GROWTH AND DEVELOPMENT STUDIES WITH BROCCOLI
(Brassica oleraceae var. italica)

A thesis presented in partial
fulfilment of the requirements for the degree
of Doctor of Philosophy
in Horticulture at
Massey University

Misael T. Diputado, Jr.
April 1989

Abstract

The influence of temperature on the growth and development of broccoli was studied in the field, the greenhouse and in controlled climate experiments at Massey University in 1985-88. In the field experiment, 6 sowings at 2-month intervals of four cultivars of broccoli were made. The effect of temperature on a number of growth and development parameters of the plant was assessed using the heat unit system. The greenhouse and controlled climate experiments were conducted as follow-up studies to determine the independent effect of temperature on the development, growth, maturity characteristics and curd quality of broccoli. In all the studies, growth analysis using the functional approach was employed.

Temperature, through the use of the heat unit system, was found to account for a major proportion of the variation between sowing dates in the rate of dry matter accumulation, rate of leaf production, times to curd initiation and maturity, and rate of curd growth. Dry matter accumulation could be expressed as a logistic function of heat unit summation (HUS) above a base temperature of 3C; rate of leaf production, a linear function of HUS above -2C; and curd growth (increase in curd diameter), as a quadratic function of HUS above 3C.

Time to curd initiation expressed as number of heat units was calculated above a base temperature of 0C. The varietal constants (total HUS from sowing to curd maturity) were calculated to be 1188, 1123, 1217 and 1347 heat units for Premium Crop, Mercedes, Idol and Fordhook Late, respectively.

The final number of leaves did not vary with sowing date but varied among the cultivars and was related to the time to curd initiation. The longer the time to curd initiation, the more leaves were formed.

The economic yield varied with sowing date and was related mainly to differences in total dry matter accumulation potential. With the cultivars, the harvest index was equally important. Differences in total dry matter accumulation between cultivars were not closely linked to differences in the relative growth rate (RGR) or any growth parameter, but were related more to the growth duration. There was some indication of a relationship between harvest index and net assimilation rate (NAR) at curd initiation time. NAR was found to be inversely related to the specific leaf weight (SLW) which is indicative of the thickness of the leaves.

High temperature regime (30C) reduced the RGR and NAR of plants relative to a 20C regime. It did not affect rate of leaf production and did not prevent or delay curd initiation. When imposed before the curd initiation stage 1-week exposure to high temperature did not reduce curd quality. When imposed at the early or late curd development stages it reduced curd quality with the reduction being more pronounced at the latter stage. When treatment exposure was increased to two weeks similar results were obtained. Growing the plants under continuous high temperature caused a range of curd morphological abnormalities such as the presence of bracts throughout the surface of the curd, suppression of the growth of the buds or irregular elongation of curd internodes.

Acknowledgments

To Dr. Michael A. Nichols for his guidance and supervision throughout the course of the study;

To Dr. David J. Woolley and Dr. Keith J. Fisher for their constructive comments and suggestions;

To the Plant Physiology Division, DSIR for making available the climate rooms and other facilities;

To Wattie Frozen Foods for some financial assistance;

To the Visayas State College of Agriculture (ViSCA), Leyte, Philippines and the New Zealand Ministry of Foreign Relations and Trades for the scholarship grant;

To the staff and post graduate students, Dept. of Hort. Sci. and the Filipino students at Massey U. for their help during the conduct of the experiments;

To the Filipino community and all friends in New Zealand for their pleasant company;

To my parents, brothers and sisters for their great moral support;

And to my wife, Mylou for her help in computer programming and for her encouragement, patience and understanding;

MY SINCERE THANKS AND APPRECIATION.

Table of Contents

List of Figures

List of Tables

List of Plates

List of Appendices

List of Abbreviations

Abbreviation	Meaning
CI	Curd Initiation
CM	Curd Maturity
CV	Coefficient of Variation
DFS	Days from Sowing
EGA	Endogenous Gibberellin Activity
EMS	Error Mean Square
HUS	Heat Unit Summation
LAR	Leaf area ratio
LWR	Leaf weight ratio
NAR	Net Assimilation rate
RGR	Relative growth rate
SD	Sowing Date
SLW	Specific leaf weight

Introduction

Yield and quality are two important attributes which will determine success in the commercial production of broccoli for processing or for the fresh market. Although total market returns are determined primarily by crop yield, curd quality can be as important as it determines the marketability and the value of the crop. On the other hand, a knowledge of the rate of development and maturity characteristics of the crop would be useful in formulating sowing and harvesting schedules. These enable the efficient use of farm resources and are important in marketing aspects.

The rate of development, yield and curd quality of broccoli may be influenced by the genotype-environment interaction. Thus, along with crop selection, plant breeding and optimization of agricultural inputs to improve yield, studies on the effect of the environment on different crop cultivars are also important. To date, there is quite an extensive research on the effect of the environment on the growth and development of cauliflower but only a few studies have been done on broccoli. The two crops may be closely related but their physiological responses to the environment have been shown to be quite different.

Based on these research needs three experiments were carried out. The field experiment was designed to examine in detail the effect of the environment, with emphasis on temperature on the growth, development, yield and maturity characteristics of four important cultivars of broccoli. An attempt was made to determine the applicability of a model to predict the curd maturity of broccoli using the heat unit concept. The greenhouse and controlled climate experiments were conducted to study further the effect of controlled temperature treatments on the growth and development of broccoli with emphasis on curd quality. In particular, the greenhouse experiment looked into the effect of short-period treatment (1 wk) at low temperature (10C) or at high temperature (30C) at different stages of plant development of broccoli under a more optimal temperature (20C). In the controlled climate experiment, the effect of continuous and 2-wk treatment at high temperature (30C) on plants under optimum temperature (20C), and vice versa was studied.

Chapter 1

Review of Literature

1.1 Classification, General Characteristics and Use

Broccoli (Brassica oleraceae var Italica) is fast becoming an important fresh market and processing vegetable crop in many parts of the world (Morelock, Peerson and Motes, 1982; Magnifico, Lattanzio and Sarli, 1979). In New Zealand, broccoli has been a popular crop in the home garden and in small commercial acreages. Field trials have produced a number of promising cultivars for the fresh market and the processing industry (Bussell, 1984; Geelen and Greaves, 1984; McErlich, 1984) which could well be suitable for large commercial plantings.

The crop is grown for its edible curd which has become a popular item in the kitchen because of its good organoleptic properties and high nutritive value (Feher, 1986). Compared with other brassica vegetables it has been found to have the highest protein, dietary fibre and vitamin C content (Wills, Lim and Greenfield, 1984).

The curd is morphologically similar to that of cauliflower (Brassica oleraceae var botrytis) although certain characteristics such as branching and time of floral initiation are different (Wiebe, 1975). Broccoli produces a green curd with long and slender floret-stalks bearing fertile flower buds while cauliflower produces a single compact white curd which forms fertile flower buds only after the normal harvest stage. The maturity of the broccoli curd is primarily determined by the developmental stage of its florets. It is harvested shortly before it loses its compactness or just before buds start to open (Marshall and Thompson, 1987a).

1.2 Growth and Development

1.2.1 General Pattern of Growth and Development

Magnifico, Lattanzio and Sarli (1979) have described typical growth curves in broccoli. They found that the growth rate was very slow at the start but then increased dramatically as the vegetative buds underwent transition to the reproductive state and as the main stem elongated. It then declined as the main head developed and increased again as the main head neared marketable maturity. They found that leaves constituted 52.4%, stems 20.8%, heads 19%, and roots 13% of the total dry matter.

Salter (1960) applied the heat unit concept (see section 1.2.4.2) in studying the pattern of dry matter accumulation in cauliflower. He found that dry matter accumulation was a logistic function of accumulated heat units from sowing to flowering. The end of the period of exponential growth coincided with the economic maturity of the curd and the maximum leaf weight of the plant although the weight of the whole plant continued to increase until flowering time when the maximum dry weight was attained.

In their study on the growth and development of winter heading cauliflowers, Wurr and Kay (1981) found that when considering four varieties of the crop the patterns of development of leaf area as well as the distribution of the dry matter were remarkably similar although the varieties represented a wide range of season of maturity. The only difference was in the dry weight accumulation into roots, later maturing varieties having a greater root dry weight and a higher proportion of dry matter as root than the earlier maturing varieties. The leaf lamina provided the greatest percentage of dry matter followed by the petiole and midribs, the stem and the roots.

The production of lateral shoots in cauliflower and broccoli as influenced by temperature has been described by Wiebe (1975). At any temperature level, temperate cauliflower cultivars did not produce lateral shoots but the tropical cauliflowers (described by Swarrup and Chatterjee (1972) as a separate variety group which at low temperatures is known to form an infloresence and exhibit branching similar to broccoli) produced lateral shoots which decreased in number with increasing temperature. At low temperature (12C), broccoli cultivars showed the strongest branching. At high temperature (27C) they produced many small lateral shoots without curds.

1.2.2 Reproductive Initiation

1.2.2.1 Physiological and Biochemical Changes During Curd Initiation

In broccoli, curd initiation represents the first step towards the transition from the vegetative to the reproductive state of the plant. Flowering in plants is a unitary and integrated process but can generally be divided into the two major phases of flower initiation and development (Bernier, 1988). The events occurring in the apex that commit it to flower formation were called floral evocation by Evans (1969). Bernier (1988) cited two views concerning the nature of evocation. One holds that the switch to flowering primarily requires a change in gene expression in the meristem, specifically the "turning on" of the genetic program concerned with the control of sexual reproduction (Zeevart, Brede and Cetas, 1977). Another view proposes that evocation is essentially an unspecific activation necessary to eliminate the vegetative pattern of morphogenesis.

Gene expression was indeed found to be highly regulated during flower development in tobacco (Kamalay and Goldberg, 1980) and tomato (Gasser, Smith, Sachs, McCormick and Hinchee, 1987). In tobacco, almost half of the genes expressed in the anther or ovary are not expressed in the leaf and vice versa. In tomato, several specific cDNA clones appear to be expressed in different organs of the flower. In cauliflower, a 20-fold increase in the volume of nucleoli and a 3-fold increase in the volume of nuclei were found during floral induction and the concentrations of nuclear and cytoplasmic proteins were found to vary between normal and induced apices (Sadik and Ozbun, 1968). These changes may also be related to changes in gene expression during curd initiation and development in cauliflower.

In support of the second view of unspecific activation, Austin (1970) as cited by Wurr, Akehurst and Thomas (1981) proposed that initiation can occur when the amount of promoter in the plant reaches a critical level and that the rates of formation and destruction of the promoter are proportional to the differences between the "cold threshold' and mean temperature and to the number of leaves in the plant. This may support the findings of Kato (1964) and Fujime and Hirose (1981) about the promotive effect of seed chilling on curd initiation. However, although a plant may be capable of accumulating a growth promoter as a result of cold stimulus for a long period of time, results of the different studies as will be discussed suggest that there is a particularly sensitive phase during development when the plant is responsive to low temperature. Thomas, Lester and Salter (1972) demonstrated that this sensitive phase coincided with a definite peak of endogenous gibberellin activity in the apex. They concluded that gibberellin is the promoter particularly since the treatment of cauliflowers with gibberellin has been shown to promote cauliflower curd development (Leshem and Steiner, 1968). Further, they suggested that for a cold treatment to be effective in synchronizing curd maturity it should coincide with the increase in natural gibberellins occurring prior to curd initiation. Since cold treatment at this stage did result in increased gibberellin activity, they concluded that there was probably a direct relationship between temperature, gibberellin synthesis and curd initiation.

Wurr et al. (1981) illustrated the probable relationships between the phases of cauliflower growth, leaf production and endogenous gibberellin activity (Fig. 1.1). The hypothesis suggests that the curd induction phase occurs between leaf numbers A and B, coinciding with the peak (GI) of naturally occurring gibberellin activity. This is considered to be the phase responsive to the cold treatment.

Thomas et al. (1972) observed cytokinin activity in the apices of untreated plants which occurred in 3 major peaks. The third and largest peak of activity occurred just before initiation was apparent. Since cytokinins are known to

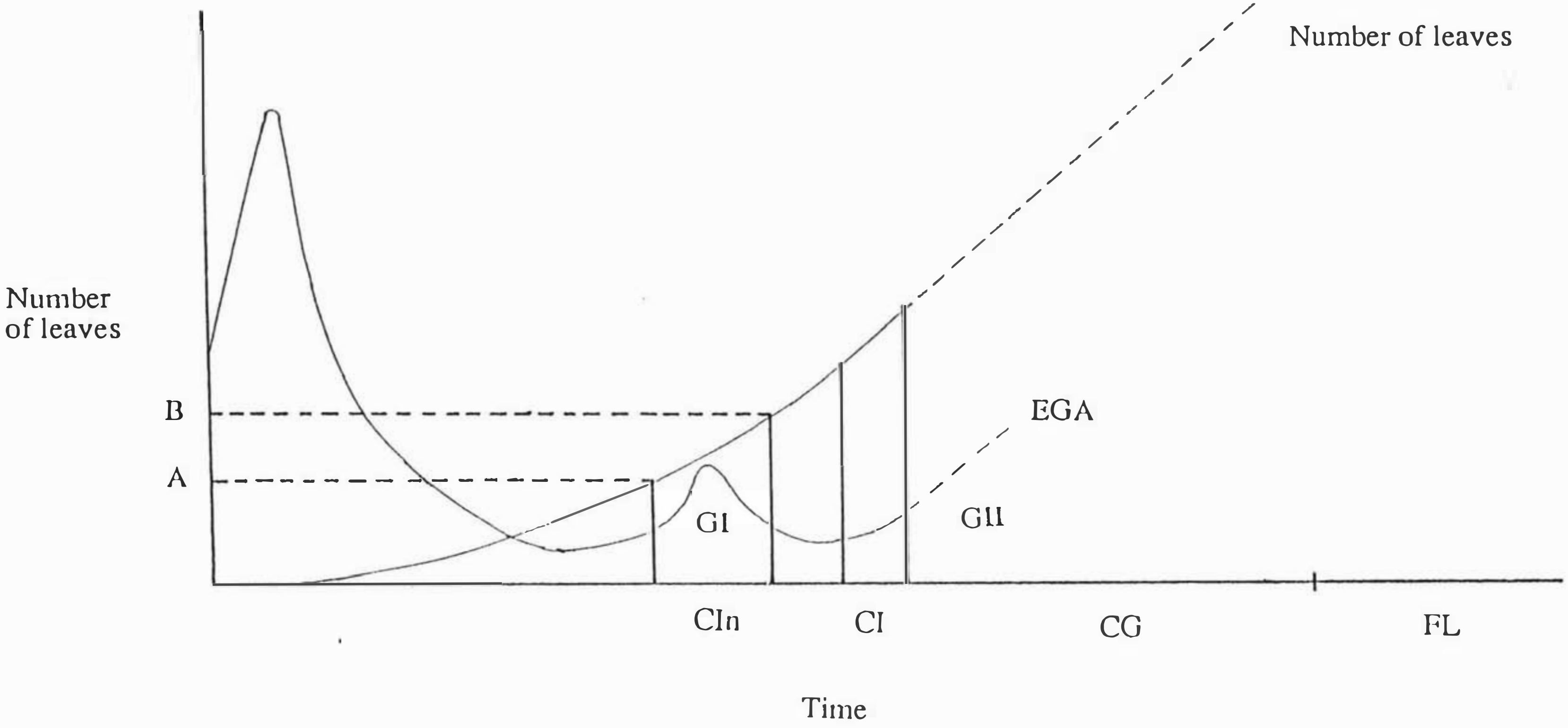


Figure 1.1 A diagrammatic representation of the relationships between the phases of cauliflower growth, leaf production and endogenous gibberellin activity. Codes: CIn - curd induction; CI - curd initiation; CG - curd growth FL - flowering; EGA - endogenous gibberellin activity; GI - first EGA peak; GII - second EGA peak. Number of leaves include bracts within a curd. Source: Wurr et al. (1981).

stimulate cell division it seems likely that this increased cytokinin activity may have been utilized during the early stage of development of the highly parenchymatous curd tissue.

Results of some studies show that under some conditions the concentration of carbohydrates found in the shoot tips of broccoli and cauliflower is correlated with floral induction (Sadik and Ozbun, 1968; Fontes and Ozbun, 1972; Sadik and Ozbun, 1967). However, Fontes and Ozbun (1972) found that if plants are grown continuously at a warm temperature then a high concentration of carbohydrates was not correlated with flowering which suggests that the association between carbohydrate concentration and floral induction under certain conditions is only coincidental and carbohydrate accumulation is not directly responsible for floral induction.

