX	
Applied gibberellin:	GA_3	GA_{4+7}	GA_3	GA_{4+7}
Leaf number	45	39	38	33
Leaf dwt g	26.9	23.3	24.9	22.6
Stem dwt g	7.9	12.3	12.9	19.4
Stem length cm	31	40	33	48

Each value represents the mean of 9

Leaf number	SED	cultivars . gibberellins	= (1.40; d.f. = 32)
Leaf dwt	SED	"	= (1.37; d.f. = 26)
Stem dwt	SED	"	= (0.66; d.f. = 32)
Stem length	SED	"	= (2.50; d.f. = 32)

displayed the greater response, the stem length being increased by 15 cm to 48 cm as compared to 33 cm measured in plants treated with GA_3. In cv Perfection foliar applications of GA_{4+7} or GA_3 resulted in stem lengths at curd appearance of 40 cm and 31 cm respectively.

7.2 Effect of GA_{4+7} on curd initiation under sub-optimal chilling conditions

In a preliminary study not described here applied gibberellin had no effect on curd initiation in plants chilled for four weeks at 5°C. This chilling treatment would have more than satisfied the vernalization response. The objective of the experiment described here was therefore to compare the effect of GA_{4+7} applied during shorter chilling treatments of one and two weeks with similar GA_{4+7} treatments applied during four weeks' chilling.

7.2.1 Materials and methods

Seeds of cvs Perfection and White Fox were sown on 8 September 1986. Germination and general plant husbandry were as described in section 2.1.1. On attainment of maturity characterised by the initiation of 14 and 19 leaves in cvs Perfection and White Fox respectively (refer to Chapter 4), plants were transferred to controlled environment conditions at a constant 5°C $\pm$ 1°C for a period of one, two or four weeks, the latter being the control treatment. GA_{4+7} at a concentration of 100 ppm was applied as a foliar spray (refer to section 2.7) coincident with the chilling treatments. In order to reduce the possible interaction of applications with time all plants, irrespective of chilling duration, received three applications of GA_{4+7} in the first week of chilling. Dates of transfer to

and from chilling and the timing of GA_{4+7} applications are summarised in Table 7.2. Applications of Tween 20 to control plants were made at the same time.

During chilling plants were illuminated by a bank of 80 W warm white fluorescent tubes providing an irradiance of 50 ± 5 Wm^{-2} incident at plant height for 16 h each day. On completion of chilling (Table 7.2) plants were returned to warm glasshouse conditions (c. 20°C) to continue growth. Natural glasshouse irradiance was supplemented using 400 W SON/T lamps, providing an additional 65 ± 5 Wm^{-2} at plant height for 16 h each day commencing at dawn. The natural November photoperiod of c. 10 h was therefore extended in line with that used under controlled environment conditions both here and in the preceding experiment (refer to section 7.1.1).

Promotion or retardation of curd initiation resulting from the application of GA_{4+7} was assessed as the number of leaves initiated before the curd. Development of individual shoot components was also measured as described elsewhere (section 2.6).

Experimental treatments were arranged in a completely randomised design, with nine plants per treatment sampled at curd appearance.

7.2.2 Results

Application of GA_{4+7} significantly reduced ($p < 0.001$) by 10 the number of leaves initiated before the curd when applied to plants of cv White Fox chilled at 5°C for one week (Fig 7.1b). No similar effect was observed in cv Perfection (Fig 7.1a). The number of leaves recorded in the remaining treatments (Fig 7.1) were not significantly affected by GA_{4+7}. Increasing the duration of chilling from one to four weeks did,

Table 7.2 Dates of transfer to and from chilling and time of GA_{4+7} applications

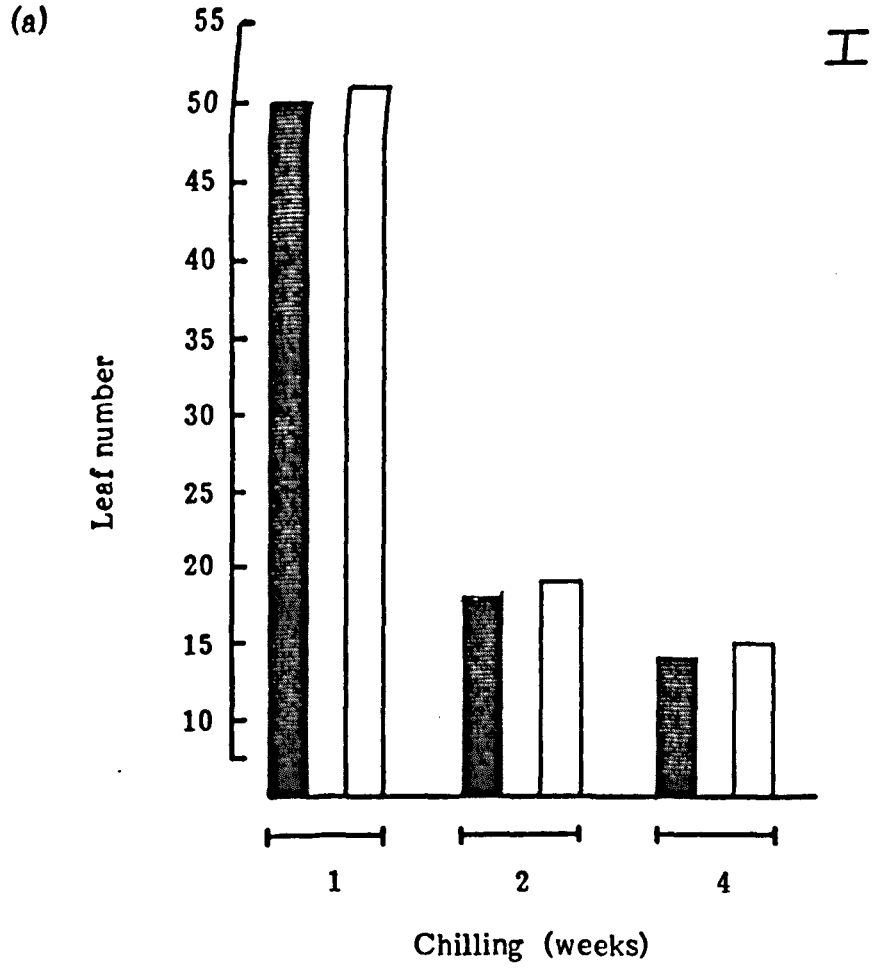
Cultivar	Chilling at 5°C			GA_{4+7}; foliar applications		
	Start chilling	Duration (weeks)	Finish chilling	1	2	3
Perfection	3.10.86	1	10.10.86	5.10.86	7.10.86	9.10.86
		2	17.10.86	"	"	"
		4	24.10.86	"	"	"
White Fox	17.10.86	1	24.10.86	19.10.86	21.10.86	23.10.86
		2	31.10.86	"	"	"
		4	14.11.86	"	"	"

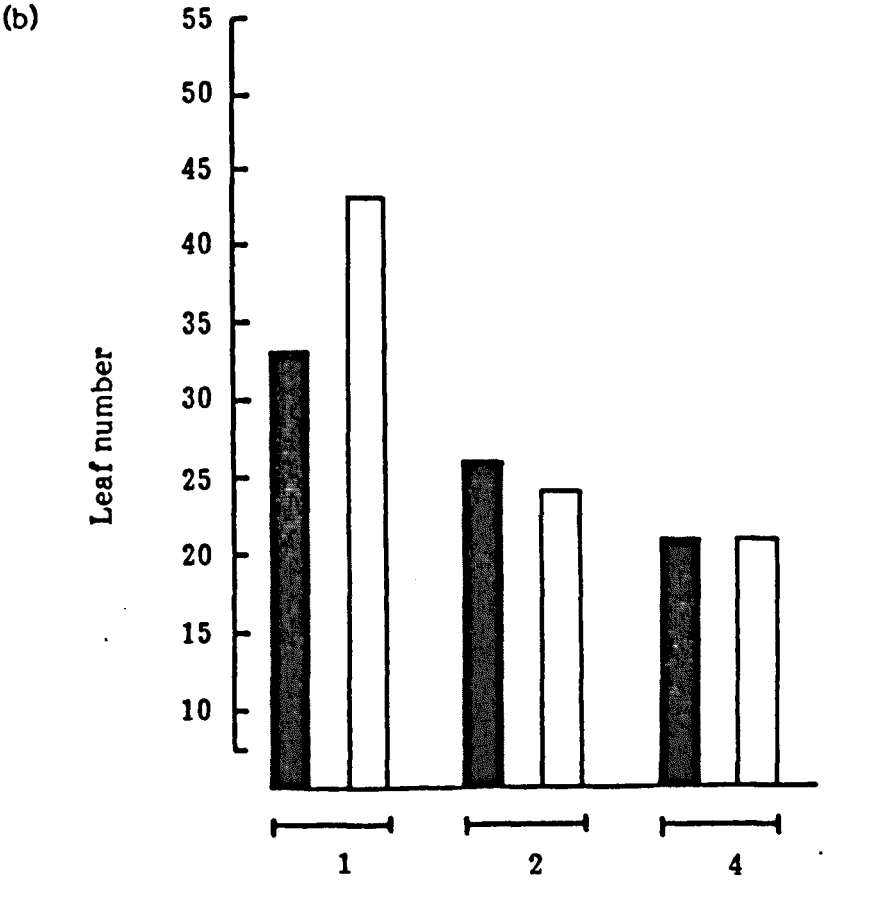
Fig 7.1 Effect of GA_{4+7} applied during chilling treatments of one, two or four weeks at 5 °C, on leaf number at macroscopic curd appearance in cvs Perfection (a) and White Fox (b)

GA_{4+7}

Tween 20 (control)

SED (d.f. = 86)


(a)
55
50
45
40
35
30
25
20
15
10
Leaf number
1
2
4
Chilling (weeks)


(b)
55
50
45
40
35
30
25
20
15
10
Leaf number
1
2
4

however, cause a marked reduction in the number of leaves initiated before the curd in both cvs Perfection and White Fox.