1.2.2.2 Morphological Age at Curd Initiation

The morphological age of the plant at curd initiation time as measured by the final number of leaves can vary among varieties depending upon the period of maturity. Salter (1969) showed quantitatively the relationship between the final number of leaves and time to curd initiation in cauliflower. He found that plants with earlier times to curd initiation had progressively smaller final leaf numbers than those initiating curds later.

Wurr and Kay's work (1981) showed that the difference in morphological age in cauliflower differed not only with varieties but with sowing dates as well. This suggests that there is no specific morphological age at the time of curd initiation for a particular variety since the final number of leaves can be influenced also by the climatic variables during a particular growth season. This was supported by the findings of Gauss and Taylor (1969a) who found that in sprouting broccoli (cv Coastal) the average number of macroscopically visible leaves formed prior to curd initiation increased as the temperature was increased from 13C to 29C. Moreover, Wiebe (1975) observed that cauliflower, sprouting broccoli and tropical cauliflower differ in the time to curd initiation and that this was correlated positively with the final leaf number. He found that the temperate cauliflower cultivars had the most leaves while the tropical cauliflower and the broccoli cultivars formed considerably fewer leaves. At higher temperature the leaf number in tropical cauliflower was found to approach that of the temperate cauliflower but in broccoli cultivars the leaf number was less influenced by temperature.

1.2.2.3 Chronological Age at Curd Initiation

The few studies on the effect of temperature on the time of curd initiation in broccoli gave quite contrasting results. Fontes, Ozbun and Sadik (1967) found that in two cultivars (Waltham and Green Mountain) curd initiation was earlier in plants grown at 5C than at 10C. They also observed that low temperature was only effective in hastening floral induction when treatments were done on plants which were at least 4 weeks old and concluded that sprouting broccoli has a juvenile stage during which the initiation of floral primordia can not be induced. Fujime and Hirose (1982) have reported similar results. Broccoli plants previously exposed to 25C/15C day/night treatment then transferred to natural conditions produced curds before those from a constant 25C treatment. Gauss and Taylor (1969a), however, claimed that temperature alone had no influence on the chronological time to curd initiation following observation that plants (cv Coastal) exposed to 13C initiated curds at the same time as those exposed to 29C. They also claimed that there is no qualitative and quantitative cold requirement for inflorescence formation since in their earlier study (Gauss and Taylor, 1969b), reproductive initiation occurred when daily minimum and maximum temperatures were at 10 and 30C, respectively. They also raised doubt on the claim of other workers that plants would only respond to cold treatment if they have gone past their juvenile stage. They pointed out that it is possible that older plants used by other workers appeared to respond to cold treatment more readily because their apices were more advanced or were already reproductive prior to cold treatment, and that the other workers might have overlooked this since they did not examine the apices of the plants prior to cold treatment. Thus, they concluded that low temperature may not be influencing growth directly. It may slow down vegetative growth when applied during this stage or allow the accentuation of the reproductive phase of growth when applied during the early phase of this stage of development.

The effect of daylength and its interaction with temperature was also covered in the study of Gauss and Taylor (1969a). They observed that, in contrast to temperature, an increase in daylength caused a rapid linear decrease in the chronological time to curd formation but not in the number of leaves formed prior to curd formation. This suggests that daylength simply influenced plant growth and not development. There appeared to be an interaction with daylength and temperature. At 13C an increase in daylength from 8 to 24 hours resulted in a marked reduction in the time to curd formation (initiation) whereas at 29C, a reduction in the time to curd formation was observed when daylength was increased from 8 to only 16 hours. A further increase to 24 hours resulted in an increase in time to curd formation. This increase was attributed to the high temperature-continuous light environment which promoted rapid vegetative growth and retarded reproductive growth. This marked effect of low temperature under continuous light provided evidence that daylength, light energy or light quantity may play important roles in the flowering response of broccoli. In the particular cultivar used it was established that only at the environment consisting of 13C temperature and 24 hour daylength were the reproductive differentiation and curd initiation hastened chronologically.

One mechanism postulated by the authors with regard to the daylength-temperature interaction is that continuous light possibly converts Pr to Pfr and low temperature simultaneously retards the breakdown or reversion of Pfr to Pr. Under these circumstances one would expect earlier curd formation if the plants were grown at low temperature under continuous light. However, they still stressed the need for further investigation of the possibility of a low temperature-mediated phytochrome system taking part in the control mechanism of flowering in broccoli.

From the same study, it was found that seed vernalization only showed a promotive effect on the advancement of the apex toward the reproductive stage under continuous light. This finding corroborated the those of other workers such as Gott, Gregory and Purvis (1955) who worked on winter rye and

McCown and Peterson (1964) on Lolium perenne. They all noted a greater response to seed or whole plant vernalization when the plants were grown subsequently under continuous light than when diurnal photoperiods were employed. Friend (1965) using red radiation on winter rye proposed the mechanism that continuous light increases the stabilization of the vernalization response since seed vernalization preceded exposure to continuous light.

The response of cauliflower to cold treatment appears to be different from that of broccoli. Most workers have reported that there is both a quantitative and a qualitative cold requirement for flowering in cauliflower. Sadik (1967) pointed out this requirement and added that the effectiveness of the cold treatment is dependent on the type of cultivar and is increased as the duration of the cold treatment is prolonged, and as the age of the plant is increased. He also claimed that the 2 cultivars he used have a juvenile stage before the end of which plants cannot be induced to initiate curds by cold treatment. He reported distinctive cold requirements for curd formation and flowering for the 2 cultivars used, one behaving as a summer cultivar since it formed a curd with or without a cold treatment but required a cold treatment for flowering while the other behaved as a winter cultivar since it required a cold treatment for both curd formation and flowering. Other workers (Wellington, 1954; Skapski and Oyer, 1964) are in general agreement that there is an optimum temperature range below and above which curd formation starts to be inhibited.

Cold treatment can also promote uniformity of curd initiation time (Wurr, Akehurst and Thomas, 1981) and crop maturity (Salter and Ward, 1972; Wurr, Akehurst and Thomas, 1981) in some cauliflower cultivars. These workers agree that the receptive stage of plant growth to cold treatment varies among cultivars and it seems likely that the number of leaves at this receptive stage increased with later maturing cultivars.

The effectiveness of a cold treatment can be altered by the condition under which plants are raised prior to cold treatment. For instance, Salter and James (1974) found that cold treatment following the raising of plants under controlled higher temperatures had no effect on the length of harvest period, while cold treatment of frame-raised plants at the same stage of growth reduced the maturity period. Moreover, Wiebe (1975) found that the variation in curd size was reduced by cold treatment only if plants had been raised under warm conditions.

Kato (1964) and Fujime and Hirose (1981) have shown that seed chilling can promote curd initiation in certain cultivars indicating that the cold requirement for initiation can start to be satisfied at germination.

Moreover, in contrast to findings from studies on broccoli, findings of other workers indicate that cold treatment was independent of daylength (Sadik, 1967) and that daylength had no influence on curd and flower formation in cauliflower (Eguchi, 1947; Parkinson, 1952 as cited by Sadik, 1967).

1.2.3 Curd Morphology Development and Growth

1.2.3.1 Morphology of the Curd

Several studies have been done to describe the morphology of the curd particularly that of the cauliflower. Earlier workers described the curd as being composed of fasciated and hypertrophied flower stalks which produce only rudiments of abortive flowers. Sadik (1962), however, claimed that a curd is composed of lateral, non-fasciated (lack of extensive fusion) and non-hypertrophied first-order branches arising acropetally in spiral succession from the main shoot. A curd can be dissected sequentially around the axis into a set of segments or metamers. Sadik (1962) estimated that a 500 g curd of Romanesco broccoli can have 150 distinguishable metamers on the main stem and on each of these metamers the subtended branch itself comprises metamers - nodes plus internodes, plus subtending branches, plus subtended secondary branches. Each secondary branch continues the sequence until about seven orders of branching are achieved. Curd growth therefore does not simply show hypertrophy.

The form of the curd is characterized by 3 main changes in the growth pattern of the plant:

1) leaf development is curtailed so that only bracts are present throughout the curd;

2) all lateral buds are elongated into shoots whose apices make up the convex surface of the curd; and

3) the internodes of the shoot system are elongated.

1.2.3.2 Development of the Curd

The morphological changes of the stem apex during the transition from the vegetative to generative state of both broccoli and cauliflower have been described by several workers. Gauss and Taylor (1969b), working on broccoli, cv Coastal observed that an increase in the chronological and morphological age of the plant is associated with an increase in the width and depth of the apex. At the 10-leaf stage the apex was broad (227μ) and practically flat. They considered this to be indicative of the early reproductive nature of the plant. Associated changes during this period were the marked increase in the tunica layer and the cupping of the uppermost leaves over the apex in a horizontal fashion. The apex then proceeded to become large, extremely flat but somewhat raised when first-order floral stalk primordia were initiated. During the period marked by rapid formation and elongation of first-order floral stalk, width of the apex decreased while depth continued to increase. The decrease in apical width was attributed to a reduction in size of the peripheral zone of the apex with the initiation of floral stalk primordia. When the apex was already in advanced reproductive stage, apical zonation still persisted. The last expanding leaf subtending the primary growing point became markedly elongated and strap-shaped in form.

Salter (1960) observed a progressive change in the appearance of the stem apex associated with the initiation of the curd. In cv Finney, development of the curd started when the normal apical dome was about 200μ in diameter. The dome widened to about 350μ and bracts were initiated in the axils of which secondary meristems developed and formed the primary peduncles of the inflorescence. Further bracts and secondary peduncles were initiated at the apices of the primary peduncles and in turn yielded a further order of peduncles. Bracts are present throughout the curd but become progressively smaller in later stages. Disruption of the curd begins at the time of floral initiation, when some of its branches begin elongation.

1.2.3.3 Growth of the Curd

Salter (1960) showed that growth of the cauliflower curd in terms of dry weight, fresh weight, mean diameter or volume was related to accumulated heat units. Without correcting for supraoptimal temperature, the form of the relationship was adequately fitted by the Gompertz curve. However, when the log dry weight of the curd was plotted against accumulated temperature between 5.5 and 13C the growth curve was almost logistic in form until maturity. Supraoptimal temperature appeared to be partially responsible for the apparently declining growth rate of the curd. Boswell and Jones (1941) as cited by Salter (1960) have also suggested that high temperatures may retard the growth of the curd. After maturity the gradual senescence of the leaves with the resulting reduction in the supply of photosynthates to the curd, may possibly have contributed also to the decline in the growth rate of the curd. When other time scales such as accumulated solar radiation, were used the growth curves for the 2 seasons were dissimilar.

In his succeeding experiment, Salter (1969) found that after considering several base and maximum temperatures, accumulated day degrees between 2.75C and 15.4C gave the best fit to the experimental points and the least residual error. This was found to be applicable to all the cultivars used.

No studies have been carried out on broccoli to describe the rate of curd growth as a function of any climatic factors.

1.2.4 Use of Environmental Time Scale

1.2.4.1 General Concept

Many studies have been done to describe plant growth patterns under field conditions. Frequently, studies show that the growth pattern for a particular crop can vary markedly between sowings because of the effects of variable weather conditions (Salter,1960). For example, when a time scale such as number of days from sowing is used against which to plot the growth of plants, the resultant plant growth curves can differ markedly from season to season. Nelder, Austin, Bleasdale and Salter (1960) introduced the idea of replacing chronological time in such growth equations by a time scale based on some suitable combinations of meteorological factors. The use of cumulative measurements of the main climatic variables as "time scales" may thus provide a common scale from season to season.

1.2.4.2 Heat Unit System

Of the various climatic variables, most attention has been given to temperature (e.g. Wurr and Kay, 1981 and Salter, 1960 on cauliflower; Marshall and Thompson, 1987a and 1987b on broccoli; Wurr and Fellows, 1984 on lettuce) as it has been considered a major environmental factor determining variations in plant growth. The use of accumulated day degrees or heat unit summation as a time scale is a convenient and simple method of integrating temperature with time to take into account temperature differences over different periods of time. It is a system for studying plant-temperature relationships by the accumulation of daily mean temperature above a threshold temperature.

Results of some work on this field are quite variable. Salter (1960), in his study on the growth and development of cauliflower found that using accumulated heat units as a common time scale in plotting growth curves resulted in the two seasons' growth being sufficiently similar to be adequately expressed by a single equation. Using a normal time scale resulted in irregular curves which were dissimilar between 2 seasons. The use of accumulated gram calories of solar radiation instead of temperature as the time scale was also tried but resulted in dissimilar curves for the two seasons. Moreover, regression analysis suggested that the growth of cauliflower plants was more closely related to temperature than to solar radiation. Nichols (1970), who used a four-parameter logistic equation to describe the growth of lettuce, also showed that the use of environmental time scales (solar radiation and heat unit summation) resulted in a better fit compared to the use of a chronological time scale. Austin, Nelder and Berry (1964) who used the same model on carrots found that for leaf growth the use of the sums of solar radiation, day degrees, or evaporation from an open water surface did not give curves that fitted the growth data better than those obtained with time in days. Yearly differences in leaf growth appeared to be related to corresponding differences in rainfall amounts. They thus suggested that a scale taking account of soil moisture tension might have given a better fit to the model. In another study (Austin, 1964) similar findings were obtained where the yearly differences in the growth curves of red beet were as great with the meteorological time scales as with the age scale, and they appeared to be related to yearly variations in plant density and rainfall. Wurr and Fellows (1984) found that in three lettuce varieties a quadratic curve relating the time of maturity to the time of sowing accounted for a high proportion of the variance while a linear relationship was established when the times of sowing and maturity were both expressed as a heat unit scale.

Initially, the heat unit system has found widespread use in predicting the date of harvest and in scheduling successive plantings. Further applications have been in scheduling spraying programmes for insect, disease and weed control and for the selection of suitable farming areas and of appropriate crop varieties for these areas (Arnold, 1959). Because of its value in satisfying these practical needs it is still being used in a variety of crops at present (e.g. Friis, Jensen and Mikkelsen, 1986 on peas; Kristenssen, Friis, Henrikssen and Mikkelsen, 1986 and Wurr and Fellows, 1984 on lettuce; Marshall and Thompson, 1987a and 1987b on broccoli).

In addition to temperature, Marshall and Thompson (1987a) considered solar radiation as a further determinant variate in the duration to crop maturity in broccoli (cv Corvet). They found that temperature accounted for a major proportion of the variation (74.3%) while solar radiation contributed a further 17.7% of the variation.

1.2.4.3 Selection of Appropriate Base Temperature

Arnold (1959) has reported that in earlier studies two methods have been used in the determination of the base temperature, namely, the least variability method and the regression coefficient method. In the former, the heat unit summations from a series of plantings were calculated on a number of base temperatures and the one giving the least variation is found by the process of elimination. The latter involves a calculation of a regression equation relating mean temperature and the heat unit summations. A correct base temperature is the one which gives a zero regression coefficient. In his review of literature he pointed out some flaws in the use of this system. The error manifests itself as a variation in the number of heat units required for a particular variety to complete a particular phase of development and was related to the selection of an incorrect base temperature. He pointed out three procedural errors, namely:

1) the use of standard deviation in the least variability method;

2) the rejection of the right base temperature on the basis that it is too low to be physiologically feasible; and

3) the failure to take into account the effect of some environmental factors in the computation of the base temperature. Based on his own study, he concluded that the base temperature resulting in the lowest coefficient of variation instead of the standard deviation is shown to be the appropriate one, and that this agreed closely with the regression coefficient method.

1.2.2.4 Limitations to the Use of the Heat Unit System

The heat unit concept is, however, open to some criticisms. These were summarized by (Wang, 1960) as follows:

1) plants may respond differently to the same environmental factors during various stages of their life cycle;

2) the threshold temperature as it was employed in heat unit computations is considered a constant but may change with the advancing age of the plant;

3) direct proportionality may not exist between growth rate and temperature;

4) several other environmental factors influence plant growth and development.

Because of these criticisms, modifications have been made to the heat unit concept by a number of workers. For instance, Brown (1975) used a system to calculate heat unit summation for corn which distinguishes between daytime and nighttime development rate of the crop, i.e, development rate is linear above a certain base temperature at nighttime and non linear during daytime. Friis, Jensen and Mikkelsen (1987) considered a 2-component model in vining peas which consists of a sowing-to-emergence soil temperature sums (Tb=3C) and an emergence-to-harvest air temperature sums (Tb=5.5C) as prediction criteria.

Other workers incorporate into the heat unit system other meteorological factors. Kish, Ogle and Loadholt (1972) incorporated available soil moisture in predicting maturity date of snap beans. Coligado and Brown (1975) developed a model which incorporates a genetic factor, mean daily temperature, photoperiod, temperature range and a development potential factor as predictor variates to predict tassel-initiation-time in corn.

1.3 Growth Analysis

1.3.1 Methods of Growth Analysis

Woodhouse (1980) as cited by Hunt (1982) stated that growth analysis, when properly handled, is at best a useful method for obtaining preliminary descriptions of plant growth as a framework for more detailed studies of the underlying biological processes, and at worst an end in itself leading on to nothing.

There are 2 general approaches to plant growth analysis, namely, the classical and the functional approach. The development of the first approach dates back to the 1920's in the work of Gregory and of Briggs, Kidd and West (Richards, 1969). The method involved a comparison of the growth rates over a time interval based on the weight of the plants harvested at the start and end of the interval. To obtain a sufficient accuracy in the analysis large but relatively infrequent harvests are done. The different quantities involved in growth analysis namely, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) are calculated based on the following formulae (Causton, 1983):

$$\mathrm{RGR} = (\log_e W_2 - \log_e W_1)/(t_2 - t_1)$$
$$\mathrm{NAR} = (W_2 - W_1)(\log_e L_2 - \log_e L_1)/(L_2 - L_1)(t_2 - t_1)$$
$$\mathrm{LAR} = L/W$$
$$\mathrm{SLW} = L/Lw$$
$$\mathrm{LWR} = Lw/W$$

where: W = plant dry weight; L = leaf area/plant;
Lw = leaf weight/plant; t = time; the subscripts
1 and 2 denote first and second harvests.

The main disadvantage of this method is that interharvest variability tends to yield markedly irregular time trends in the derived relative growth rate, net assimilation rate and other parameters.

In the second approach, a continuous assessment of gain in dry weight and in leaf area with time is obtained by fitting the values at each harvest interval to an appropriate equation defining the curve (Hurd, 1977). From the equation further equations defining changes in the various growth parameters can then be derived.

Hunt (1982) pointed out that the two approaches are not mutually exclusive if time and space are no objects but it is not often that such a scheme makes the most efficient use of the material available.

In recent years the functional approach to growth analysis has become increasingly popular. Causton, Elias and Hadley (1978) summarized the advantages of this approach as follows:

1) the function fitted provides a convenient summary of the data;

2) a series of estimates of the growth attribute may be calculated at as many times as desired, and these estimates are less disturbed by the biological variability;

3) the logarithmic form of the function may be differentiated to produce a relative growth rate function;

4) if the function employed is based on some biologically meaningful model, then the parameters of the function may provide useful information, either by themselves or in various combinations.

1.3.2 Growth Models

In the functional approach, the use of the polynomial exponential family of functions has been popular because of the great flexibility of the curves and also because the model can be fitted to the data easily by the straightforward regression methods, and a confidence band can be defined easily about the fitted curves (Venus and Causton, 1979). However, Causton et al. (1978) pointed out that these functions are not based on any biological model and usually nothing of significance can be inferred from the parameters derived. Interpretation of results can be very difficult. For instance, the relative growth rate trend with time obtained from a second degree polynomial fitted to data is linear while that derived from higher order polynomials exhibit various forms of curvilinearity and often the results are not biologically satisfactory. Hurd (1977) also showed that the use of exponential polynomials did not provide similar patterns of growth that would be expected between closely related steady-state treatments.

There are a number of alternative functions to polynomials which are based on a simple but more realistic model. However, these functions are statistically not linear so that the definition of confidence bands is not exact and considerable computation is necessary (Venus and Causton, 1979).

Among these functions are the following (Hunt, 1982):

a) The Logistic function

$$W = a/(1+be^{-kt})$$

b) The Gompertz function

$$W = ae^{-be^{-kt}}$$

c) The Richards function

$$W = a(1+e^{(b-kt)})^{-1/d}$$

where a is the asymptote; b is a measure of the starting size of the system; k, a rate constant; and d, a measure of the point of inflection of the curve.

A summary of the extensive application of the logistic and the Gompertz function on a variety of crops was presented by Hunt (1982).

The Richards function was proposed by Richards (1959) and, unlike the logistic or the Gompertz function which contains only 3 parameters, it contains a fourth parameter, d which determines the point of inflection of the curve.

Nelder (1961) proposed a development of the logistic equation which is related to the Richards function and which takes the form:

$$W= a/(1+e^{-(b+kt)/d})^{d}$$

and is otherwise known as the generalized logistic equation. This was applied satisfactorily by Austin (1964) who worked on red beet, Austin, Nelder and Berry (1964) on carrots and Nichols (1972) on lettuce.

One advantage of these asymptotic functions is that the individual members of families of related curves may each be fitted by the function without losing their family identity, a property not shared by a collection of polynomials of comparable complexity (Hunt, 1982).

1.3.3 The Growth Parameters as Indicators of Plant Response to the Environment

The relative growth rate (RGR) concept is a very old concept but at present it still provides a convenient and equitable performance for different plants (Hunt and Lloyd, 1987). It is a measure of the efficiency of the material comprising an organism in the production of new material, and the measure is an average over the whole organism (Causton, 1983). In plants, the relative growth rate may be partitioned into two components:

1) the net assimilation rate (NAR), which may be regarded as a measure of net photosynthetic rate on a whole plant basis; and

2) the leaf area ratio (LAR).

LAR may in turn be partitioned into a further 2 components:

1) the specific leaf area (SLA) which gives an indication of the thickness or density of the leaves; and

2) the leaf weight ratio (LWR) which is a measure of the leafiness of the plant.

The effect of some environmental factors particularly temperature and light intensity on the different growth parameters have been studied on a range of crops. The investigations of Blackman, Black and Kemp (1965), Black (1955) and Hodgson (1967) as reviewed by Rajan, Betteridge and Blackman (1973) showed common trends in NAR and RGR of sunflower and soybean with solar radiation. In each case, increasing solar radiation enhanced NAR and RGR but depressed LAR. In contrast, the responses to changes in the mean diurnal air temperature were less clear. Warren-Wilson (1966a) in his controlled climate experiment found that in rape, sunflower and maize both NAR and RGR rose with temperature up to a maximum and fell with further increase in temperature. LAR and SLA also tended to increase with temperature while LWR was generally unaffected. In all these species the optimum temperature for NAR and RGR was found to lie between 20C and 30C. In a separate study Warren-Wilson (1966b) related the pattern of early vegetative growth of the three crops to seasonal changes in an arid climate and he found that for each species, NAR was a function of radiation receipt, but was positively temperature-dependent only for sunflower and maize. From the results of his two separate studies Warren-Wilson (1966b) suggested that for plants under natural climate the effect of temperature on NAR and RGR must vary according to whether the prevailing temperature lies above or below the optimum for the species under consideration.

Findings from other workers also suggest a complex interaction between the effects of light intensity on NAR, LAR and RGR of different crop species (Rajan et al. 1973; Elias and Causton, 1975; Evans and Hughes, 1961; Hughes, 1965).

Elias and Causton (1975) emphasized the importance of LAR and LWR in studying the response of a plant to a particular environment. They formulated two hypotheses to determine the relative importance of these ratios:

1) the optimisation of leaf area is achieved through leaf area affecting the partition of matter between the leaves and the rest of the plant through some kind of feedback mechanism; or

2) the optimisation of leaf area can only occur within limits laid down by the inherent trends of LWR with time.

The findings that LWR was unaltered with temperature and or light intensity treatments (Evans and Hughes, 1961; Warren-Wilson 1966a) supports the second hypothesis. However, those of Elias and Causton (1975) or Rajan et al. (1973) where both LWR and LAR were affected by temperature and light intensity do not lend support to any hypothesis.

Nichols (1972) observed differences in NAR between 2 cultivars of lettuce and attributed the differences to differences in SLW. As this was exhibited only at the time when the plants were small and not competing for light, he argued that at high densities all the light would be absorbed by the crop canopy and thicker leaves would no longer offer any advantage.

Barnes, Pearce, Carlson, Hart and Hanson (1969) and Dornhoff and Shibles (1976) found that specific leaf weight correlated well with CO_2 exchange rate.

Gifford and Evans (1981) pointed out that the importance of SLW depends on its relationship with leaf area development as expansion of leaf area and thickening of leaves can be inversely related. They advanced the idea that a sound strategy might be to produce plants which expand large thin leaves early in the season and then thick leaves after the canopy intercepts all the light.

1.4 Yield in Relation to Dry Matter Partitioning and Plant Photosynthetic and Storage Capacity

In the past, the yield of economically important crops has been increased through plant breeding and optimisation of growing conditions. These resulted in substantial improvement in both dry matter production in the leaves and accumulation of dry matter by harvestable organs (Ho, 1988).

Improvement of the photosynthetic capacity of the modern cultivars of important crops has been achieved mainly by increasing the light-intercepting area of leaves. This has been made possible by increasing the number of leaves, attaining a larger individual leaf area or modifying leaf posture (Evans and Dunstone, 1970; Tanaka, Kawano and Yamaguchi, 1966). Attempts to improve yield by increasing plant photosynthetic rate per unit leaf area have had very little success. Selection for the component processes of photosynthesis such as photophosphorylation (Hanson and Grier, 1973; Treharne, 1972) or chlorophyll content (Ferguson, Eslick and Aase, 1973) had little influence on yield. Direct breeding for high CO_2 exchange rate (CER) and for low photorespiration has also been unsuccessful (Hart, Pearce, Chatterton, Carlson, Barnes and Hanson, 1978; Kaplan and Koller, 1977; Murthy and Singh, 1979). A few cycles of selection may have been sufficient to eliminate completely an apparent inefficiency which nature or agricultural practice had not already overcome (Wilson, 1978).

Harvest index is the ratio of the economic yield to total plant biomass and reflects the dry matter accumulation capacity of the harvestable organs. Increase in harvest index has been accomplished mainly by increasing the number and size of the different yield components of the crop (Evans and Dunstone, 1970;

Tanaka et. al, 1966).

At different times, either source- or sink-limiting situations may exist as the capacity of dry matter production in leaves may either be higher or lower than the capacity of dry matter accumulation in the sinks. While there is a dynamic relationship between the production and utilization of dry matter within a plant (Wareing and Patrick, 1975) the regulation of the partitioning of dry matter into different organs can be independent from the production of assimilate (Ho, 1988). Evans (1975) thus pointed out that the present scheme in crop productivity improvement should involve the enhancement of the efficiency of partitioning along with the improvement of both photosynthetic and storage capacity of the plant in a more or less coordinated way.

The subjects of dry matter partitioning and source-sink relationships have been reviewed extensively (Snyder and Carlson, 1984; Gifford and Evans, 1981; Hunt and Lloyd, 1987; Ho, 1979).

In particular, Snyder and Carlson (1984) pointed out that dry matter partitioning can be influenced by some environmental factors such as temperature, light, water and minerals, carbon dioxide and oxygen and plant stand density depending on the crop species. Hunt and Nicholls (1986) as cited by Hunt and Lloyd (1987) emphasized the importance of below- and above-ground environmental stress, and the growth potential of the species on dry matter partitioning.

Gifford and Evans (1981), in their review on photosynthesis, carbon partitioning and yield, concluded that continuation of the improvement in the ratio of the economic sink to total plant still seems to be the most effective route until it is at the expense of light-intercepting leaf surface. The key to understanding distribution of photosynthate assimilate to particular organs seem to lie not so much in the leaf mesophyll or the phloem loading system nor in the translocation system, but more in the determination of the properties of the sinks themselves. Similarly, Hardwick (1984) argued that the growth of yield organs should be regarded as a special case of the general problem of plant morphogenesis. His study on the sink development, phyllotaxy and dry matter distribution in a cauliflower curd presented evidence against the "bicycle pump model" of source-sink relationship. It revealed that there are strong local controls of sink development in cauliflower. In a curd, he found that there are substantial variations in mass between florets which could not be interpreted using a competition function. These variations appeared to originate at the apical meristem as variations in the timing of promordial initiation. He proposed the 'clock face model' which postulates that the position of successive primordia at the apical meristem is determined as if there were a steadily rotating radius vector receiving signals from the older primordia and determining the position of new primordia in response to these signals. The role of mechanical stress as a morphogenetic trigger (Lintilhac, 1974) which determines the positioning of new primordia at the apical meristem and the importance of some plant growth regulators have been pointed out.

There is nothing in the literature to explain the nature of the mechanism controlling the rate of growth of individual metamers of a curd after initiation, and about factors which control the cessation of growth. The economic yield may be associated with the mass or area of leaves per plant but the relationship between size of source and eventual size of sink in a plant is in general not very close (Ho, 1988).

Chapter 2

Field Experiment: The Effect of Sowing Date and Cultivar on the Growth and Development of Broccoli.

1.1 Introduction

Growth and development, maturity charateristics and yield of vegetable crops are determined by the response of the genotype to the environment. Studies on the effect of the environment on cauliflower are quite extensive (e.g., Wurr and Kay, 1981; Sadik, 1967) but few studies have been done on broccoli. The two crops are closely related but the limited studies on broccoli to date indicate that their responses to the environment may be quite different.

This experiment was conducted to determine the effects of genotype and environment on the growth and development of broccoli. Six bimonthly sowings were done in order to cover all the critical changes in season throughout the year. Four commercially-important broccoli cultivars, representing different periods of maturity, were used in order to examine the genotype-environment interaction.

Specifically, the study aimed to:

(1) determine the effect of sowing date and genotype on the different growth and development parameters of broccoli including rate of dry matter accumulation, times to curd initiation and maturity, leaf production, yield and total dry matter production;

(2) assess the contribution of temperature to the variation in the different parameters with sowing date using the heat unit concept;

(3) determine the applicability of using a unified, temperature-based time scale in describing the growth rates of the plant; and

(4) apply a model to predict curd maturity of the different broccoli cultivars.

2.2 Materials and Methods

2.2.1 Experimental Design and Treatments

A 2-factor factorial experiment in randomized complete block design (RCBD) with 3 replications was used in this study. The following were the treatments:

Sowing Date
- a) 18 September 1985
- b) 19 November 1985
- c) 17 January 1986
- d) 21 March 1986
- e) 22 May 1986
- f) 22 July 1986

Cultivar
- a) Premium Crop
- b) Mercedes
- c) Idol
- d) Fordhook Late

2.2.2 Production of Transplants

Seed of the different cultivars of broccoli was sown in cellular trays on heated beds inside a glasshouse. The propagation medium consisted of 95% fine peat and 5% fine sand by volume with fertilizer additions (Appendix 1b). As soon as the first true leaf emerged the trays were taken outside the glasshouse into the natural environment. Liquid feed (72 g KNO_3/100 l) was applied to the developing seedlings 2-3 times a week. At the 4-leaf stage the seedlings were transplanted into the field.

2.2.3 Cultural Management Practices

2.2.3.1 Land Preparation and Planting

The field was ploughed and then rotavated a number of times until the soil was friable and free from perennial weeds. Plots measuring 2m x 18m with 2 rows spaced at 0.75m were laid out. Seedlings were then transplanted into each row 0.35m apart.

2.2.3.2 Fertilizer Application and Weed Control

A week before transplanting, a complete fertilizer (12-10-10) at 1 t/ha and borax at 30 kg/ha were broadcast over the plots. The soil was rotavated to thoroughly mix the fertilizer. In the first planting trifluralin was used to control weeds but in the other plantings mechanical means of weed control was used.

2.2.3.3 Irrigation and Pest and Disease Control

Irrigation was supplied during the drier months when rainfall was not adequate. A trickle system of irrigation using biwall and alkathane pipes was used.

Pesticides were applied regularly from emergence onwards using a spray programme outlined in Appendix 2. Slug infestation was controlled using Mesurol(R) slug bait. To prevent rabbit damage an electric fence was installed around the field.

2.2.4 Growth Analysis

Sampling for growth analysis commenced one week after seedling emergence. Four plants of each cultivar per replicate were harvested. The root was separated from the shoot at the base of the cotyledons. The shoot was subdivided into the leaf and the stem. The leaf was separated at the base of the lamina. In the field, groups of 8 plants within each plot were randomly designated as to time of sampling. At each sampling time the inner four plants from each group were harvested. Whole plants were dug up using a fork to recover as much of the root system as possible. The roots were separated and thoroughly washed. The plant parts (leaves, stem, root and curd) were oven-dried at 80C for 48 hours and their dry weights were obtained. Sampling was done at weekly intervals during the warmer months (October 15 to April 14) when plant growth was faster and biweekly during the cooler months (April 15 to October 14) when growth was slower.