Changes in individual shoot components resulting from the application of GA_{4+7} or increased chilling duration reflected trends described elsewhere (refer to preceding experiment and section 3 respectively). Detailed analysis of the data has therefore been omitted. No correlations between changes measured in shoot components with the time of curd initiation were evident under the conditions employed here.

7.3 GA_{4+7} and curd initiation in modular raised transplants grown under field conditions

The objective of the experiment described here was to ascertain whether the application of GA_{4+7} to modular raised plants during propagation could substitute, at least in part, for a period of 'relative' cold and accelerate curd initiation following transplanting into the field. The influences of GA_{4+7} on both the spread of curd maturity and curd quality were also considered.

7.3.1 Materials and methods

The application of GA_{4+7} to modular grown plants of cv White Fox was an additional treatment incorporated into the field trial described in detail in section 6.5.1. Within each of the three nitrogen treatments of 50, 100 and 200 ppm, GA_{4+7} at a concentration of 100 ppm was applied at two stages of development marked by the initiation of 14 and 19 leaves respectively. A third control treatment comprising surfactant only (Tween 20) was applied at the 14 leaf stage, and methods of application were as detailed in section 2.7.2. It was postulated that at leaf numbers

between 14 and 19 (approaching phase transition) plants may display increased sensitivity to exogenous GA_{4+7}. Inability to attain 19 leaves during propagation in Hassy 308s (volume : 14 cm^3) meant that GA_{4+7} treatments to plants with 19 leaves were given under field conditions shortly after transplanting on 8 July. Foliar applications of GA_{4+7}, or Tween 20 in the case of control plants, were made on three occasions over the period of fourteen days.

Crop husbandry, sampling and measurements of plant material and assessment of both curd maturity and quality were as detailed in section 6.5.1.

7.3.2 Results

As the effects of GA_{4+7} applications on plant growth were independent of those recorded for nitrogen nutrition and module size described in a preceding section (refer to section 6.5.2), it was possible to present the results separately.

7.3.2.1 Leaf growth during propagation Leaf dry weight prior to transplanting was significantly increased ($p < 0.001$) by the application of GA_{4+7} to plants which had initiated 14 leaves, the leaf dry weight being increased from an average of 0.9 g for control plants to 1.5 g. As application of GA_{4+7} at 19 leaves was carried out in the field these plants could not be considered here. The number of leaves initiated and leaf area attained during propagation were not significantly affected by the application of GA_{4+7}.

An interesting observation was the marked 'greening' effect in plants which had been treated with GA_{4+7} (Plate 5). It may be suggested

Plate 5 'Greening' effect resulting from the application of GA_{4+7} demonstrated on the right. Plants on the left received Tween 20 only

that possible increased photosynthetic activity in these plants could account for the measured increase in leaf dry weight.

7.3.2.2 Curd initiation under field conditions Application of GA_{4+7} significantly decreased ($p < 0.001$) the number of leaves initiated before the curd by five (Table 7.3). Maximal reduction in leaf number compared to the average of 36 recorded for control plants occurred when GA_{4+7} applications were commensurate with phase transition at 19 leaves, resulting in an average of 31 leaves being initiated before the curd.

Table 7.3 Leaf number initiated before the curd in plants treated with GA_{4+7}

Treatment	Leaf number at time of application	
	14	19
GA_{4+7}	33	31
Control (Tween 20)	36	

Application of GA_{4+7} had no significant effect on the leaf area or leaf dry weight recorded at the time of curd initiation. The absence of any response was consistent with results reported for nitrogen nutrition and module size (section 6.5.2.2). Data are therefore not presented here.

The slight promotory effect of applied GA_{4+7} on curd initiation was not reflected in the spread of curd maturity. This did not differ significantly between gibberellin treatments. Similarly curd size and quality was unaffected.

7.4 Summary

1. GA_{4+7} accelerated curd initiation by six and five leaves in unchilled plants of cvs Perfection and White Fox respectively as compared to the 45 and 38 leaves initiated before the curd following application of GA_3.

2. GA_{4+7} applied to unchilled plants of cv Perfection significantly reduced leaf dry weight at macroscopic curd appearance by 6.6 g compared to plants treated with GA_3. Stem dry weights were increased by 4.4 g and 6.5 g in cvs Perfection and White Fox respectively when treated with GA_{4+7} compared with those treated with GA_3. Stem lengths were extended by 15 cm and 9 cm by the application of GA_{4+7} in plants of cvs Perfection and White Fox respectively, compared to GA_3 treatments.

3. Stem dry weight and leaf number at curd appearance were shown to be negatively correlated ($r = -0.76$). This correlation is consistent with the time of curd initiation being controlled by stem dry matter content.

4. GA_{4+7} applied to cv White Fox in conjunction with one weeks' chilling at 5°C significantly reduced ($p < 0.001$), by ten, the number of leaves initiated before the curd.

5. GA_{4+7} at a concentration of 100 ppm applied to modular grown plants of cv White Fox which had initiated 14 leaves increased the average leaf dry weight per plants by 0.6 g to 1.5 g immediately prior to transplanting.

6. Curd initiation under field conditions was accelerated by the application of GA_{4+7}. Maximal reduction in leaf number occurred when applications were commensurate with phase transition at 19 leaves; leaf number before the curd was reduced by five to 31.

Chapter 8

DISCUSSION

The purpose of this discussion is to consider together the results of the investigations described in the earlier chapters of this thesis. Whilst wishing to minimise repetition, further reference to results was considered necessary to allow a full discussion.

Acceleration of curd initiation in the cauliflower by chilling was measured here both as a reduction in the leaf number beneath the curd and as a decrease in the number of days to macroscopic curd visibility. The extent of the low temperature effect was dependent both on the genotype and age of the plant, and on the duration and temperature of the chilling treatment. This agrees with previous observations of Sadik (1967), Wurr, Akehurst and Thomas (1981), Liptay (1981) and Wiebe (1983). Maximal reduction in leaf number resulted from four weeks' exposure to 5°C, but curds could be initiated even in plants grown at 25°C, emphasising the quantitative nature of the low temperature effect.

The early summer cvs Perfection and Alpha Cliro initiated curds following exposure of six week old plants to 5°C for four weeks, without initiating any more leaves. It may therefore be concluded that the 19 and 18 leaves initiated at the start of chilling in cvs Perfection and Alpha Cliro respectively were equal to or greater than the leaf number marking transition from the juvenile to mature forms. A less marked vernalization effect of chilling was apparent in younger plants of both cv Perfection, with 12 leaves, and Alpha Cliro with 9. Further studies demonstrated that during chilling at 5°C for four weeks, approximately four more leaves would initiate (Chapter 5). This suggested that phase transition could occur during chilling and if the chilling treatment was long enough plants would then be vernalized.

The late summer cvs Dok and White Fox appeared less responsive to low temperature than the early summer cultivars. There were two possible explanations for this. Firstly, later cultivars may have a requirement for longer than four weeks at 5°C to express maximum promotion of curd initiation. Secondly, later season cultivars may have a longer juvenile phase where phase transition is marked by a higher leaf number than that achieved by plants used for this study. The second explanation is favoured here and is discussed later with reference to juvenility. Similar observations have previously been reported for summer cauliflowers (Sadik, 1967; Salter and James, 1974; Wiebe, 1974) and for the Roscoff winter heading varieties St Thomas and St Gwithian (Wurr et al., 1981). The number of days to macroscopic curd visibility following exposure to low temperature also showed a maximal reduction after four weeks' exposure to 5°C. Time of curd initiation could be calculated from this date if the rate of early curd growth was known and was shown to be constant between cultivars.

Maximum suppression of vegetative growth measured as a reduction in leaf dry weight was associated with rapid promotion of curd initiation. This may suggest an element of competition between vegetative growth and shoot apex development.

In cold responsive plants low temperature is reported to induce flowering and simultaneously to increase the level of carbohydrates in the shoot tip (Trione, 1966; Sadik and Ozbun, 1968). Although evidence is lacking for a causal relationship between carbohydrate level and flowering in cauliflower (Sadik and Ozbun, 1968), temperature treatments that reduce carbohydrate levels also reduce the number of plants flowering. Similarly with broccoli (Fontes, Ozbun and Sadik, 1967) low temperature

enhanced flowering, and higher growing temperatures of 24-27°C blocked flowering.

On the basis of results obtained from this preliminary study, further experiments were restricted to two cultivars, Perfection representing the early summer cauliflowers and White Fox, the mid to late season cultivars. The selection of Perfection was based primarily on its having a clear, large vernalization response to short chilling treatments. It also had a distinct juvenile phase during which no significant vernalization response was measured. Propagation of cv Perfection was simple and it was possible to reproduce plant material of high uniformity. The commercial importance of Perfection, as indicated by its inclusion in the National Institute of Botany's list of recommended varieties, was also a consideration. The reasons for selecting cv White Fox were less strong. This cultivar was used primarily to provide contrasts with Perfection and also because of its commercial importance.

Reducing the total irradiance receipt caused marked delays to curd initiation and hence an increase in the leaf number beneath the curd in both cvs Perfection and White Fox. Irradiance exerts a strong effect on flower initiation in many other plants (Halevy, 1974; 1984; Cockshull, 1984). In tomatoes low irradiances experienced during early seedling growth delay inflorescence initiation (Calvert, 1959; Wittwer, 1963). In a growth room study, Calvert (1959) showed that reducing the illuminance level from 10,000 to 2,500 lux delayed flower initiation by up to 29 days and allowed up to approximately seven more leaves to be produced before the inflorescence was initiated. Effects of light were greater at high temperatures (25°C) than at lower temperatures (15°C). These results are analogous to those found here with cauliflowers. In many woody plants

transition to reproductive development is controlled mainly by irradiance (Jackson and Sweet, 1972).

Slower leaf initiation in the later season cv White Fox was consistent with the findings of previous studies, notably Wurr, Fellows and Crisp (1982) which demonstrated that both final leaf number and rate of leaf production differed substantially according to variety. An interesting feature of their work may account for the high rate of leaf initiation observed in the cv Abundantia (section 3.1). Although included in experiments here as a late summer cultivar, Abundantia was originally thought to belong to the over-wintered, spring heading (biennial) group. Wurr et al. (1982) showed marked negative correlations across varieties between leaf production (rate and number) and rate of curd expansion. Their results further suggested that fast rates of curd expansion follow slow rates of leaf production, and that in annual varieties such as Perfection and White Fox, growth is biased towards curd production while in the biennial varieties leaf growth predominates.

Rate of leaf initiation was shown here also to be under the control of irradiance receipt. Higher light integrals accelerated leaf initiation. These findings are consistent with results from studies with other plants such as that on Cucumis (Milthorpe and Newton, 1963) where the rate of leaf initiation is related to irradiance ($MJm^{-2}\ d^{-1}$). Regressing leaf number on light integral showed that the light integral incident at plant height required for the initiation of one leaf was constant throughout experiments at 6.6 and 7.8 MJm^{-2} for cvs Perfection and White Fox respectively. There were however significant displacements of the fitted lines observed in both cvs between shaded and unshaded treatments. Whilst differences in light quality and air temperature were unlikely to cause this

displacement, the intensity of natural radiation can affect tissue temperature and consequently developmental processes (Gates, 1968; Rickman, Klepper and Peterson, 1985). However, because of the cooling effect of transpiration the mean temperature of a leaf freely supplied with water rarely departs from the temperature of the ambient air by more than $\pm$ 2.0°C, even in bright sunshine (Monteith, 1981b). It was more probable that the seedlings under shading treatments in experiments here were watered less than those on open benches. This would account for the observed displacement in the fitted lines.

Growth in dry matter and leaf area was also depressed under imposed shading. Growth in shoot weight, comprising stem and leaf components and associated leaf area was shown to increase exponentially over the irradiance range 125 to 350 MJm^{-2}, but was not maintained at integrals greater than 350-400 MJm^{-2}. The similarity of quadratic curves for individual shoot components is not surprising as differences in weight gain and leaf area during early vegetative growth should be comparable. Whilst all growth curves might first be fitted as quadratic curves, since early growth is logarithmic and inevitably diminishes with time (Hurd, 1977), comparison of individual shading treatments would suggest a reduction in light utilisation efficiency with increased growth in individual shoot components.

The conversion efficiency of incident light energy to chemical energy in tomato plants ranges from 15 per cent in seedlings in low continuous light diminishing with increasing light integral and plant age to about six per cent (Hurd and Thornley, 1974). Similarly in a study of bulb development in onion (Brewster, Mondal and Morris, 1986), lower efficiency of conversion of intercepted radiation coincided with periods of high mean

temperature and irradiance. A decrease in the efficiency of the leaf canopy might be expected as a result of self shading with increasing plant size. Net photosynthetic efficiency of leaves has also been shown to decline with age as the plant approaches harvest (Woolhouse and Jenkins, 1983) and the ratio of 'maintenance respiration' to photosynthesis can increase as the plant or crop increases in weight (Biscoe and Gallagher, 1975). It can be expected therefore that irradiance receipt will influence both leaf and curd initiation in the cauliflower. High irradiance integrals serve to accelerate leaf initiation, reducing, at least chronologically, the duration of the juvenile stage and accelerating curd initiation, probably by increasing carbohydrate availability to the stem apex.

Carbohydrate availability to the shoot apex has been implicated in the control of vernalization and floral initiation in a wide range of species (Bodson, 1984; Bodson and Bernier, 1985; Sachs, 1987). In Sinapis alba the sucrose concentration of the apex increased by more that 5% within 10 hrs of the start of an inductive 'displaced short day' (Bodson and Outlaw, 1985). Flower initiation in the quantitative long-day plant Brassica campestris was earlier and at a lower final leaf number when sucrose was added to the medium in which plants were grown in sterile culture (Friend, Bodson and Bernier, 1984). A possible role for carbohydrates in low temperature induction has already been considered earlier in this discussion. Whilst conclusive evidence of a regulatory role for carbohydrate in the initiation of cauliflowers is still to be obtained, other studies undertaken in this laboratory (Williams, 1988) and circumstantial evidence derived here from studies of low temperature and irradiance receipt indicate that an early physiological event in initiation is the increased availability of carbohydrates at the shoot apex.

Post-vernalization photoperiod was shown to influence the time of curd initiation but only when the duration of the preceding vernalization treatment was restricted to one week. Photoperiods of 24 h then delayed curd initiation, marked by an increase in leaf number subtending the curd. Chilling for one week had previously been shown to be sub-optimal for vernalization (section 3.1). Accelerated curd initiation observed under short photoperiods following sub-optimal vernalization may represent an additive effect or true substitution by short days for low temperature. The phenomenon whereby short day treatment may substitute either partly or entirely for cold is often referred to as "SD vernalization" and is seen in certain winter cereals (Purvis, 1958; Lang, 1965) and vegetables (Atherton, Basher and Brewster, 1984).

Failure of previous studies to demonstrate an interaction between photoperiod and vernalization in cauliflower (Parkinson, 1952; Sadik, 1967) may be attributable to varietal differences in response to time of application of photoperiodic treatments (Parkinson, 1952). In the latter study plants were grown under field conditions and probably received saturating vernalization treatments.

Continuous lighting also caused maximum stem extension irrespective of the duration of the preceding vernalization treatment. The high correlation between stem length and leaf number at curd initiation may indicate that delayed initiation under a 24 h regime was a consequence of increased stem extension rather than a direct photoperiodic effect. In previous studies where tungsten filament lamps have been used in preference to fluorescent lamps to extend natural short days, as with the present study, internodes were longer. This phenomenon which is also observed in tomato and Glycine max cv Biloxi (soya) (Downs, Borthwick and

Piringer, 1958) has been attributed to the higher content of far-red light in the emission spectrum of tungsten filament lamps.

Stem dry weight at curd initiation in plants which had received one week's vernalization was lowest following growth under a 16 h photoperiod as compared with 8 h or 24 h regimes. As leaf number was positively correlated with stem dry weight, 16 h would appear to be the optimum photoperiod for curd initiation following sub-optimal vernalization. Studies on spring barley (Cottrell and Dale, 1986) concluded that growth and development of the ear was controlled by rate of use of available soluble carbohydrate which in turn was subject to photoperiodic control. Correlations of stem dry weight with leaf number below the curd suggests that there may be a similar control mechanism determining time of curd initiation. Similar mechanisms of flower induction have been proposed elsewhere for other plants (Pryke and Bernier, 1978; Bernier, Sachs and Kinet, 1981).

Initiation of a critical number of leaves was shown to mark the end of the juvenile phase and sharply define transition to the mature form in both cvs Perfection and White Fox. This attainment of competence to respond to a vernalization stimulus was marked by the initiation of 14 and 18 leaves in Perfection and White Fox respectively. Competence to respond to vernalization was acquired rapidly at that stage of development, phase transition being complete within two plastochrons. Attainment of a minimum leaf number is consistent both with preceding studies here (section 3.1) and with those elsewhere (Wiebe, 1972a; 1974; Salter and James, 1974; Wurr, 1981). Observations that later season cvs possess a juvenile phase that terminated at a higher leaf number were also consistent with findings from earlier studies (Wiebe, 1974; Wurr, Akehurst and Thomas, 1981).

Effective manipulation of curd initiation by imposed chilling to bring about more uniform curd initiation and consequently curd maturity (Salter, 1969), is heavily dependent on an accurate determination of the duration of the juvenile phase. Failure to do so may account for many of the inconsistent results achieved with the artificial chilling of cauliflower transplants recorded in the past (Salter and Ward, 1972; Salter and James, 1974). Whilst chilling applied after phase change would promote curd initiation, chilling during juvenile development would cause a delay (section 3.1).