At every sampling, apices of the plants were observed under a dissecting microscope for curd initiation. When initiation was evident, curd diameter measurements were taken periodically up to curd maturity. A curd was considered to be mature at the time just before it started to lose compactness or just before the buds started to open.

2.1.5 The use of the Heat Unit System

Daily maximum and minimum temperatures and sunshine hours were obtained from the meteorological station at DSIR situated about 300m from the experimental site. Accumulated day degrees or heat units above various base temperatures were calculated for each sowing date using a formula (Anon, 1954) based upon the following:

a) If $T_{min} > T_b$
   $HU = T_{mean} - T_b$
b) If $T_{min} < T_b$ and $T_{mean} > T_b$
   $HU = (T_{max} - T_b)/2 - (T_b - T_{min})/4$
c) If $T_{max} > T_b$ and $T_{mean} < T_b$
   $HU = (T_{max} - T_b)/4$
d) If $T_{max} < T_b$
   $HU=0$

where: HU = heat unit; Tmax = maximum temperature;
Tmin = minimum temperature; $T_{mean} = (T_{max} + T_{min})/2$;
Tb = base temperature

2.2.6 Fitting Growth Data into the Modified Richards Function

A computer programme which fits growth data into the modified Richards function (Nelder, 1961) was developed for an IBMPC, using both chronological, i.e. number of days, and heat unit summation time scales. The equation has the form:

$$W = A/(1 + e^{-(b+kt)/d})^{d}$$

or its logarithmic form:

$$\log_e W = \text{loge } A - d\log_e (1+e^{(b+kt)/d})$$

where: W = weight
A = W asymptote
b = loge W intercept
k = initial RGR
d = point of inflexion
T = time (chronological or temperature-based)

The procedure used in choosing the base temperature was based on the least variability method as suggested by Arnold (1959). This consisted of estimating the error mean square (EMS) about the logistic function when total plant dry weights for all the sowing dates and cultivars were fitted into a single curve against the heat unit summation time scale. A number of base temperatures were tried and the one yielding the least EMS was considered to be the most appropriate.

2.2.7 Fitting Curd Growth Data and Estimating the Time to Curd Initiation

Curd growth data which consisted of weekly (or biweekly) measurements of curd diameter were fitted into polynomial models relating $\log_e$ curd diameter to heat unit summations at different base temperatures. Based on the significance of the components of the model (i.e., linear, quadratic and cubic) the appropriate model was determined. The appropriate base temperature was chosen on the basis of the goodness of fit (measured as r^2) of the regression equation. To derive a common regression for all the sowing dates, the intercepts were adjusted such that at time to curd initiation, heat unit summation was equal to zero. The base temperature resulting in the best fit (highest r^2) was chosen.

From the established equations, the heat unit summation (HUS) from sowing to curd initiation time for each cultivar was estimated by extrapolating to a curd diameter of 0.6 mm. This size was taken to be the diameter of the shoot apex at curd initiation time for cauliflower (Wurr and Kay, 1981) and will be considered in this study to be also appropriate for broccoli. From the estimates, the chronological time at curd initiation (CI) was determined. Based on these chronological times, heat unit summations at different base temperatures were calculated. The appropriate base temperature for curd initiation was the one which resulted in the least variation (lowest CV) between sowing dates.

2.2.8 Leaf Production

At every harvest the number of leaves longer than 1 cm was counted. When the curd was already visible, the number of leaves was considered final. After this stage, only bracts are formed which subtend secondary curd meristems (Wiebe, 1975). The final number of leaves was considered to be the morphological age of the plant at curd initiation time. The number of leaves was fitted against both chronological and heat unit summation time scales and the appropriate base temperature was chosen using the goodness of fit method.

2.2.9 Calculating the Growth Analysis Parameters

The different growth data (leaf area, leaf dry weight and total dry weight) were fitted to the model using a heat unit time scale above the chosen base temperature. From the equation, predicted values were determined and from these values the different growth analysis parameters, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf weight (SLW), and leaf weight ratio (LWR) were calculated. The pattern of changes in these growth parameters during specific stages of plant development (early seedling, curd initiation and curd maturity stages) were analysed.

2.2.10 Dry Matter Production and Partitioning

The time when 50% of the plants in the field had mature curds was considered to be the time of curd maturity. The final dry matter yield at curd maturity was taken and analysed. The patterns of dry matter partitioning during the three development stages were analysed based on the raw data and not on the predicted values.

2.2.11 Application of a model to predict curd maturity

Marshall and Thompson (1987a) described a model that predicts the number of days from sowing to curd maturity (henceforth called crop duration) given a knowledge of the daily maximum and minimum air temperature and daily receipt of solar radiation (Appendix 9). The model was simplified in this study as

$$R-\bar{\bar{R}} = a(\bar{H}-\bar{\bar{H}})+E \quad \text{(Model A)}$$

with heat unit summation (Tb=3C) as the single component of the model, or

$$R-\bar{\bar{R}} = a(\bar{H}-\bar{\bar{H}})+b(\bar{S}-\bar{\bar{S}})+E \quad \text{(Model B)}$$

with sunshine hours as a second variate. R is the reciprocal of crop duration (1/D), $\bar{H}$ and $\bar{S}$ are the total heat unit summation and sunshine hours averaged over crop duration (HUS/D and S/D, respectively), a and b are the corresponding regression coefficients, $\bar{\bar{R}}$, $\bar{\bar{H}}$ and $\bar{\bar{S}}$ are the grand means of the variates, $\bar{R}$, $\bar{H}$ and $\bar{S}$, respectively, and E is the error term.

For the second model, a sequential F-test was done to determine the significance of the contribution of sunshine hours as a second explanatory variate.

The models were fitted separately for each cultivar and the predicted crop durations were computed.

2.3 Results

2.3.1 Growth and Development

2.3.1.1 Growth and the Heat Unit System

Table 2.1 shows the error mean square (EMS) about the regression of total plant dry weight from all sowing dates against heat unit summation above different base temperatures. The regression parameters are shown in Appendix 4. Using a base temperature of 3C resulted in the smallest error variance. When a chronological time scale (i.e. no. of days from sowing) was used the function could not be fitted. This was presumably because of too large an error variance, the rate of dry matter accumulation at different sowing dates being so variable that a common regression could not be derived. Even within each sowing date, data could not be fitted against a chronological time scale. Thus, throughout the succeeding analysis of plant growth, heat unit summation above 3C was used as the time scale.

The trend in the monthly heat unit accumulation above 3C covering the whole experimental period is shown graphically in Fig. 2.1. It ranged from as high as 518 heat units on January to as low as 141 heat units on July.

2.3.1.2 Pattern of Dry Matter Accumulation

The patterns of dry matter accumulation of broccoli at different sowing dates, averaged over cultivar means, are shown in Figs. 2.2 and 2.3. In the former figure a common initial relative growth rate (parameter k of the equation) was fixed for all the sowing dates. The k value of the regression equation of dry matter accumulation against HUS (Tb=3C) common to all sowing dates (App. 4) was used. It can be seen that the predicted curves for the September and July sowings did not provide as good a fit as did those of the other sowings presumably because of the large deviations from the actual initial RGR. The latter figure shows the different curves when the k parameter was not fixed. Some variations in the initial RGR are evident but that of March, May

Table 2.1 Error mean square (EMS) about logistic function of total plant dry weight against heat unit summation at different base temperatures.

BASE TEMP (C)	EMS
0	0.52
1.0	0.48
2.0	0.44
2.5	0.43
3.0	0.39
4.0	0.45
5.0	0.54

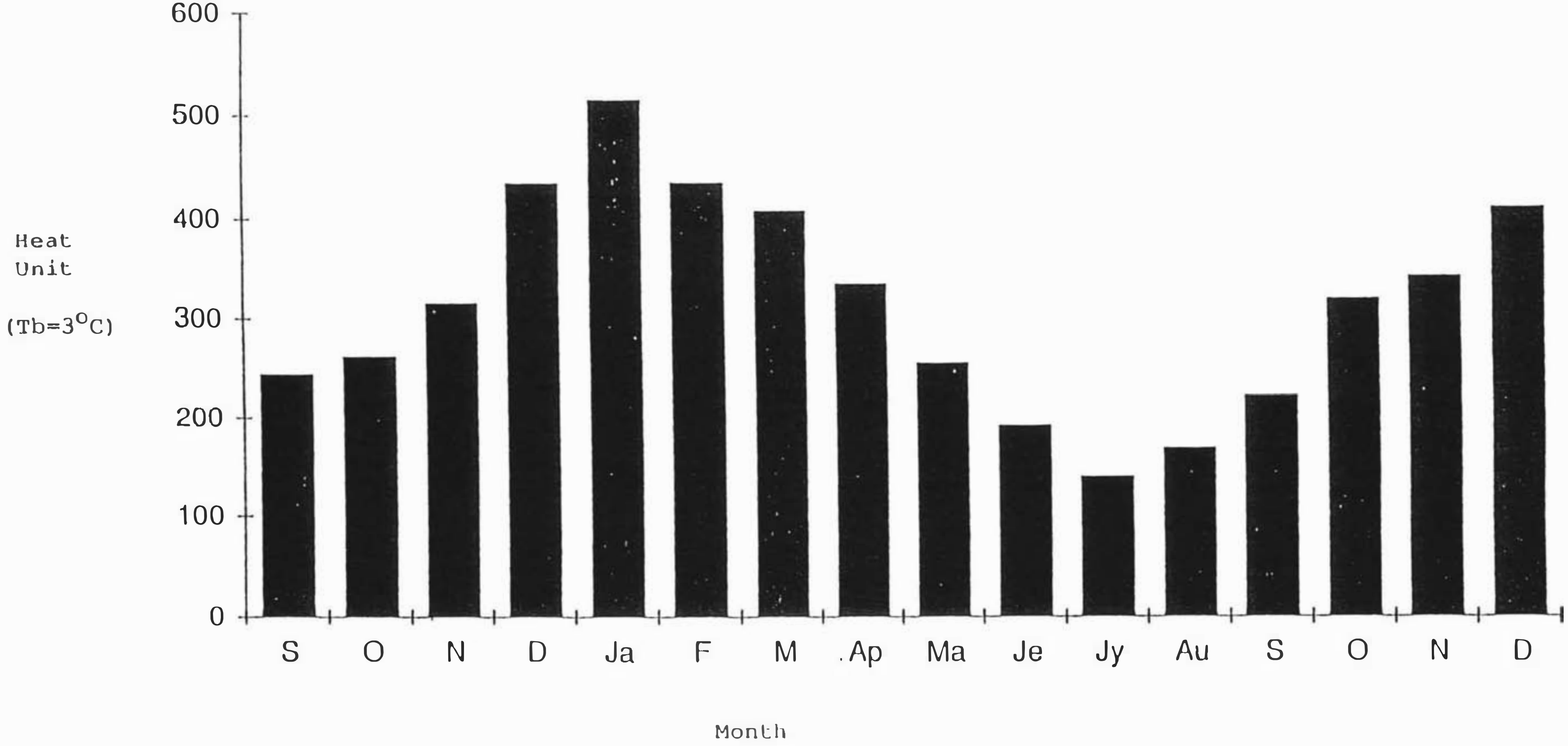


Fig. 2.1 Monthly heat unit accumulation above 3C from September, 1985 to December, 1986.

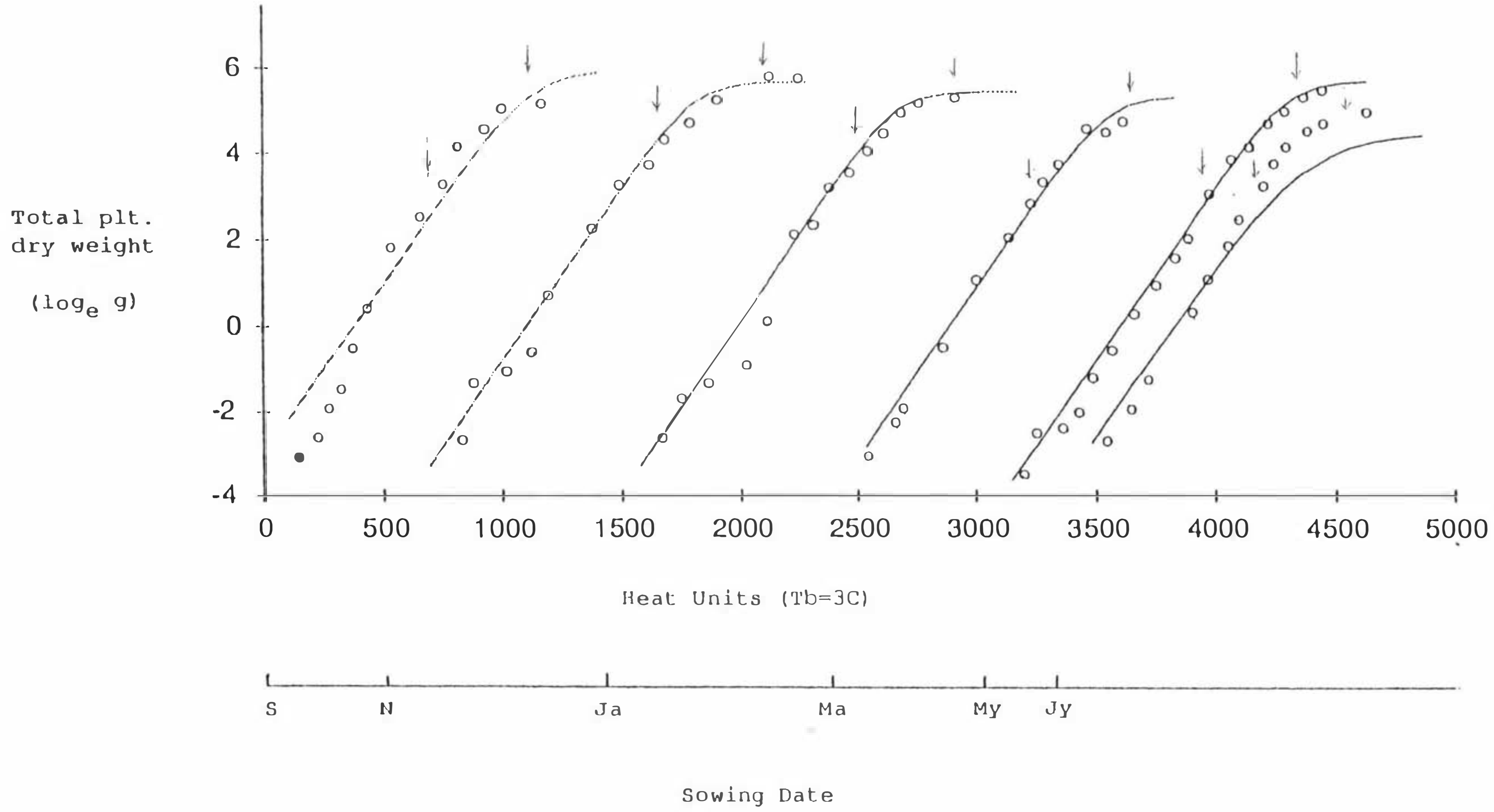


Fig. 2.2 Dry matter accumulation of broccoli (mean of 4 cultivars) at different sowing dates (assuming a constant initial RGR). Data fitted to a logistic equation. First and second arrows for each sowing date represent the curd initiation and curd maturity stages, respectively.

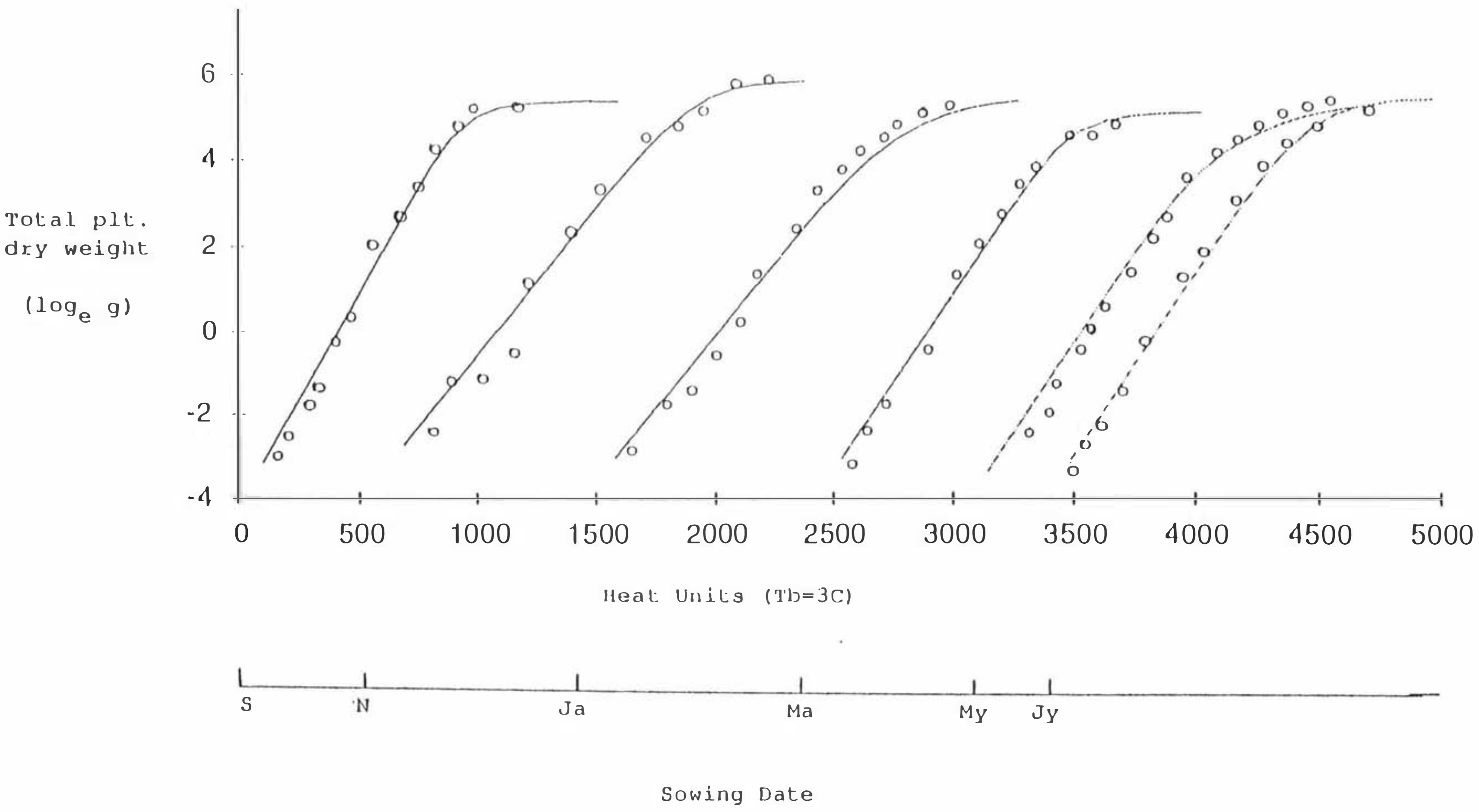


Fig. 2.3 Dry matter accumulation of broccoli (mean of 4 cultivars) at different sowing dates. Data fitted

and July sowings are close enough to be described by a single parameter. The statistical analysis of this parameter is dealt with in the succeeding section. Generally, the end of the exponential growth (i.e. log linear phase) coincided with the stage between curd initiation and curd maturity. Thereafter, the rate of dry matter accumulation declined then levelled off.

2.3.1.3 Growth Analysis

The trends in the different growth analysis parameters (average of cultivar and sowing date means) derived from the predicted values of total plant dry weight, leaf dry weight and leaf area are shown in Fig. 2.4a and Fig. 2.4b. Relative growth rate (RGR) assumed an inverse sigmoid curve. Net assimilation rate (NAR) increased with time and peaked just after the curd initiation stage and, thereafter, declined. Leaf area ratio (LAR) and specific leaf weight (SLW) were higher early on and declined progressively with time. Leaf weight ratio (LWR) was constant at the start and declined slightly during the curd development stage.

The growth curves for the different sowing dates are shown in Figs. 2.5a and 2.5b, and for the different cultivars in Figs. 2.6a and 2.6b. It is difficult to compare the trend of the different curves for the different sowing dates without referring to specific developmental stages, as obviously, the patterns with time are influenced by the time and duration of these development stages which varied appreciably with sowing dates. Tables 2.2 - 2.6 show the values of the different parameters at three stages of plant development namely: the early seedling (ES); curd initiation (CI); and curd maturity (CM) stage. Identification of these three stages is discussed in Section 2.2.1.5. Initial RGR (early seedling stage) was higher during the September, March, May and July sowings than during the November and January sowings. This was obviously associated with the growth duration of the plant (i.e. total number of heat units), the shorter the duration the higher was the initial RGR. The same trend can be seen during the curd initiation stage. At curd maturity RGR values for the different sowing dates became more uniform.

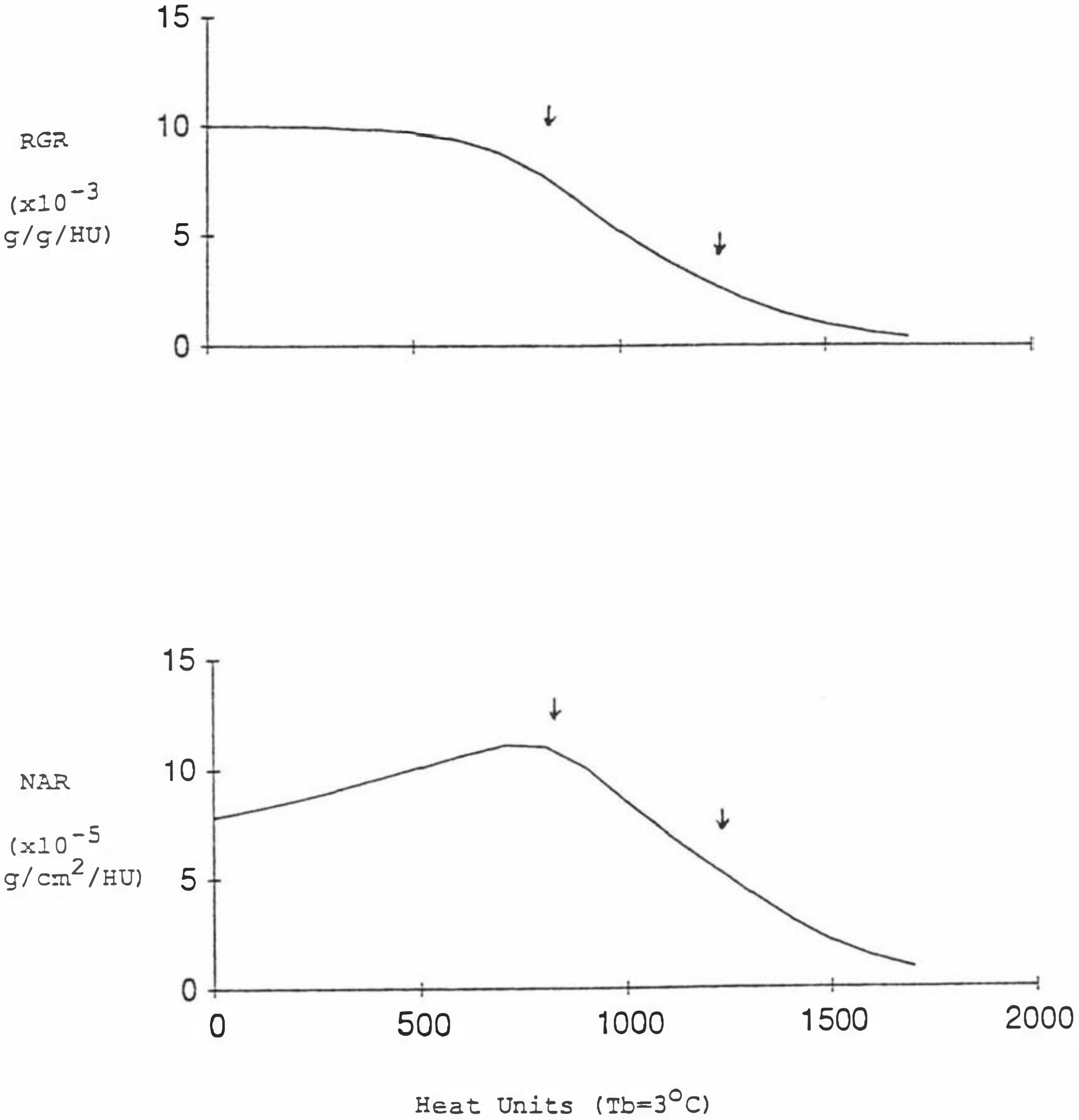


Fig. 2.4a Trends in relative growth rate (RGR) and net assimilation rate (NAR) with cumulative heat units (mean of 4 cultivars and 6 sowing dates). Primary data fitted to a logistic equation. First and second arrows represent the curd initiation and curd maturity stages, respectively.

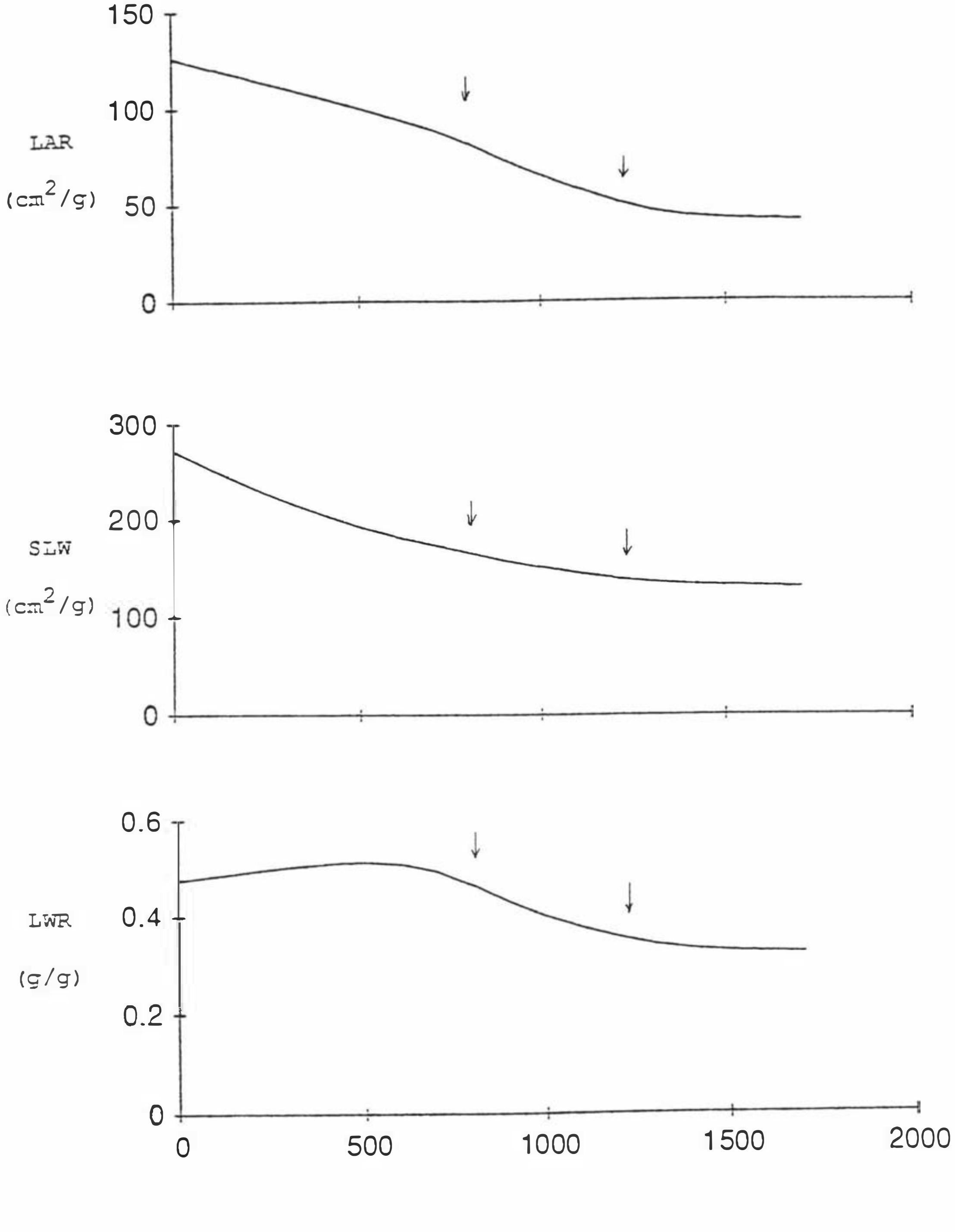


Fig. 2.4b Trends in leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) of broccoli with cumulative heat units (mean of 4 cultivars and 6 sowing dates). Primary data fitted to a logistic equation. First and second arrows represent the curd initiation and curd maturity stages, respectively.

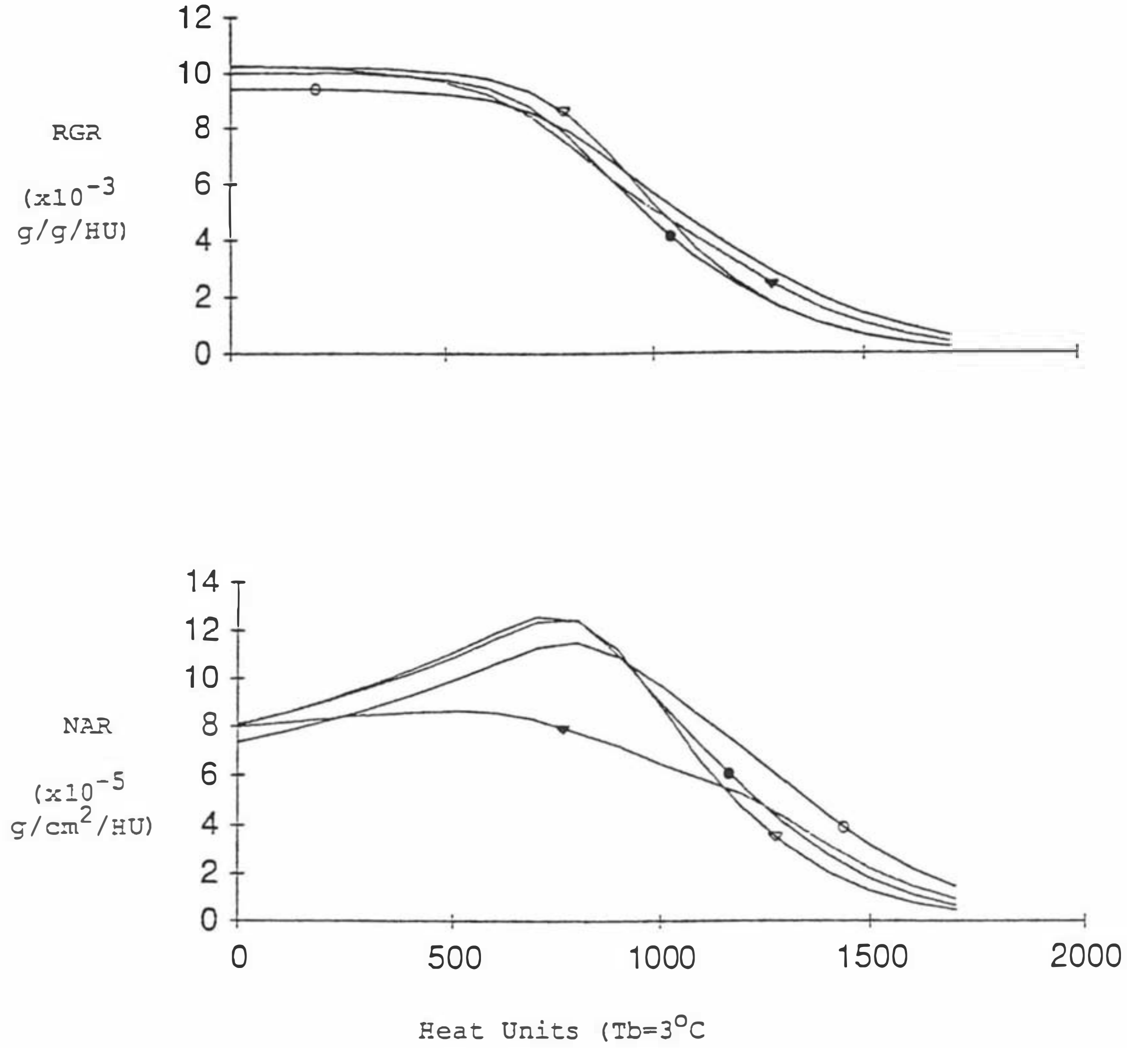


Fig. 2.5a Relative growth rate (RGR) and net assimilation rate (NAR) of different cultivars of broccoli (-○- P. Crop; -●- Mercedes; -▽- Idol; -▼- Fordhook Late) averaged over 6 sowing dates. Primary data fitted to a logistic equation.