Competence to respond to a vernalization stimulus after phase change was retained in plants with leaf numbers as high as 36. These plants displayed accelerated curd initiation when chilled (section 4.1). This is in stark contrast to earlier studies (Salter and Ward, 1972; Thomas et al., 1972; Wurr et al., 1981) where the curd induction phase was suggested as being analogous to a narrow 'window' delineated by specific numbers of leaves. Salter and Ward (1972) observed that cold treatments reduced the length of the curd harvesting period of cvs Le Cerf B and Hylite when applied to six week old plants but were ineffective on eight week old plants. The cvs Le Cerf B and Hylite were therefore competent to respond to a vernalization stimulus at leaf numbers of 11.5 and 10.2 respectively, but were apparently unable to do so after initiating 17.9 and 12.9 leaves. A further study however (Salter and James, 1974) demonstrated that all growth stages of the three autumn cultivars responded to the cold treatment by a reduction in the length of the harvest period. In attempting to explain the lack of a discrete induction phase in the second study, Salter suggested that individual plants comprising a population may enter the inductive phase at different leaf numbers. In addition, individual plants

were suggested to have differing quantitative cold requirements for curd induction. No evidence to support these views was derived from the present study. Accurate determination of the juvenile phase is clearly essential for the full interpretation of Salter's studies.

The presence of a longer juvenile phase in later maturing varieties is clear from this present study. Whilst this is both consistent with previous work (Sadik, 1967; Wiebe, 1974), it is in contrast to Salter's findings where plants of the autumn cultivars Le Cerf B and Hylite were able to respond to chilling after initiation of only c. 10-12 leaves.

Parameters of leaf growth other than leaf number examined here could not be used as stable markers for phase transition. The ease with which leaves may be lost during sampling also favours leaf number as a marker of phase transition, as scars may be counted in the absence of the leaves themselves. As the log of shoot dry weight was linearly related to leaf number it was anticipated that this could also be a stable, practical marker of phase transition.

Pre-vernalization high temperatures of 18°C and 25°C during juvenile growth did not reduce the response to vernalization. This is in contrast to results observed in studies with cabbage (Heide, 1970) and Chinese cabbage (Elers and Wiebe, 1984). Earlier studies with cauliflower (Salter and James, 1974) indicated that the temperature at which plants are raised can influence their response to a subsequent cold treatment. However, the contrasting conditions under which Salter's plants were raised do not facilitate direct comparison with the present study. Where Salter's plants were raised in Dutch lights they may have partially satisfied their low temperature requirement before the cold treatment began. Plants in Salter's second treatment raised under an 18/13°C day/night regime would

only have received the 14 day cold treatment which may have been insufficient to satisfy completely the cold requirement as observed from results in the present study (section 3.1). Salter's result may therefore reflect partial vernalization rather than a temperature effect on competence. Clearly juvenility had not been considered in that work in relation to raising temperatures.

Increases in the rate of leaf initiation with increasing temperature over the range 2 to 20°C would cause the chronological duration of juvenility to vary considerably with plant raising temperature. Decline in the rate of leaf initiation with further increase in temperature from 20 to 25 and 35°C observed here suggested an optimum temperature for leaf initiation of c. 20°C. A base temperature for leaf initiation of c. 2°C was also indicated. The dependence of leaf initiation rate on temperature has implications for the timing of any cold treatment to be applied after phase transition. The need to measure juvenility in terms of leaf number and not time both in experimental investigations and in manipulation of commercial crops is clear. The influence of raising temperature on leaf initiation described here is largely consistent with the findings of Wiebe (1972c) in which the rate of leaf 'formation' was shown to increase with increasing temperature up to 22°C.

Uniform curd initiation was expected to be achieved (Wiebe and Krugh, 1974) by raising plants at high temperatures (c. 20°C) and then, after phase transition, subjecting them to a standard cold treatment of 2 weeks at 2°C. However, in the present studies a highly significant linear relationship was established when regressing leaf number on shoot dry weight during juvenile and early vegetative growth. As a result, large plants were produced at high temperatures both here and in earlier studies

(Wiebe, 1972c). Transplanting large plants is known to increase the incidence of buttoning (Chapter 1) and would seem to negate the value of this plant raising procedure. This conclusion was arrived at by Wiebe himself in a later publication (Wiebe, 1983).

Manipulation of phase change and establishment of uniform initiation would require an understanding of differences in juvenility between cultivars. In addition to differences in critical leaf number at phase change, the time of this event would also be determined by a cultivar-dependent rate of leaf initiation. Wurr, Fellows and Crisp (1982) showed rates of leaf initiation to be slower in later maturing types than in earlier types. Duration of the juvenile phase in Brussels sprout cultivars was found here to be solely dependent on rate of leaf initiation; slower rates associated with later maturing types (Thomas, 1980). No differences were found there in critical leaf number for phase change.

A thermal time procedure was used to measure leaf initiation in these studies. Justification for this is given in section 4.3. A base temperature of 2°C was determined here for leaf initiation in cv Perfection. This was close to that reported for other temperate crops (Angus et al., 1981; Baker and Gallagher, 1983a). The similarity in thermal time requirements for leaf initiation calculated on this basis for plants growing under different temperature regimes supported the use of this procedure. Gallagher and co-workers (Gallagher, 1979a; Baker and Gallagher, 1983b) have shown that the production of leaf and spikelet primordia, leaf appearance, lamina expansion and the duration of leaf growth of field grown wheat and barley may all be described in terms of thermal time.

Thermal requirements for leaf initiation measured in degree-days during juvenile and mature phases of development were calculated as 50 and 18°C d per leaf respectively. These were in close agreement with the values 41 and 19°C d derived from a preliminary study. Differences in the rate of leaf initiation during juvenile development when comparing the first and second studies probably resulted from the relatively few measurements taken during the earlier study. Leaf initiation rate is known to be influenced by irradiance (section 3.3) whilst photoperiod is known to interact in a multiplicative manner with temperature in controlling leaf initiation in wheat (Kirby, 1974; Gallagher, 1979; Baker and Gallagher, 1983b). Interactions between temperature and irradiance on leaf initiation were not examined in the present study.

Increased rates of leaf initiation just prior to floral initiation are widespread in a range of photoperiodically sensitive species (Evans, 1960; Dale and Wilson, 1979). A similar phenomenon is seen following phase change in Hedera (Hackett, Cordero, and Srinivasan, 1987). Despite a close relationship between transition to flowering and rapid leaf initiation, there appears to be no causal relationship (Bernier, Kinet and Sachs, 1981). Treatments which hasten leaf initiation need not result in floral initiation. Shortening of the plastochron may be considered either as a necessary but insufficient component of evocation or as an indication of an underlying physiological event associated with evocation.

Faster rates of leaf initiation found here in cauliflower after phase change may reflect enhanced availability of nutrients to the stem apex. Consistent with this hypothesis are the observations that environmental changes effective in accelerating leaf initiation, such as higher irradiance (section 3.3; Milthorpe and Newton, 1963), longer

photoperiods (Dale and Wilson, 1979) and increasing temperature in the range 10 to 20°C (section 4.3; Dale and Milthorpe, 1983) also enhance assimilate supply.

Chilling imbibed seed proved to be ineffective in reducing the number of leaves initiated before the curd in both cvs Perfection and White Fox. The observations are consistent with the studies of Wiebe (1972a) in which seed of the cvs Aristokrat and Sesam were chilled at 1°C for periods of 0 to 12 weeks. Subsequent curd initiation at temperatures of 10, 15 and 20°C was unaffected. Reports of effective seed vernalization (Kato, 1964; Fujime and Hirose, 1979) are open to question. Kato (1964) reported that seed vernalization in cauliflower cvs Sakata-gokuwase and Nozaki-wase, both summer maturing types, was only effective when supplemented with plant vernalization. As chilling treatments imposed by Fujime and Hirose (1979) lengthened from 0 to 45 days, the number of leaves initiated before the curd decreased by approximately five in the cv Nozaki-wase; a small reduction when compared with that achieved by the vernalization of mature plants reported here. Where plants were grown at a constant 15, 20 or 25°C following seed vernalization (Fujime and Hirose, 1979), curds were formed at 20°C when seeds had been chilled but not in unchilled controls. There was no effect of seed vernalization at 15°C, where plants formed curds regardless of chilling or at 25°C where plants failed to initiate curds even when seeds were chilled.

One of the main aims of this thesis was to investigate techniques for the prediction of curd initiation from a knowledge of curd initiation responses to various environmental factors. As the main environmental factor regulating curd initiation was temperature, the thermal time procedure of Gallagher (1979a) and Garcia Huidobro et al. (1982a) was investigated.

The use of 'thermal time' here has two main advantages over the traditionally used 'heat sums'. Firstly, while the use of heat sums as the basis of predictive systems has been widespread (Brown, 1960; Dickson, Reiger and Peterson, 1961; Cross and Zuber, 1972) the selection of the appropriate base temperature is often arbitrary, in the present study it is defined experimentally. Secondly, it is often assumed in simple heat sums systems that all temperatures above the base are equally effective in eliciting a response. The thermal time procedure used here allows the optimum temperature for the process to be determined and the correct adjustments to the model to be made when this is exceeded.