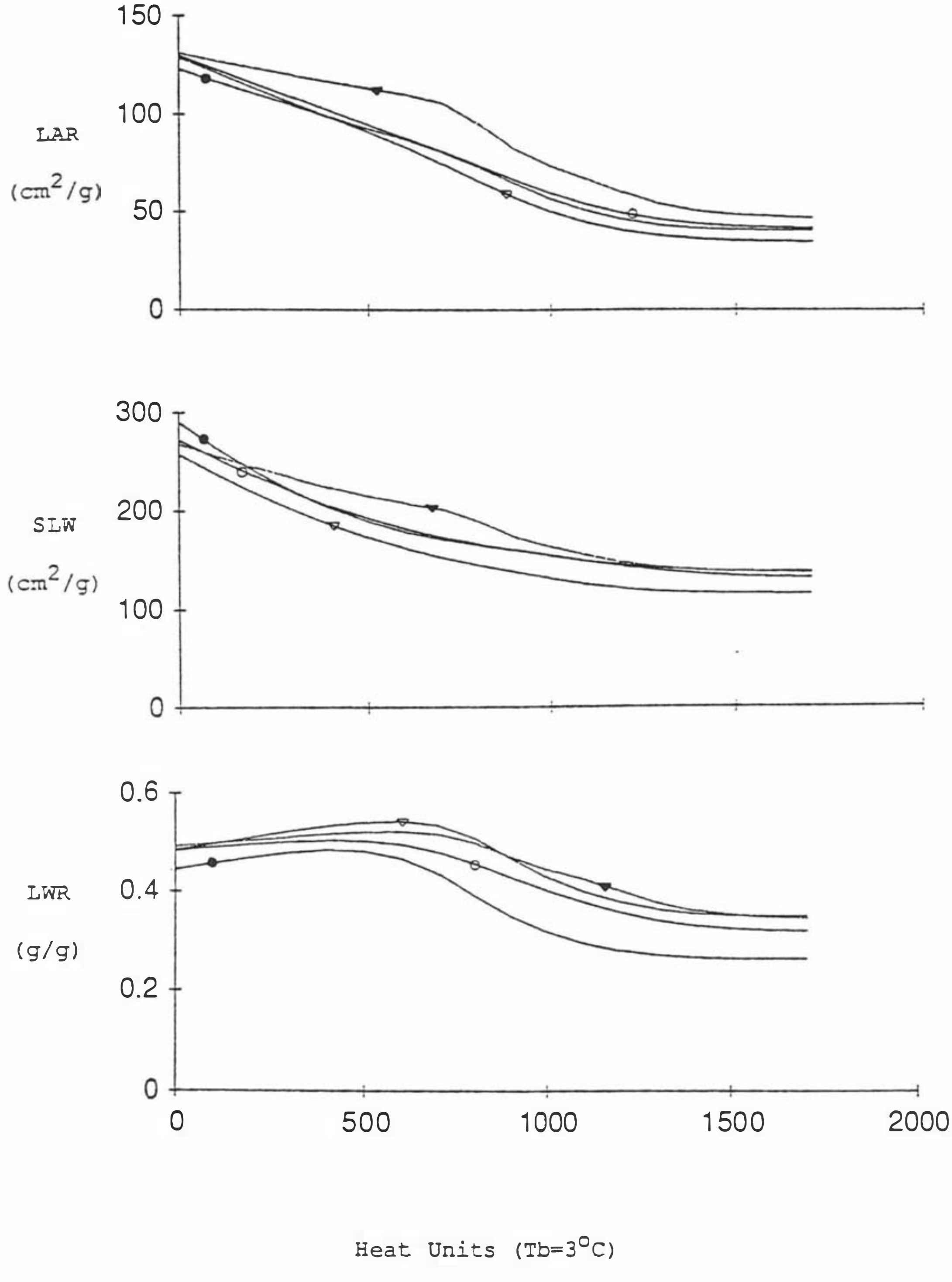


Fig. 2.5b Leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) of different cultivars of broccoli (-o- P. Crop; -●- Mercedes; -▽- Idol; -▼- Fordhook Late) averaged over 6 sowing dates. Primary data fitted to a logistic equation.

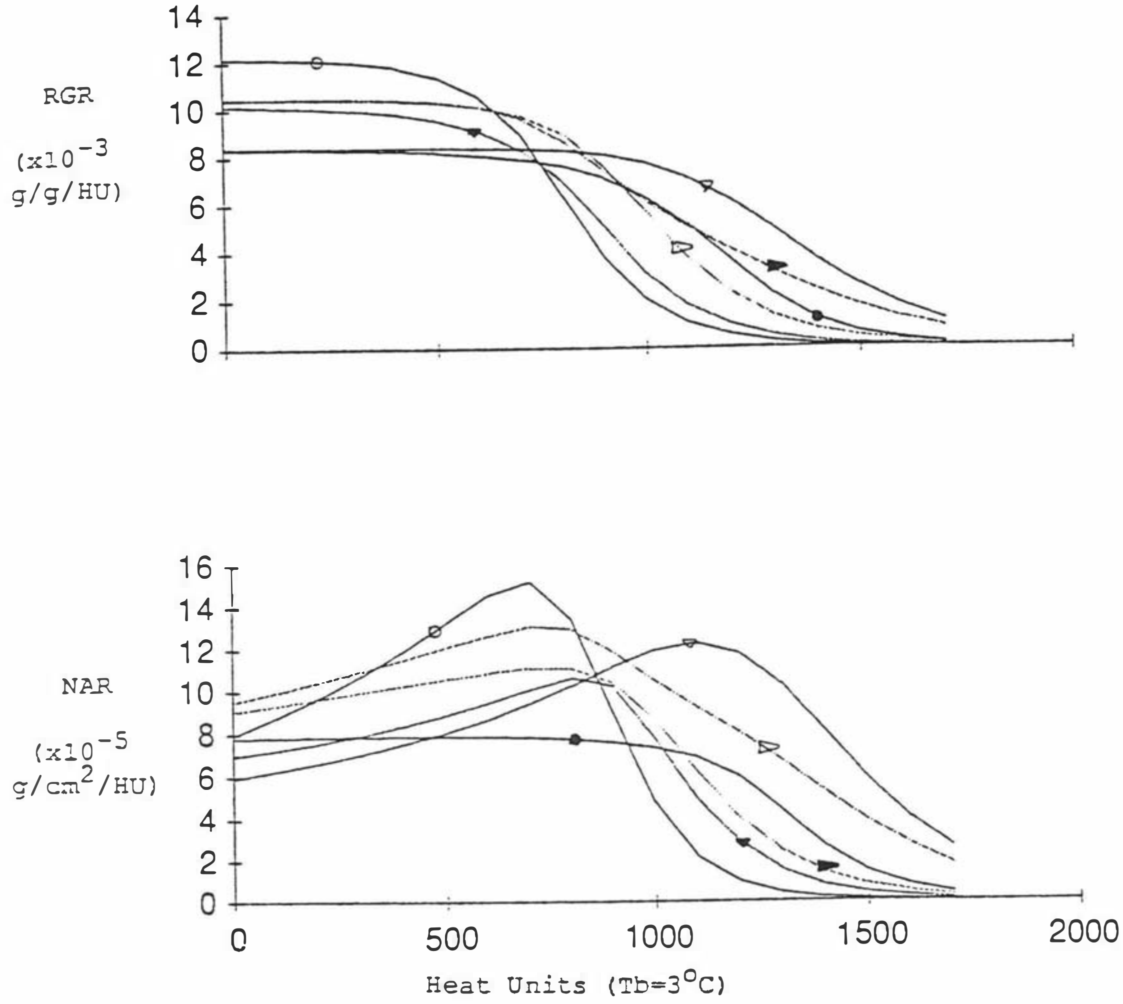


Fig. 2.6a Relative growth rate (RGR) and net assimilation rate (NAR) of broccoli at different sowing dates (-o- Sept; -●- Nov; -▽- Jan; -▼- March; ▷ May; ► July) averaged over 4 cultivars. Primary data fitted to a logistic equation.

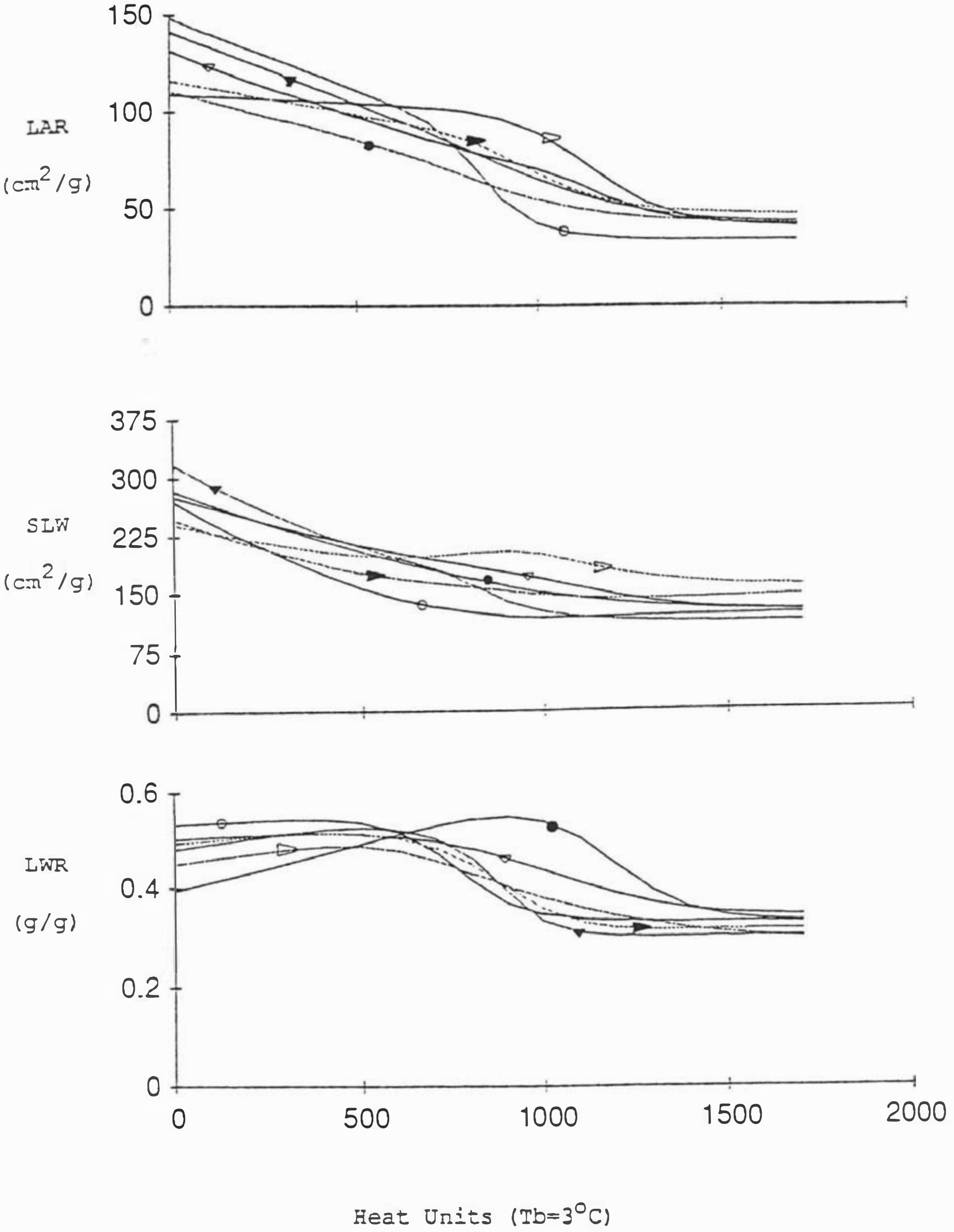


Fig. 2.6b Leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) of broccoli at different sowing dates (-o- Sept; -●- Nov; -▽- Jan; -▼- March; ▷ May; ► July) averaged over 4 cultivars. Primary data fitted to a logistic equation.

Table 2.2 Relative growth rate (RGR) of broccoli at threestages of plant development (cultivar and sowing date means).

FACTOR	RGR (x 10^{-3} g/g/HU) Stage of Development ES	CI	CM
CULTIVAR			
Premium Crop	9.38 b	8.47 ab	4.35 a
Mercedes	9.99 ab	8.67 ab	4.64 a
Idol	10.21 a	9.07 a	3.57 ab
Fordhook Late	10.24 a	7.94 b	2.22 b
s.e.	0.262	0.317	0.61
SOWING DATE			
18 Sept	12.14 a	9.93 a	3.72 ab
19 Nov	8.32 c	6.35 d	3.00 ab
17 Jan	8.38 c	8.08 c	3.95 ab
21 March	10.15 b	8.62 bc	2.22 b
22 May	10.34 b	8.62 abc	3.93 ab
21 July	10.42 b	9.59 ab	4.35 a
s. e.	0.276	0.34	0.62
s. e. (SD5)+	0.51	0.62	1.14

Means for each factor having a common letter are not significantly different at 5% level.

+ Standard error for May sowing with only 1 replication.

Table 2.3 Net assimilation rate (NAR) of broccoli at three stages of plant development (cultivar and sowing date means).

FACTOR	NAR ($\times 10^{-5}$ g/cm^2/HU) Stage of Development ES	 CI	 CM
CULTIVAR			
Premium Crop	7.41	11.85 a	8.56
Mercedes	8.10	11.61 a	8.03
Idol	8.15	11.94 a	7.81
Fordhook Late	8.03	8.64 b	4.19
s. e.	0.32 ns	0.91	1.55 ns
SOWING DATE			
18 Sept	7.95 b	14.18 a	9.35 a
19 Nov	7.78 b	7.29 c	5.20 ab
17 Jan	5.94 c	10.64 b	10.28 a
21 March	6.98 b	9.59 b	3.89 b
22 May	9.83 a	13.23 ab	6.78 ab
21 July	9.04 a	11.14 ab	7.39 ab
s. e.	0.33	0.96	1.58
s. e. (SD5)+	0.62	1.77	2.92

Means of each factor having a common letter are not significantly different at 5% level.

ns non significant

+ Standard error for May sowing with only one replication.

Table 2.4 Leaf area ratio (LAR) of broccoli (cultivar and sowing date means) at 3 stages of plant development.

FACTOR	LAR (cm^2/g) Stage of Development ES	 CI	 CM
CULTIVAR			
Premium Crop	128.71	74.45 b	47.73
Mercedes	127.65	79.10 b	45.42
Idol	129.45	82.58 ab	48.34
Fordhook Late	129.10	98.16 a	52.96
s. e.	5.30 ns	6.18	1.55 ns
SOWING DATE			
18 September	154.99 a	73.74 b	40.94 c
19 November	109.02 b	92.37 ab	56.30 ab
17 January	141.40 a	76.13 b	48.78 bc
21 March	147.37 a	99.99 a	38.48 c
22 May	103.36 b	68.88 b	44.84 bc
21 July	116.24 b	90.33 b	62.32 a
s. e.	5.58	6.51	4.15
s. e. (SD5)+	10.30	12.00	7.67

Means of each factor having a common letter are not significantly different at 5% level.

ns non significant

+ Standard error for May sowing with only one replication.

Table 2.5 Specific leaf weight (SLW) of broccoli at 3 stages of plant development (cultivar and sowing date means).

FACTOR	SLW (cm^2/g) Stage of Development ES	CI	CM
CULTIVAR			
Premium Crop	267.73	152.66 b	137.34
Mercedes	288.59	175.63 ab	143.76
Idol	266.82	161.98 ab	126.51
Fordhook Late	262.94	191.25 a	145.50
s. e.	11.70 ns	10.86	11.33 ns
SOWING DATE			
18 September	291.72 a	149.61 b	119.45 b
19 November	271.74 a	168.95 a	136.26 b
17 January	283.26 a	162.94 ab	132.78 b
21 March	305.96 a	187.79 a	120.03 b
22 May	236.11 b	160.68 ab	147.63 ab
21 July	240.33 b	192.32 a	173.50 a
s. e.	12.33	11.45	11.53
s. e. (SD5)+	22.75	21.11	21.33

Means for each factor having a common letter are not significantly different (5% level).

ns non significant

+ Standard error for May sowing with only one replication.

Table 2.6 Leaf weight ratio (LWR) of broccoli at 3 stages of plant development (cultivar and sowing date means).