Adaptation of the thermal time procedure (Chapter 5) was dependent on establishing the cardinal temperatures for curd initiation, the rate of curd initiation being measured both as reciprocal of leaf number subtending the curd and the reciprocal of the number of days to macroscopic curd visibility. Analysing the response in terms of rate has several advantages (Roberts and Summerfield, 1987). First, a consideration of rate rather than time is probably one step closer to the basic cause of developmental processes: the reason why an event happens in a short time is because the rate of progress was rapid, and not vice versa. Secondly, because the relation between temperature and rate is typically linear, data from only a few environments (theoretically only two) are required to define and quantify it. The reciprocal of days to macroscopic curd visibility being the reciprocal of a process duration is therefore a measurement of rate. Whilst reciprocal of leaf number does not consider time and therefore cannot be a true rate ($^{1}/$Duration) it was considered here to be a good marker of the 'rate of progress' towards curd initiation. In addition the linear relationship between rate and temperature which

enabled the cardinal temperatures to be determined also satisfied one of the basic prerequisites for the application of the thermal time procedure (Gallagher, 1979a; Garcia Huidobro et al., 1982a). Linear regressions fitted to both sub- and supra-optimal temperatures enabled temperatures exceeding T_o to be incorporated into subsequent thermal time calculations. Taking account of supra-optimal temperatures was considered to be important as the relationship between development and thermal time breaks down when the temperature exceeds the optimum for a substantial part of the period over which it is integrated (Monteith, 1977).

The nature of the linear response described here, and its possible relevance to physiological changes occurring during vernalization, may be considered in the light of mechanisms discussed by Schwabe (1971). Schwabe proposed that the overall effect of vernalization depended upon a balance in the plant between two separate reactions of differing Q_{10} that possibly competed for the same substrate. One reaction was considered as promoting flowering while the other was considered inhibitory. Furthermore these reactions differed in their cardinal temperatures. The inhibitory reaction was characterised by a high base temperature. Lowering the temperture would arrest the inhibitory reaction sooner, possibly at a temperature close to the optimum for vernalization. The promotive reaction on the other hand could still continue at a lower temperature. Increasing the temperature from T_b to T_o would therefore favour the promoting reaction. Increasing the temperature further from T_o to T_m would increase the rate of inhibitory reactions more than those of a promotive nature. At T_m, insufficient promoter would be formed for vernalization to proceed. Evidence supporting this hypothesis has not been obtained and the biochemical nature of such reactions is not understood.

Why the relationship between temperature and the rate of development processes reported here should be linear is not clear (Monteith, 1981). Simple in vitro biochemical reactions conform to the Arrhenius relationship in which the rate is exponentially related to absolute temperature. In a logarithmic notation, the log of the rate constant is a linear function of the reciprocal of absolute temperature. Reviewing the problem of growth rate and development responses to temperature in vivo, Gallagher (1976) concluded that the Arrhenius equation;

$$k = Ae^{-E/RT}$$

where k = rate constant, T = temperature in K, R = gas constant, A = constant, E = activation energy of the reaction,

or in logarithmic notation:

$$\text{Ln } k = \text{Ln } A \frac{-E}{RT}$$

often did not provide a satisfactory description. Many reports have shown that the rate/temperature relationship was linear rather than exponential (refer to Chapter 1). It is probable, as suggested by Schwabe (1971), that the rate of a biological process is determined by a complex of reactions each independently affected by temperature, the rate limiting reactions involved combining to give a linear dependence of rate on temperature over a wide range of temperatures (Hegarty, 1973).

Roberts and Summerfield (1987) speculated that the effect of temperature on rate of development would be linear. They reasoned that relative growth rates and rates of development often relate linearly to the logarithm of the concentrations of limiting substances. The Arrhenius relation implies that a linear change in temperature would induce a similar

change in the logarithm of the concentration of some limited factor. Hence, a logarithmic change in concentration of the limiting factor causes a linear change in rate of development.

Effective temperatures for curd initiation in cv Perfection (section 5.1.2.3) ranged from a base of -1.25°C to a maximum of 23.5°C; the optimum being 5.5°C. The temperature range over which vernalization occurred in cv White Fox was wider, with T_b and T_m being -3°C and 31.5°C respectively with an optimum of 8.6°C. Whilst these optima, particularly that of cv White Fox, are in close agreement with the optimum of 7 to 12°C derived for cvs Aristokrat and Sesam (Wiebe, 1972b) a full comparison of all three cardinal temperatures is not possible as Wiebe's relationship took the form of an optimum curve over the range 2 to 17°C. Wiebe measured the 'relative portion of daily temperature effect for covering the cold requirement of cauliflower'. That is to say the effectiveness of a given temperature was expressed as a percentage of the total cold requirement. At temperatures of 2 and 17°C prolonged vernalization was required to achieve the same effect. An increase in vernalization temperature also increased the number of leaves initiated before the curd as in the present study. Clearly a simpler system of describing thermal requirements of vernalization is required for use in a predictive model.

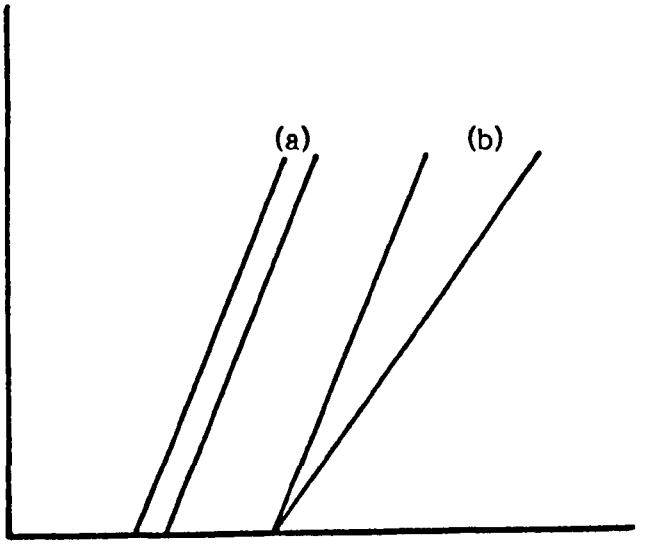
Cardinal temperatures for vernalization measured as rate of curd appearance were -4.5°C, 12.0°C and 29.5°C for T_b, T_o and T_m respectively. The corresponding cardinal temperatures for White Fox were -3.5°C, 15.8°C and 28.3°C. The higher optima of 12 and 15.8°C for cvs Perfection and White Fox may as reported earlier (section 5.1.2.1) be the result of combined temperature optima for the processes of curd initiation

and early curd growth. Differing optima may, from Figure 8.1, be seen to result from similar rates of development but different base temperatures (a), or different rates but similar base temperatures (b). The second of the two hypotheses (b) is consistent with the results of studies with pearl millet (Ong, 1983b) and groundnut (Leong and Ong, 1983) where base temperatures for different developmental processes appear to be similar. In contrast however, Wielgolaski (1974) has postulated that base temperature is highest during periods of active metabolism. Base temperatures have been shown to increase by 5-7°C from germination to flowering in pea, potato and wheat (Wielgolaski, 1974; Angus et al., 1981). Further support for hypothesis (b) comes from Ong and Baker (1982) who state that curvature in rate/temperature relations at high temperatures is common and may be a consequence of other environmental factors such as low light.

Cardinal temperatures used here for the calculation of thermal time of vernalization were based on reciprocals of leaf number as a measure of curd induction. Base temperatures of -1.25 and -3°C were used for cvs Perfection and White Fox respectively. Whether this represents a significant difference in base temperatures is questionable. For many different cultivars of cowpea, Vigna unguiculata (Hadley, Roberts and Summerfield, 1983) and groundnut, Arachis hypogea (Leong and Ong, 1983) it has been reported that little error is introduced in assuming a common base temperature.

The base temperature is usually defined as the lowest temperature at which plant development will proceed. However, as with the present study, the most appropriate base temperature for use in a linear system need not coincide with the physiological base temperature (Arnold, 1959). The appropriate base temperature might therefore be

Figure 8.1



Hypothetical relationship between rate of development and temperature in two processes having similar rates but different base temperatures (a) and different rates but similar base temperatures (Modified from Garcia-Huidobro et al., 1982a)

better defined as that temperature which when used in a linear heat unit system gives the least variation in heat unit summations over the temperature range that is normally experienced in the phase of crop development involved. Base temperatures derived in the present study were therefore considered appropriate for use in calculating thermal time sums. In previous studies base temperatures have been rejected as too low to be physiologically feasible (Nuttonson, 1948; Madariaga and Knott, 1951). Arnold (1959) has highlighted the pitfalls of attempting to rectify this discrepancy by arbitrary substitution of what appear to be more physiologically acceptable base temperatures. This would increase the discrepancy in the higher temperature range and thereby increase the error because of the greater frequency with which these temperatures are likely to be encountered.

Regression of leaf number below the curd on thermal time of vernalization showed differences in the vernalization requirement between cvs Perfection and White Fox. Regression of final leaf number for cv Perfection on thermal time was described by a quadratic curve. Reduction in leaf number below the curd required a longer thermal time of vernalization for leaves 21 to 16 (counted acropetally) than for leaves 42 to 29. Clearly change in leaf number of cv Perfection was less dependent on accumulated thermal time than in younger plants. This may be consistent with the quantitative cold requirement displayed by some cauliflower cultivars (Haine, 1959; Sadik, 1967; Wiebe, 1972). In these examples cauliflowers will initiate curds eventually when grown under warm conditions; leaf number initiated before the curd is then correspondingly high. Less thermal time of vernalization may be required at these high leaf numbers. In contrast, the relationship between leaf number subtending

the curd in cv White Fox and thermal time of vernalization was shown to be linear; the thermal time required for decreasing the number of leaves before the curd was therefore constant.