FACTOR	LWR		
	Stage of Development		
	ES	CI	CM
CULTIVAR			
Premium Crop	0.45 ab	0.48 ab	0.35 b
Mercedes	0.44 b	0.45 b	0.31 c
Idol	0.48 ab	0.53 a	0.38 a
Fordhook Late	0.49 a	0.51 a	0.37 ab
s. e.	0.014	0.02	0.011
SOWING DATE			
18 September	0.54 a	0.50 a	0.35 ab
19 November	0.39 c	0.55 ab	0.41 a
17 January	0.50 ab	0.47 ab	0.37 b
21 March	0.48 b	0.52 b	0.32 b
22 May	0.44 bc	0.43 b	0.31 bc
21 July	0.49 b	0.48 b	0.36 bc
s. e.	0.014	0.022	0.012
s. e. (SD5)+	0.026	0.040	0.022

Means for each factor having a common letter are not significantly different (5% level).

+ Standard error for May sowing with only one replication.

Net assimilation rate also varied with sowing date but showed no consistent trend at the different development stages. Initial NAR was higher during the May and July sowings than the other sowing dates. At CI stage NAR was comparable in the last four sowings (January - July), was significantly lower in the November sowing and higher in the September sowing. At curd maturity, it was lower in the March sowing although this was not significantly different from the May, July and September sowings.

LAR, SLW and LWR also varied with sowing date. There appears to be a reversal in the trends in LAR and SLW at ES and CM stages. In September and March, SLW and LAR were higher at the ES stage but becomes lower at the CM stage. There are no clear trends in the other sowing dates. Compared to the other parameters, LWR showed the greatest stability with sowing date.

The different cultivars showed some slight variations in the different parameters. Fordhook Late had a relatively lower NAR but a higher LAR and SLW at the CI and CM stages (Tables 2.2 - 2.5).

2.3.1.4 Leaf Production

The appropriate base temperature for leaf production appeared to be much lower than that for dry matter production. Table 2.7 shows that plotting leaf number from all sowing dates against heat unit summation above -2C resulted in the best fit (highest r^2) and consequently the most uniform rate of leaf production (CV=20.8%) with different sowing dates.

In Fig. 2.7 the trend in leaf production during the different sowing dates is shown. A linear model best described the trend with accumulated heat units in all sowing dates and cultivars. The use of heat unit summation time scale did not totally eliminate variation in the rate of leaf production (Table 2.8) as in the rate of dry matter accumulation. During the May sowing rate of leaf production was considerably slower and was faster during the March sowing. At the other sowing dates the rate was fairly constant.

Table 2.7 The coefficient of determination (r^2) as a measure of the goodness of fit of the number of leaves of broccoli cultivars against chronological or heat heat unit summation at different base temperatures.

TIME SCALE	r^2 (%)			
	Cultivars			
	P. Crop	Mercedes	Idol	F. Late
Days	69.80	66.70	69.20	76.10
HU (-5C)	91.10	89.50	89.90	93.30
HU (-2C)	92.40	90.90	90.90	93.80
HU (0C)	90.40	89.00	88.70	90.90
HU (3C)	86.50	84.60	84.40	86.00
HU (5C)	77.30	74.50	74.90	77.60

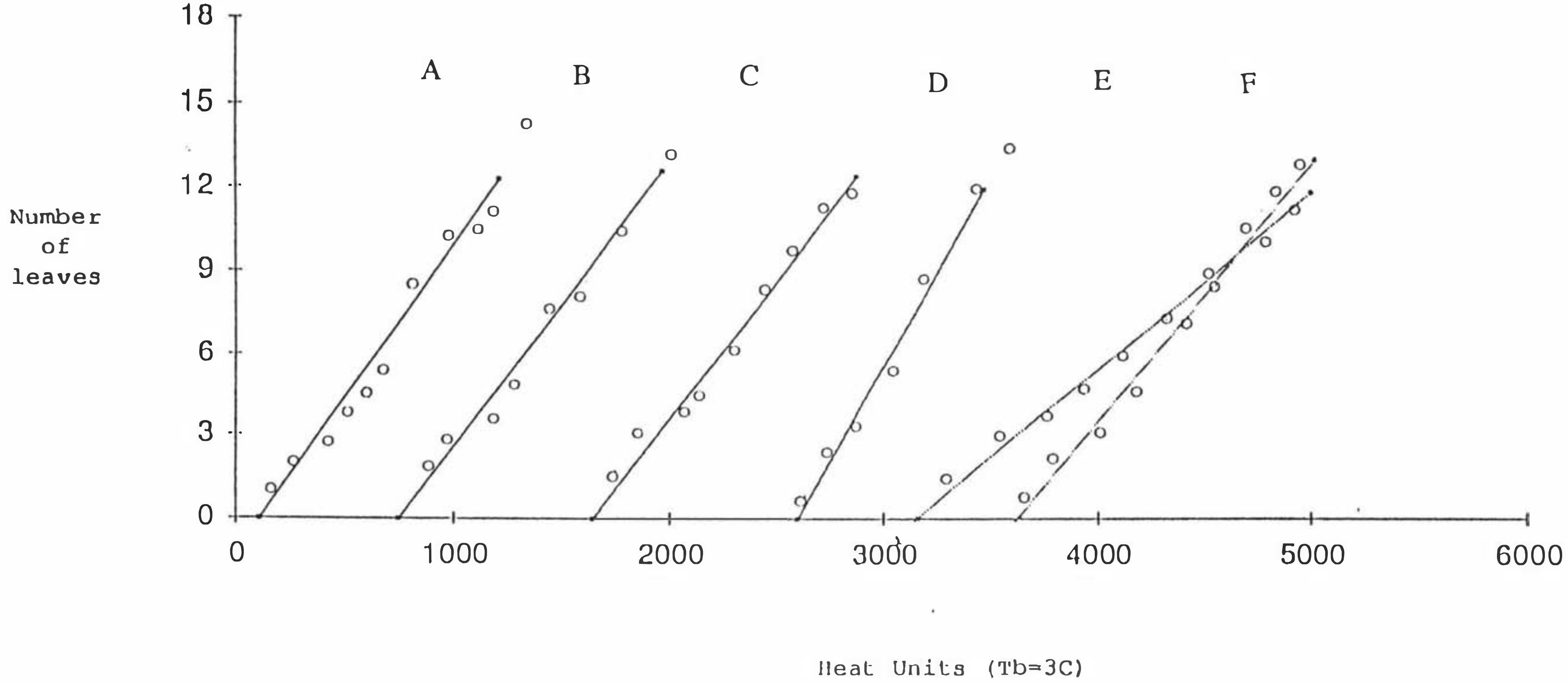


Fig. 2.7 Rate of leaf production of broccoli at different sowing dates (mean of 4 cultivars). Codes: A-September; B-November; C-January; D-March; E-May; F-July.

Table 2.8 Rate of leaf production and final number of leaves of broccoli (cultivar and sowing date means).

FACTOR	RATE (No. of Lvs./100 HU)	FINAL NO. OF LEAVES
CULTIVAR		
Premium Crop	0.97	11.9 b
Mercedes	1.01	11.1 c
Idol	1.02	12.3 b
Fordhook Late	1.03	14.1 a
s.e.	0.027 ^{ns}	0.23
SOWING DATE		
18 September	1.11 b	12.3 ab
19 November	1.02 bc	12.6 ab
17 January	0.99 c	12.4 ab
21 March	1.32 a	11.9 ab
22 May	0.67 d	11.8 b
21 July	0.95 c	13.0 a
s.e.	0.033	0.28

Means having a common letter are not significantly different (5% level).

^{ns} non significant

No significant differences in the rate of leaf production were noted among cultivars (Table 2.8).

The final number of leaves, which is the index of the morphological age of the plant at curd initiation time, were almost similar for the different sowing dates (Table 2.8). It was not correlated with the mean heat unit summation, (Tb=-2C) per day ($r=0.44^{ns}$). In the cultivars the number of leaves appeared to be related to the time to curd initiation. Fordhook Late which initiated curds the latest had the most number of leaves while Mercedes which initiated curd the earliest had the least number of leaves.

2.3.1.5 Curd Initiation and Growth

A second degree polynomial (quadratic) model best described curd expansion of broccoli at different sowing dates. When a common regression was derived for all the sowing dates, a heat unit summation time scale above 3C resulted in the best fit (Table 2.9). With a chronological time scale the fit was very poor. The following were the derived equations for the different cultivars:

a) Premium Crop

$$\log_e Y = -2.708 + 0.0219X - 0.000021X^2$$

b) Mercedes

$$\log_e Y = -2.820 + 0.0195X - 0.000017X^2$$

c) Idol

$$\log_e Y = -2.632 + 0.0203X - 0.000020X^2$$

d) Fordhook Late

$$\log_e Y = -2.588 + 0.0187X - 0.000018X^2$$

where: Y = curd diameter (mm); X = heat unit summation (Tb=3C).

The relationships are shown graphically for the sowing date and cultivar means (Fig. 2.8). For the purpose of comparison, the curves were separated by computing at different X intercepts (e.g., V1 at 0 HU; V2 at 200 HU; etc). The different cultivars showed very similar pattern of curd expansion. With the different sowing dates, the trends were quite variable. This suggests that

Table 2.9 The coefficient of determination as a measure of the goodness of fit of curd expansion of broccoli cultivars against chronological or heat unit summation at different base temperatures.

TIME SCALE	r^2 (%)			
	CULTIVARS			
	P. Crop	Mercedes	Idol	F. Late
Days	72.98	67.43	66.56	70.89
HU (0C)	91.22	80.10	90.59	84.91
HU (2C)	87.86	82.28	91.42	86.15
HU (3C)	93.24	88.43	93.27	87.05
HU (4C)	91.56	82.62	89.62	85.93
HU (5C)	91.24	81.88	86.22	89.79

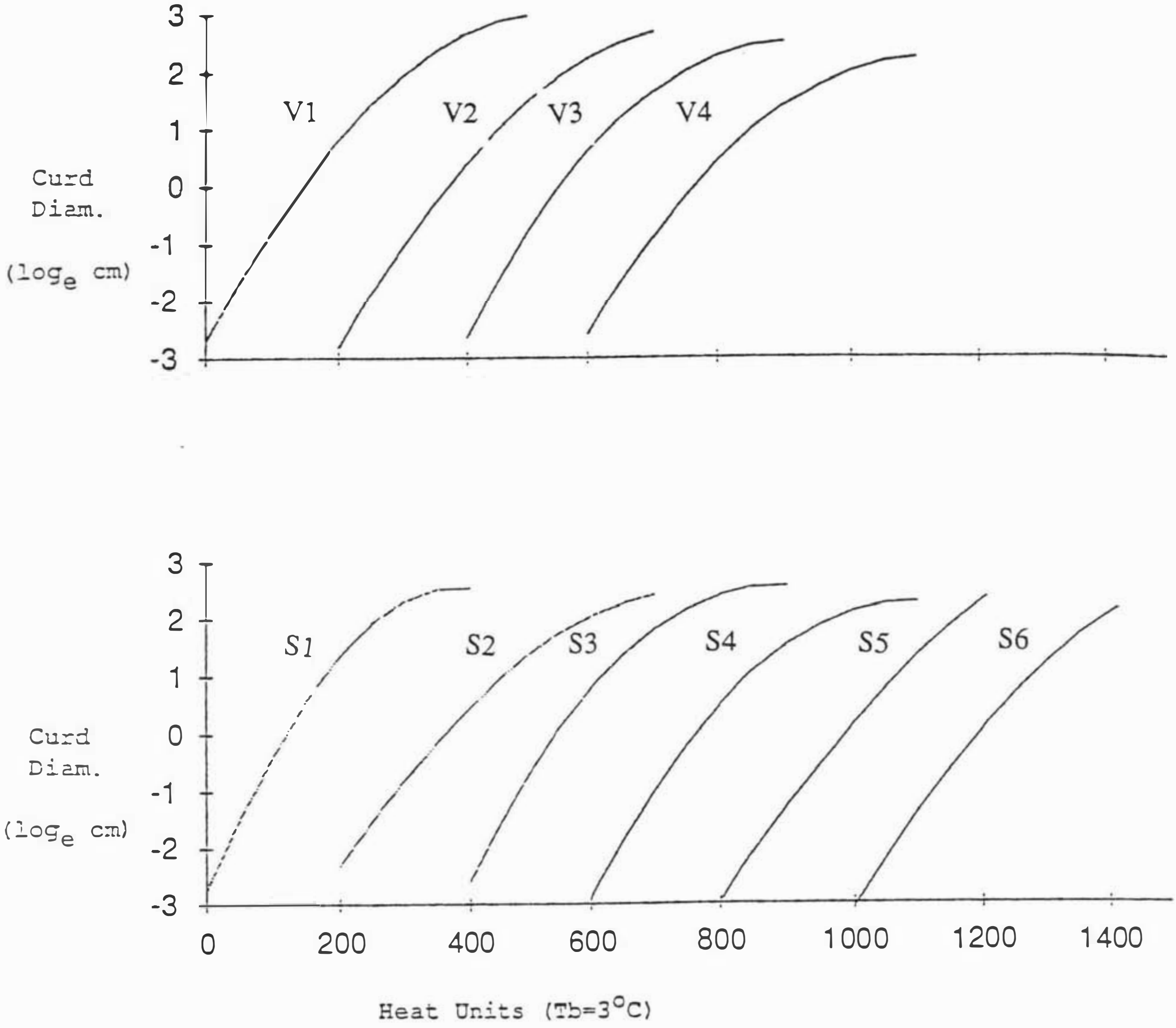


Fig. 2.8 Rate of curd growth of broccoli.
A. Cultivar means (V1 Premium Crop; V2 Mercedes; V3 Idol; V4 Fordhook Late)
B. Sowing Date means (S1 Sept; S2 Nov; S3 Jan; S4 March; S5 May; S6 July)

temperature, through the use of the heat unit system, did not account for all the variation in curd expansion during the different sowing dates.

Table 2.10 shows that overall, the appropriate base temperature for the computation of heat unit summation from sowing to curd initiation is 0C as it resulted in the lowest variation with sowing dates. The heat unit summation at curd initiation time for the different sowing dates estimated at different base temperatures are shown in Appendix 5.

The total duration from sowing to curd maturity can be broken down into 2 development stages:

1) the period from sowing to curd initiation; and
2) the period from curd initiation to maturity.

As shown in Table 2.11 it is evident that the 2 stages both contribute to the variation in the total growth duration of the plant. The length of the 2 stages varied with sowing dates and follow the same trend. It took 135 days for the plants to initiate curd during the May sowing (winter) which was more than double that from September, November, January or March sowings. The second stage was also longest when it coincided with winter (March sowing) and decreased in the summer.

The different cultivars also showed variation in the time to curd initiation. Mercedes initiated curds the earliest while Fordhook Late initiated curds the latest. The period, curd initiation to maturity was also longest for Fordhook Late and was comparable in the other three cultivars.

Table 2.12 shows a summary of the heat unit summations at curd maturity and after each development stage for the different sowing dates and cultivars. The use of a HUS time scale reduced the variation with sowing date in the durations from sowing to curd initiation and to maturity under a normal time scale by about 53% and 52%, respectively. The varietal constants (number of heat units from sowing to curd maturity) were computed to be 1188, 1123, 1217

Table 2.10 Variation between sowing dates in the number of days to curd initiation and heat unit summation at different base temperatures.

TIME SCALE	CV (%)
Days	38.78
HU (-2 C)	14.52
HU (-1 C)	14.39
HU (0)	14.35
HU (1)	14.80
HU (2)	15.72
HU (3)	17.32

Table 2.11 Number of days from sowing to curd initiation (CI) and curd maturity (CM) (cultivar and sowing date means).

FACTOR	DAYS (S - CI)	DAYS (CI - CM)	DAYS (S - CM)
CULTIVAR			
Premium Crop	85 b	36	121
Mercedes	78 c	37	115
Idol	84 b	37	121
Fordhook Late	92 a	43	135
s. e.	1.57		
SOWING DATE			
18 September	70 cd	23	93
19 November	66 de	28	94
17 January	64 e	36	100
21 March	74 c	74	148
22 May	135 a	39	174
21 July	98 b	31	129
s.e.	1.66		
s.e (SD5)+	3.06		

Means with the same letter are significantly different (5% level)

+ Standard error for May sowing with only one replication.

Table 2.12 Heat unit summation (HUS) at curd initiation (CI) and curd maturity (CM) (cultivar and sowing date means).

FACTOR	HUS TO CI (Tb=0C)	HUS CI-CM (Tb=3C)	HUS AT CM (Tb=3C)
CULTIVAR			
Premium Crop	1055 b	376	1188
Mercedes	952 c	396	1123
Idol	1035 b	414	1217
Fordhook Late	1148 a	459	1347
s. e.	19.7		
SOWING DATE			
18 September	866 c	394	1052
19 November	1186 a	434	1440
17 January	1121 b	404	1348
21 March	914 b	413	1113
22 May	1189 a	431	1265
21 July	1010 b	368	1096
s.e.	20.2		
s.e. (SD5)+	37.3		

Means for each factor having a common letter are not significantly different (5% level).