Prediction of the time of curd initiation under field conditions required extrapolation of the controlled environment studies reported in section 5.1.2.3. Under field conditions the thermal time required after phase transition for curd initiation in cv White Fox was very close to the figure of 268 °C d predicted from controlled environment studies where plants initiated curds at the same leaf number. However, this agreement only extended to plants transplanted to the field in late February and early March. The thermal time of vernalization required for later transplantings was much less than predicted. Possible explanations for this obervation are considered firstly as systematic errors in the thermal time procedure itself, and secondly as the result of interactions between temperature and other variables.

The use of mean screen temperature in this study as the basis for calculating thermal time may result in inaccuracy as it is unclear how this relates to meristem temperature. While information on the thermal sensitivity of meristems is available in a few species, ryegrass (Peacock, 1975) and maize (Watts, 1972), very little is known about how the mean meristem temperature of field crops may depend on their position and on temperature gradients. In a few cases at least (Arnold and Monteith, 1974; Gallagher, 1976) the mean meristem temperature was close to mean screen temperature because temperature gradients in one direction during the day were offset by gradients in the opposite direction at night. Under controlled environment conditions similar findings were reported by Fujime and Hirose (1984) in the summer cauliflower Nozaki-wase. In a naturally lit

cabinet kept at a constant 14, 20, 24 or 29°C (RH 80%), the shoot tip temperature (STT) was lower than room temperature (RT) at night. As RT increased the difference between RT and STT increased. During the daytime STT was higher than RT. Under field conditions STT was lower than air temperature at night, but was equal to or a little higher during the daytime as insulation increased.

Calculation of thermal time on the basis of mean daily temperature would seem to be fully justified. This takes no account of diurnal thermoperiodicity which is known to determine the rate of other developmental processes such as seed germination (Koller, Mayer, Poljakoff-Mayber and Klein, 1962). Cross and Zuber (1972) predicted flowering dates in maize (Zea mays) based on 22 different methods of computing thermal time. Their findings showed little significant improvement in accuracy when calculating daily average temperatures on an hourly basis. They showed that a daily heat stress system in which temperatures above the T_m of 30°C were subtracted, slightly improved the degree of accuracy. While computation of thermal time here ignored possible detrimental temperatures above the T_m of 31.5°C for White Fox, the effect of the latter was considered to be negligible. Even allowing for a positive thermal gradient from screen to apex, the temperature was not likely to exceed 31.5°C, at least under UK conditions. Furthermore, Fujime and Hirose (1980, 1981) concluded that although the low temperature stimulus may be reduced in effect when a high temperature day followed a low temperature day, the influence of low temperature was accumulated.

Reduction in the apparent thermal time of vernalization required for curd initiation in cv White Fox transplanted later in the year suggests

an interaction with a further factor such as total irradiance receipt. Thermal times for vernalization were derived from experiments conducted at an irradiance level corresponding to 70% of that recorded under field conditions at the first transplanting (27 February and 20 March at Kirton and Wellesbourne respectively). For later transplantings in May, June and July the experimental irradiance level corresponded to only 35%, 29% and 27% of the mean field irradiance. Clearly, it is desirable when defining the effects of a given variable, in this case temperature, to obtain non-limiting conditions of a second such as light. Van Bavel (1973) pointed out the need to elicit vital responses such as transpiration rate at levels comparable to those obtaining in nature. In most installations light levels and total radiant energy loads are too low (Van Bavel, 1973; Warrington, Edge and Green, 1978).

In temperate zones the amount of light intercepted may be a limiting factor for growth and development (Bierhuizen, 1973; Monteith, 1981b). It is suggested that the curves (Fig. 5.6a) describing the relationship of thermal time to maturity on transplanting date may represent a shift in the relative influence on curd initiation from that of low temperature to that of irradiance receipt. Stated simply, the decrease in vernalization receipt is compensated for by an increase in irradiance receipt. The high correlation between solar radiation and light may be expected to result in a standard response. The same hypothesis may explain the similarity of curves describing cauliflower maturity characteristics (Fig. 5.6b). Although the hypothesis proposed here is speculative, it has been shown that with lettuce grown under outdoor conditions in Finland (Suhonen, 1969; as cited in Bierhuizen, 1973) and south west regions of Germany (Hartman, 1969; as cited in Bierhuizen, 1973) that the seasonal

variation in the use of heat units may be ascribed to variations in irradiance level. Reducing total irradiance receipt here (section 3.2) was shown to delay curd initiation in cvs Perfection and White Fox with an increase in leaf number initiated before the curd. Conversely higher light integrals accelerated curd initiation reducing the final leaf number and increasing the rate at which individual leaves are initiated.

Flowering in geranium seedlings does not occur until they are exposed to a minimum amount of cumulative radiation (Craig and Walker, 1963). Seedlings planted when radiant flux was decreasing (October-November) required more days to reach anthesis than seedlings planted when more solar energy was available for growth.

In modelling plant weight gain, Scaife et al. (1987) noted that weights of plants from winter harvested experiments were much lower than for plants grown in other seasons. This was almost certainly due to inadequate light. Scaife and colleagues therefore sought a new time scale which would include the effect of light as well as temperature. The conventional day-degree system was modified so as to remain unchanged under non-limiting light conditions, but to reduce the effectiveness of the day-degree total for those days at sub-optimal radiation. As consistent measurements of irradiance receipt were unavailable in this study, the influence of irradiance level in modelling the low temperature induction of curd initiation must be the subject of future research. This will prove necessary before curd initiation can be accurately predicted under field conditions.

Knowledge of a relationship between curd growth and temperature would be of practical value in the development of a predictive model for curd initiation. In modelling curd initiation the reliance on leaf number

subtending the curd or the number of days to macroscopic curd visibility does not allow the precise time of curd initiation to be determined; extrapolation back from a known curd diameter would do so. The problems associated with unpredictable curd growth and subsequent fluctuations in market supply were discussed earlier (Chapter 1; Booij, 1984, 1986; Wurr, 1986). The simple relationship described here (section 5.2) of $\log_e$ and diameter on thermal time (°C d > 2°C) would, it is proposed, enable curd maturity to be predicted once the point of curd initiation is known. The time of initiation could be determined simply by a number of sample dissections.

Any attempt to model curd initiation would need to consider the role played by edaphic factors such as nitrogen nutrition and soil moisture status. Experiments were carried out for this purpose.

Accelerated curd initiation as marked by a reduction in the number of leaves initiated before the curd was recorded when higher nitrogen levels were applied to unchilled plants. Curd initiation in chilled plants, however, was unaffected by nitrogen treatments. The results would suggest that the influence of nitrogen level on curd initiation is restricted to plants under otherwise non-inductive conditions. This would tend to support much earlier work (Gott et al., 1955) in which nitrogen deficiency was shown to retard progress to flowering in unvernalized and slightly vernalized winter rye, but that it was without effect on highly vernalized plants. Similarly nitrogen deficiency only delayed flower initiation in photoperiodically sensitive plants such as glasshouse carnation (Blake and Harris, 1960) when they were grown under non-inductive conditions. Brewster (1983) demonstrated that a reduction in nitrogen concentration of nutrient solution supplied to onions grown under controlled environment

conditions greatly accelerated inflorescence initiation particularly in photoperiods and temperatures not conducive to rapid initiation. Thus it is proposed that where nitrogen nutrition influences curd initiation it is probably through mechanisms less specific than those controlled by vernalization treatments.

Blake and Harris (1960) speculated that nitrogen deficiency probably reduced levels of metabolites at the stem apex to a point where floral initiation was delayed but leaf initiation could continue. Observations on cauliflower reported here are consistent with that view. In plants grown under non-inductive conditions curds were initiated following the initiation of approximately 33 leaves provided that plant dry weight exceeded 5 g. Many more leaves were initiated before the curd where dry matter accumulation was less. A minimum dry weight of c. 1.2 g was also indicated.

Whilst the number of days to macroscopic curd visibility increased with increasing supply of nitrogen, this parameter was poorly correlated with leaf number. The contrasting high correlation with both leaf area and dry weight would support the view that in this instance curd appearance is simply governed by the size of the surrounding leaves. This may suggest that control of buttoning in the crop is largely a function of plant size; reduced leaf expansion allowing early curd visibility, consistent with reports from earlier work (Carew and Thompson, 1948; Wurr and Fellows, 1984).

Increasing use of modules for the propagation of cauliflowers (Symonds, 1984) has increased the degree to which plant growth can be manipulated by feeding and has led to further attempts to schedule accurately cauliflower production and overcome problems of continuity of

supply (Salter, Ward and Whitwell, 1972; Booij, 1986). While it is known that transplanting can be scheduled with accuracy (Martin, 1985), little was known about the effects of nitrogen nutrition on curd initiation. These must be understood as continuity is largely determined by the time of curd initiation (Chapter 1).

The combination of large modules and high nitrogen clearly increased the number of leaves initiated during propagation. The maximum leaf number attained of 22 was eight higher than that attained when growing plants in small Hassy 308 modules at low nitrogen. As cv White Fox is known to undergo phase transition at 18 leaves it is possible for those 'larger' transplants to initiate curds during propagation. Although not a prerequisite for buttoning (Wurr and Fellows, 1984) the combination of maturity attained during propagation and the check in growth at transplanting would increase the incidence of buttoning. Restricting leaf number with small modules and low nitrogen may account for the observation that plants raised in this manner are unable to initiate curds during propagation (Hiron, pers. comm.).

A limit to the dry weight attainable in different modules would suggest that cauliflowers grown in small modules, even at high nitrogen levels, will accumulate insufficient dry matter (c. 0.68 g) to initiate curds during propagation. The 1.97 g dry matter attained in large modules however exceeds the proposed minimum of c. 1.2 g required for curd initiation to proceed. A knowledge of the effect of module size and nitrogen level on leaf number and dry matter attained during propagation may enable blueprints to be drawn up for a range of commercial cultivars which would minimise the risk of buttoning and loss of crop uniformity.

The response of curd initiation to potassium nutrition was inconsistent. In unchilled plants grown in the absence of nitrogen (section 6.1.2) a maximum increase in the number of leaves initiated before the curd was associated with the lowest level of potassium, 10 mg wk^{-1}. In contrast, later studies (section 6.4.2) showed that under similar conditions increased leaf number resulted from the highest potassium level, 30 mg wk^{-1}. Clearly, further studies are needed to clarify the role, if any, of potassium in curd initiation. One hypothesis may be that potassium, as discussed for nitrogen, influences assimilate distribution. The long distance transport of sucrose has been shown to be favoured by K^+ (Mengel, 1980).

The imposition of 'severe' water stress on unchilled plants accelerated curd initiation, reducing the leaf number by three. The results reported here for cauliflower are consistent with those of Parkinson (1952) who obtained a similar effect on leaf number by subjecting plants to a 16 day dry period. Salter (1960b) also observed that 'dry' conditions reduced the final leaf number in cauliflowers; however, results were not consistent in successive trials. In contrast, Aamlid (1952) reported an increase in leaf number resulting from dry conditions.

The total number of leaves produced by the primary stem of Helianthus annuus was reduced from 29 to 21 when water stress ranging from -2000 to -3000 KPa was imposed over the period from day 10 to day 20 after sowing (Marc and Palmer, 1976). Reduction in leaf number has also been reported in Helianthus by Yeggapan, Paton, Gates and Muller (1980). Increasing the level of applied water stress gave a progressive reduction in leaf number in tomato plants (De Koning and Hurd, 1983; Othman, 1984).

Reduction in leaf number following water stress reported in these studies (section 6.6.2) may have resulted from a decrease in the rate of leaf initiation. Although curd induction would proceed slowly at the high glasshouse temperatures used here, induction may have accompanied the initiation of fewer leaves. The imposition of water stress was shown to reduce the rate of leaf initiation in Helianthus (Marc and Palmer, 1976). The possibility that the physiological activity of cells of the shoot apex was impaired by a reduction in turgor has been considered (Plaut and Ordin, 1964). Closure of stomata may also have restricted the supply of carbohydrate to the shoot apex.

The imposition of water stress resulted in a reduction in leaf dry weight at the time of macroscopic curd appearance; the severity of imposed stress appeared unimportant. In contrast, leaf area declined with increasing stress. Restriction of vegetative growth may have been the result of reduced cell expansion in the leaf and possibly a reduction in the rate of cell division itself, as was postulated for tomatoes (De Koning and Hurd, 1983). A reduction in leaf area would, it is proposed, reduce the fraction of incident radiation intercepted by foliage and the quantity of dry matter produced per unit of radiation intercepted. A close relationship between the amount of dry matter produced per unit of radiation intercepted by foliage and mean leaf water potential was reported for groundnut (Ong, Simmonds and Matthews, 1987).

Determination of either percentage dry matter or specific leaf area of leaf discs may, in future studies, give some indication of carbohydrate reserve status. Leaf water potential gives an indication of treatment effects but is difficult to measure routinely. The possibility of measuring stem water potential (McBurney and Costigan, 1982; 1984) using

a modified leaf water potential hygrometer may facilitate continuous non-destructive measurements. McBurney and Costigan (1982; 1984) showed that in Brassica plants changes in stem water potential paralleled changes in leaf water potential.

Failure to observe an increase in endogenous ABA following imposition of water stress is in contrast to many earlier studies on a wide range of species (Wright and Hiron, 1969; Wright, 1978). However, further studies have shown water stress to result in a decline in ABA levels in pearl millet (Henson, Mahalakshmi, Alagarswarmy and Bidinger, 1984) and in maize (Ilhai and Dorffling, 1982). ABA has been implicated in the manipulation of sink activity and in the distribution of assimilates (Dewdney and McWha, 1978). However, again evidence is conflicting (Mullins, 1970). Whether ABA has a role in regulating curd initiation clearly needs to be the subject of further detailed studies.

Manipulation of curd initiation and improvement of crop uniformity by the use of plant growth regulators may represent a viable alternative to the use of cold treatments.

Studies reported here demonstrated the ability of exogenous foliar applications of GA_{4+7} to accelerate curd initiation by reducing the number of leaves initiated before the curd in plants grown under warm glasshouse conditions. Acceleration of curd initiation was measured relative to the time of application of GA_3. The result described here is consistent with the observation that floral initiation resulting from the application of exogenous gibberellins may be dependent on the specific gibberellin applied (Michniewicz and Lang, 1962; Pharis and King, 1985).

The marked increase in stem dry weight at curd initiation in plants treated with GA_{4+7} in contrast to the reduced leaf dry weight may

suggest the enhanced movement of assimilates to the stem. Support for this observation is indicated from the results of Morris and Arthur (1985b). In their studies the application of GA_3 as a root drench to 16 day old plants of Phaseolus vulgaris increased upward translocation of ^{14}C sucrose to the elongation region of the stem at the expense of the hypocotyl and root system. Morris and Arthur (1985b) proposed that GA_3 acted to stimulate acid invertase activity resulting in an increased rate of hydrolysis of sucrose to hexose. Changes in the carbohydrate status in the shoot tip of cauliflower (Sadik and Ozbun, 1968) and Broccoli (Fontes and Ozbun, 1972) have been implicated in floral initiation. The application of gibberellins to flower buds of tomato plants grown under poor light conditions has been shown to prevent flower abortion and enhance flower development (Kinet, 1977b; Kinet et al., 1978; Othman, 1984; Kinet et al., 1985). Gibberellins are again considered to influence sink activity (Othman, 1984; Morris and Newell, 1987).

The hypothesis that the time of curd initiation may in part be controlled by stem dry matter content was further supported by the negative correlation evident between the number of leaves initiated and stem dry weight at curd appearance. The absence of any correlation with stem length would suggest that time of curd initiation is independent of stem length, a view consistent with previous studies (Leshem and Steiner, 1968).

The accelerated curd initiation in cv White Fox brought about by the application of GA_{4+7} during one week's chilling (section 7.2.2) is consistent with results from earlier studies (Leshem and Steiner, 1968) and the view that gibberellins may be used to advance curd initiation under sub-optimal vernalizing conditions (Booij, 1985). The reason for the

apparent absence of an effect in cv Perfection is not clear, particularly when it is considered that earlier cultivars are regarded as being more sensitive to low temperature and, by inference, to gibberellins. However, the use of exogenous gibberellins to accelerate curd initiation may not reflect the role of those which occur naturally. Individual plants are likely to contain many naturally occurring gibberellins as in the case of the cucurbit Sechium edule (Albone et al., 1984) and garden pea, Pisum sativum (Sponsel, 1985). Detailed studies with Pisum sativum (Sponsel, 1985) have revealed that there are differences both in the levels and types of GAs present in different plant organs which may change both quantitatively and qualitatively in response to genotype, developmental stage and environmental influence.

Whilst increasing the duration of low temperature to 2 or 4 weeks accelerated curd initiation, as with results reported earlier (Chapter 3), the application of exogenous GA_{4+7} had no further promotory effect. This may be explained by the presence of saturating levels of endogenous gibberellins resulting from the extended exposure to low temperature. Low temperature has been shown to enhance naturally occurring peaks in the levels of exogenous gibberellins in cauliflower plants (Thomas et al., 1972; Wurr et al., 1982). Increases in endogenous gibberellins associated with vernalization have also been reported in wheat (El-Antably, 1977), raddish (Suge, 1970) and carrot (Hiller, Kelly and Powell, 1979). Maximal increase in gibberellins in wheat was shown to occur in the shoot apices (El-Antably, 1977).

Gibberellins have also been implicated in phase transition from juvenile to mature forms in many species, such as Hedera (Robinson and Wareing, 1969) and Ribes nigrum (Schwabe and Al-Doori, 1973). It is

proposed that the first peak in endogenous gibberellins observed in cauliflower (GI) (Wurr et al., 1981) is coincident with the point of phase transition and the associated increase in the rate of leaf initiation recorded in the studies reported earlier (Chapter 4). Young leaves have been shown to be sources of gibberellin-like compounds in other plants (Abdul and Harris, 1977; 1978). It is postulated here that the flush of young leaves associated with phase transition may give rise to an increase in the level of endogenous gibberellin-like compounds at the apex. This in turn may increase the sink strength of the apex providing assimilates for curd initiation.

Further increase in the level of gibberellins associated with low temperature (Thomas et al., 1972; Wurr et al., 1981) would serve to accelerate curd initiation.

The application of GA_{4+7} to modular raised transplants of cv White Fox signifiantly increased leaf dry weight during propagation. This may have been as a direct result of the 'greening' effect observed in GA_{4+7} treated plants. Hormone directed transport of metabolites is now widely recognised (Phillips, 1975), and whilst divergent results have yet to be reconciled, gibberellins have been reported to decrease the export of photosynthate from leaves (Halevy, Monselise and Plaut, 1964). It is recognised that the results reported here for modular raised transplants do, to some degree, conflict with earlier results (section 7.1.2) where GA_{4+7} enhanced dry matter accumulation in the stem. However, the latter experiment served as a comparison between gibberellin types and not gibberellin treated plants compared with untreated controls. Retention of chlorphyll in plant tissue is a recognised bioassay for gibberellin-like compounds.

Leaf number initiated during propagation was unaffected by the application of GA_{4+7}. However, the inability of plants to initiate 19 leaves during propagation in modules here dictated that gibberellin treatments applied at the 19 leaf stage were undertaken in the field. The reduction in leaf number initiated before the curd associated with applying GA_{4+7} at 19 leaves may be explained in several ways. GA_{4+7} applied to mature (> 18 leaves) plants under field conditions may have 'topped up' the vernalization stimulus under sub-optimal vernalizing conditions; whereas GA_{4+7} applied to juvenile plants was ineffective. These observations are largely consistent with those of Booij (1984).

Curd size, quality and maturity characteristics were unaffected by the application of GA_{4+7}; again results are consistent with earlier studies (Salter and Ward, 1972). Although constituting a preliminary study, the results reported here may indicate a role for gibberellins in accelerating curd initiation under sub-optimal vernalizing conditions. Field establishment and hence crop uniformity may also be enhanced as a result of the 'greening' effect and the resultant higher photosynthetic activity. Clearly further studies are needed to clarify the role of endogenous gibberellins in curd initiation and the benefits of exogenously applied gibberellins.

The main objective of this thesis was to consider the regulation of curd initiation in the summer cauliflower. Special attention was given to the time of curd initiation in response to changing environment. Accurate characterisation and quantification of the juvenile stage and vernalization requirement for curd initiation enabled a technique for predicting curd initiation in field crops of cauliflowers to be investigated. The hypothesis was proposed that gibberellins may, in part, be the mechanism by which those conditions influencing curd initiation are mediated.

APPENDIX

Appendix 1

Calculation of an 'equivalent' temperature when $T > T_o$

If the linear response if asymmetrical direct comparison of equivalent temperatures on either side of T_o is not possible as rate is dependent on slope (Appendix figure 1).

If D (duration in days) is substituted for time t

$$1/D = K(T - T_b) \qquad \text{(eqn 1)}$$

where the constant K = slope of the line.

Thermal time Θ:

$$\Theta = 1/K = D(T - T_b) \qquad \text{(eqn 2)}$$

Linear regressions (Appendix figure 2)

$$R_1 = Ro_1 + b_1 (T_1) \qquad \text{(eqn 3)}$$

$$R_2 = Ro_2 + b_2 (T_2) \qquad \text{(eqn 4)}$$

T_1 and T_2 are the two temperatures for equivalence needs to be ascertained.

Ro_1 and Ro_2 are the intercepts of the regressions R_1 and R_2 respectively and b_1, b_2 the corresponding slopes.

Figure 1

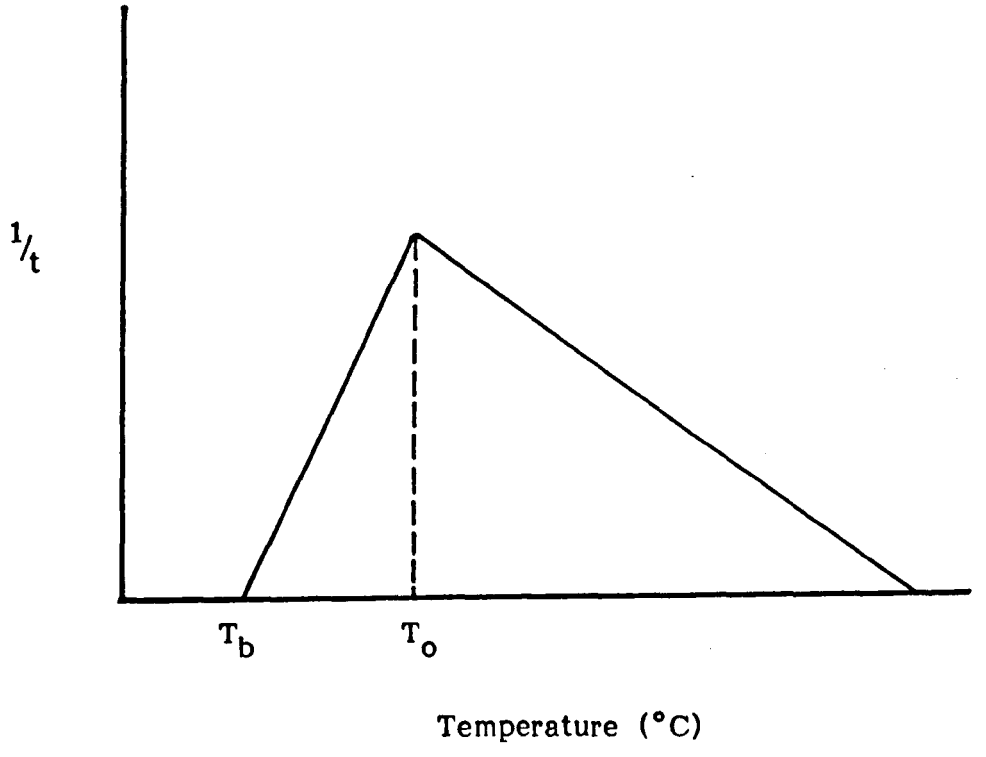
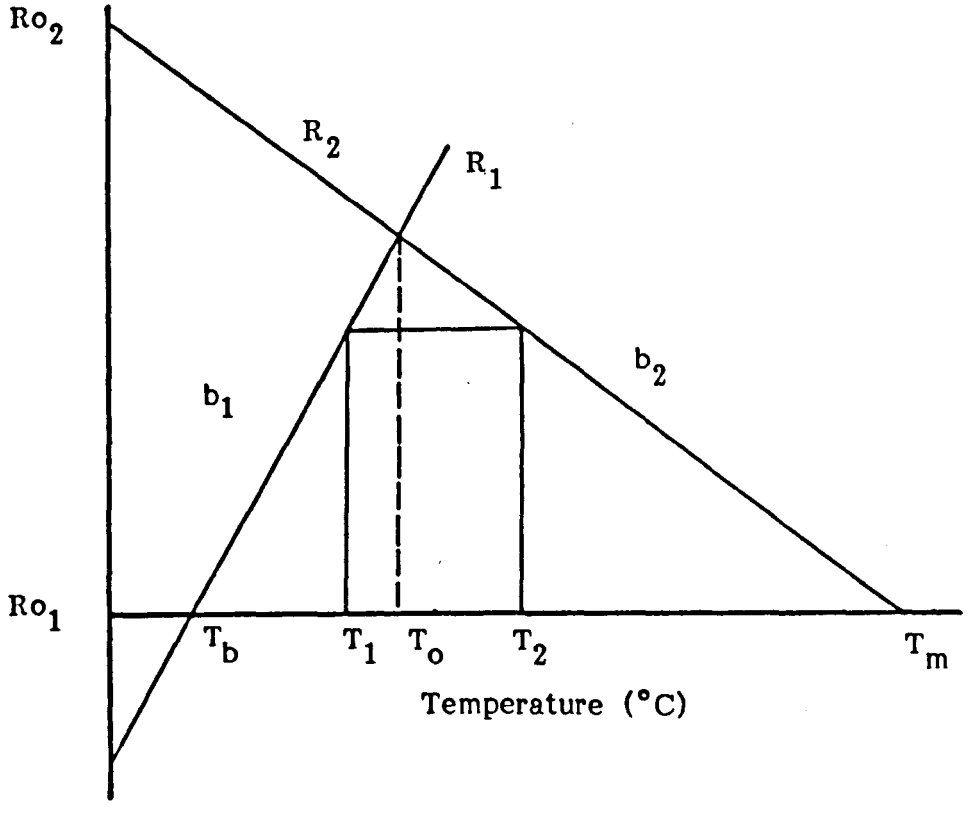


Figure 2



$$Ro_1 + b_1 (T_1) = Ro_2 + b_2 (T_2) \qquad \text{(eqn 5)}$$

$$Ro_1 - Ro_2 = (b_2 - b_1) T \qquad \text{(eqn 6)}$$

$$T = \frac{Ro_1 - Ro_2}{b_2 - b_1} \qquad \text{(eqn 7)}$$

also: $$Ro_1 - Ro_2 = b_2 T_2 - b_1 T_1 \qquad \text{(eqn 8)}$$

$$T_2 = \frac{Ro_1 - Ro_2 + b_1 T_1}{b_2} \qquad \text{(eqn 9)}$$

$$R_2 = Ro_2 + b_2 T$$

$$R_1 = Ro_1 + b_1 T \qquad \text{(eqn 10)}$$

$\therefore$ equivalent temperature Teq

$$Teq = \frac{Ro_2 - Ro_1}{b_1} + \frac{b_2}{b_1} \times Tgopt \qquad \text{(eqn 12)}$$

where Tgopt = T when $T > T_o$

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