+ Standard error for May sowing with only one replication.

and 1347 for Premium Crop, Mercedes, Idol and Fordhook Late, respectively.

2.3.1.6 A Model to Predict Curd Maturity

The simple linear model (Model A)

$$R-\bar{\bar{R}} = a(\bar{H}-\bar{\bar{H}})+E$$

(refer to section 2.1.11) was found to be significant for all the cultivars (Table 2.13). Addition of sunshine hours in the model (Model B), i.e,

$$R-\bar{\bar{R}} = a(\bar{H}-\bar{\bar{H}})+b(\bar{S}-\bar{\bar{S}})+E$$

improved the fit (higher r^2), however, a sequential F-test revealed that the contribution of sunshine hours after taking account of heat unit summation was not significant (Table 2.13). The proportions of variance accounted for by temperature and sunshine hours for each cultivar are shown in Appendix 10. Based on the two models, predicted crop duration were calculated for the different sowing dates and cultivars. These are shown in Table 2.14. In Figure 2.9, the observed and predicted crop duration at different sowing dates averaged over 4 cultivars are shown graphically. It shows that the two models gave a better prediction of crop duration for the November, January, March and July sowings.

2.3.2 Total Dry Matter Production and Partitioning

2.3.2.1 Curd and Total Dry Matter Production

Plant potential for dry matter production varied with sowing dates and with cultivar (Table 2.15). Both curd and total dry matter production were lower during winter (March and May sowings) than during the summer sowings. The curds produced by the different broccoli cultivars sown on November and May are shown on Plates 2.1 and 2.2, respectively.

Total plant dry weight, curd dry weight and curd diameter were correlated positively with the average heat unit summation per day during each growing period ($r=0.72^{*}$; $r=0.91^{*}$; and $r=0.97^{**}$, respectively).

Table 2.13 Estimates and standard errors of the regression coefficients from 2 models[1] for the prediction of curd maturity of different cultivars of broccoli

CULTIVAR	REG. COEFF.	MODEL A		MODEL B	
		Estimate[2]	Std. Err.	Estimate[3]	Std. Error
Premium Crop	a	5.99	1.40^{*}	1.72	2.12^{*}
	b	-	-	1.72	7.55^{ns}
Mercedes	a	6.97	1.62^{*}	1.60	2.22^{*}
	b	-	-	1.94	7.81^{ns}
Idol	a	5.46	1.46^{*}	0.35	2.82^{*}
	b	-	-	2.24	10.10^{ns}
Fordhook Late	a	5.18	1.83^{*}	0.76	2.34^{*}
	b	-	-	2.01	9.61^{ns}

[1] refer to Section 2.1.11

[2] $HU^{-1} \times 10^{-4}$

[3] $HU^{-1} \times 10^{-4}$ or $S^{-1} \times 10^{-5}$

* significant (5% level).

ns non significant

Table 2.14 Observed and predicted number of days from sowing to curd maturity (based on 2 models[1]) of different broccoli cultivars at different sowing dates.

CULTIVAR/ SOWING DATE	OBSERVED DURATION (days)	PREDICTED DURATION (days)	
		Model A	Model B
Premium Crop			
18 September	93	109	96
19 November	90	85	92
17 January	97	94	91
21 March	144	142	145
22 May	173	146	154
21 July	126	132	139
Mercedes			
18 September	87	105	90
19 November	84	80	87
17 January	93	88	86
21 March	138	134	140
22 May	167	141	150
21 July	122	126	132
Idol			
18 September	89	105	92
19 November	96	88	98
17 January	100	97	94
21 March	141	142	144
22 May	173	146	152
21 July	125	133	138
Fordhook Late			
18 September	102	122	108
19 November	106	98	107
17 January	111	110	103
21 March	168	163	163
22 May	184	162	172
21 July	142	146	151

---

[1] refer to section 2.1.11

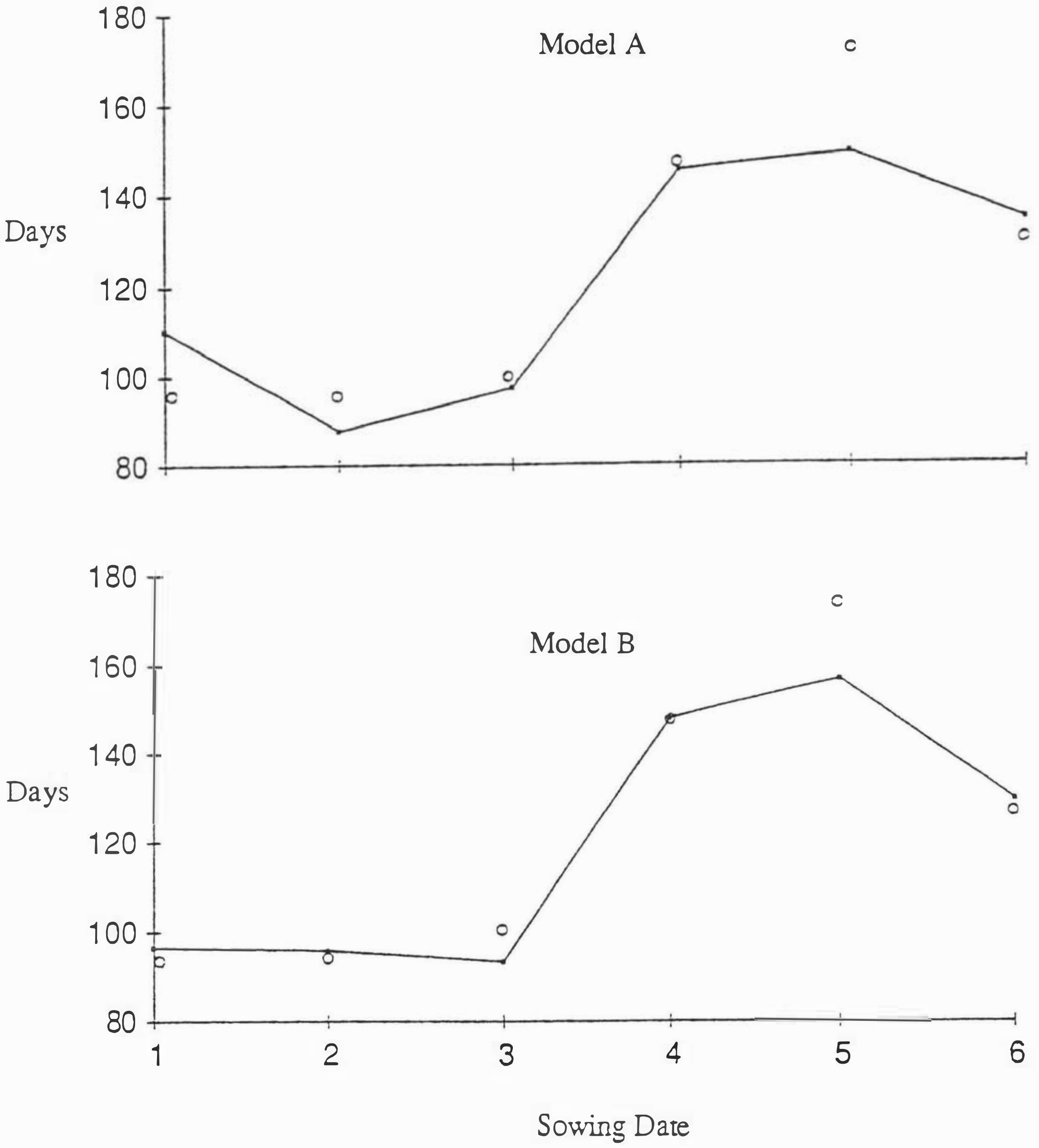


Fig. 2.9 Observed (o) and predicted (-•-) number of days from sowing to curd maturity of broccoli (mean of 4 cultivars). Predicted values based on Models A and B (refer to Section 2.1.11).

Table 2.15 Total plant dry weight, curd dry weight and curd diameter of broccoli (cultivar and sowing date means).

FACTOR	TOTAL PLT DRY WT. (g)	CURD DRY WT. (g)	CURD DIAM. (cm)
CULTIVAR			
Premium Crop	188.1 b	28.9 a	12.8 a
Mercedes	124.2 c	23.2 c	11.3 b
Idol	212.4 b	28.2 a	11.2 b
Fordhook Late	280.0 a	26.1 b	10.6 b
s. e.	12.82	0.69	0.41
SOWING DATE			
18 September	176.5 b	26.0 c	12.1 ab
19 November	304.5 a	37.7 a	13.0 a
17 January	204.7 b	32.3 b	12.5 ab
21 March	116.9 c	18.4 d	10.5 c
22 May	199.8 b	17.2 d	10.3 c
21 July	204.4 b	28.0 c	11.0 bc
s.e.	15.7	0.84	0.51

Means for each factor having a common letter are not significantly different (5% level).

Plate 2.1 Mature curds of different broccoli cultivars sown in November 1985.

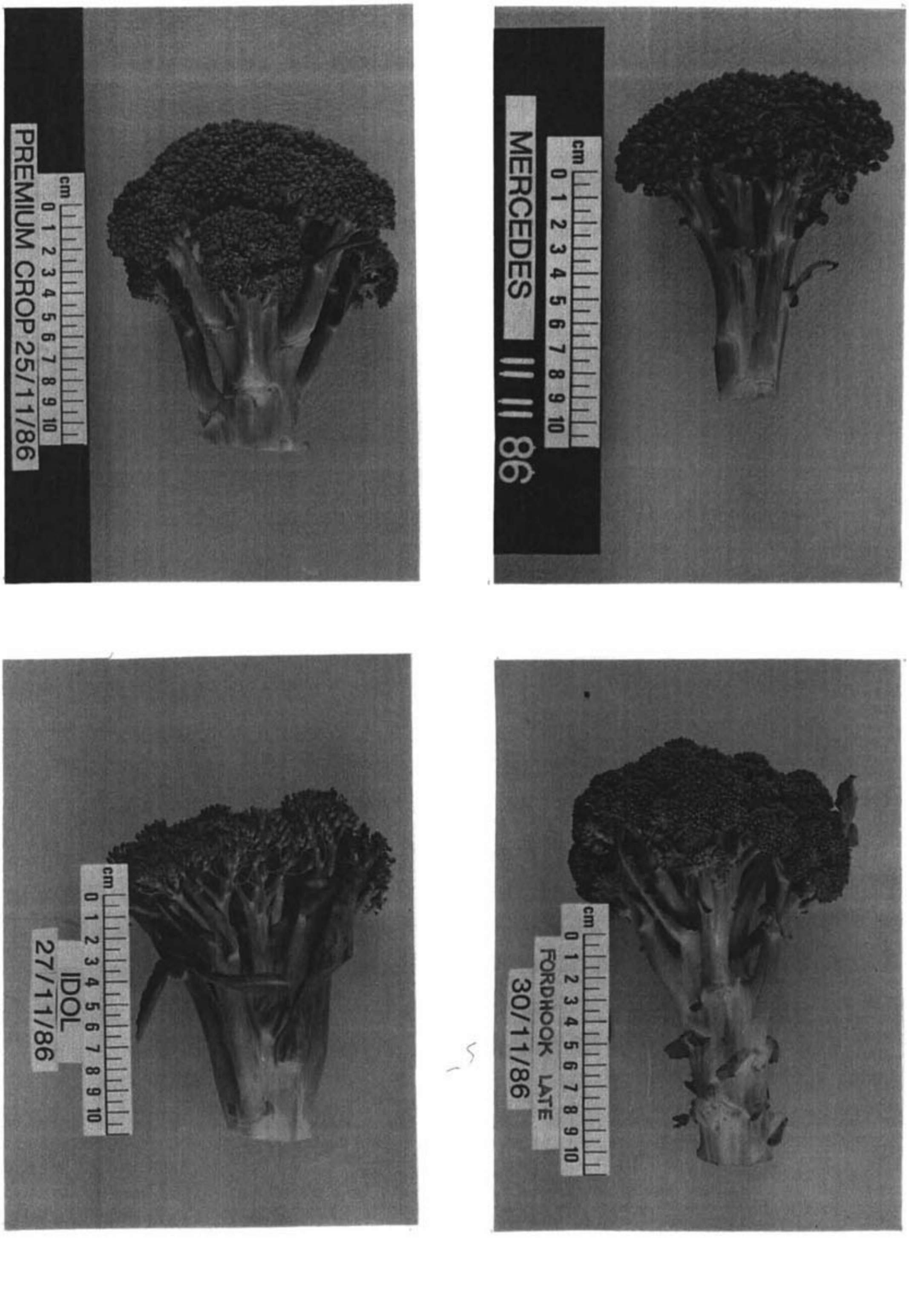


Plate 2.2 Mature curds of different broccoli cultivars sown in May, 1986.

Curd and total dry weight also varied with cultivars. Fordhook Late had the highest total dry weight but had lower curd dry weight than Premium Crop or Idol. Mercedes had the least curd and total dry weight. There was a significant cultivar x sowing date interaction effect on total dry matter production (Table 2.16). The differences in total dry weight production among cultivars was consistent in the Sept., Nov., Jan., March and July sowings but the degree of differences was quite variable. During the May sowing Premium Crop produced more dry matter than Idol.

2.3.2.2 Dry Matter Partitioning

Partitioning of dry matter into the leaves stem and root did not seem to be affected greatly by sowing date and cultivar particularly during the early seedling and curd initiation stages (Tables 2.17 - 2.19). At curd maturity stage partitioning varied with sowing date and cultivar, with the curd component being the most variable. The January, March, July and September sowings had significantly harvest index while the May sowing had the lowest. Among the cultivars Mercedes had the highest harvest index while Fordhook Late had the lowest.

Generally, in all the development stages leaves contributed the most dry matter which was about 56%, 63% and 40% during the early seedling, curd initiation and curd maturity stages, respectively. The stem proportion continuously increased from 14% to 27% to 35%. The root constituted a major proportion during the early seedling stage (33%) but dropped to 9.5% and 8.5% during the second and final stage, respectively. The general pattern of dry matter partitioning is shown graphically in Fig. 2.10.

Table 2.16 Total dry matter production of different cultivars of broccoli at different sowing dates.

SOWING DATE	TOTAL DRY WEIGHT (g/plant)			
	Cultivar			
	P. Crop	Mercedes	Idol	F. Late
18 September	158.9	101.0	187.6	258.0
19 November	267.6	180.9	309.4	463.3
17 January	190.2	141.2	229.3	258.1
21 March	104.2	75.8	131.9	155.7
22 May	206.9	116.2	191.4	284.8
21 July	200.8	130.2	226.7	259.8

s. e. = 12.49

Table 2.17 Dry matter partitioning in broccoli at early seedling stage.

FACTOR	PERCENTAGE OF DRY MATTER (%) ++		
	Leaf	Stem	Root
CULTIVAR			
Premium Crop	48.59	22.57	32.53
Mercedes	48.16	21.65	33.63
Idol	48.75	21.50	33.18
Fordhook Late	48.94	22.16	32.23
s. e.	0.44 ns	0.72 ns	0.67 ns
SOWING DATE			
18 September	50.61 a	20.70	31.80
19 November	47.00 c	22.90	33.90
17 January	49.00 bc	22.50	31.90
21 March	49.50 ab	22.80	31.20
22 May	47.70 bc	22.20	33.80
21 July	47.80 c	20.60	34.80
s. e.	0.46	0.46 ns	0.75 ns
s. e. (SD5)+	0.86	0.86	1.39

Means having a common letter are not significantly different at 5% level.

++ Arc sin transformed values.

+ Standard error for May sowing with only one replication.

ns non significant

Table 2.18 Dry matter partitioning in broccoli at curd initiation stage.

FACTOR	PERCENTAGE OF DRY MATTER (%) ++		
	Leaf	Stem	Root
CULTIVAR			
Premium Crop	52.50	31.30	18.00
Mercedes	53.60	30.90	16.80
Idol	52.40	31.30	18.50
Fordhook Late	52.30	31.60	18.20
s. e.	0.99 ns	1.10 ns	1.12 ns
SOWING DATE			
18 September	49.70 b	35.30 a	16.60
19 November	53.12 a	31.50 b	17.10
17 January	53.24 a	32.20 ab	15.60
21 March	53.54 a	30.80 b	17.40
22 May	54.46 a	28.30 b	19.50
21 July	52.12 ab	29.70 b	20.90
s. e.	1.05	1.16	1.18 ns
s. e. (SD5)+	1.93	2.14	2.17

Means for each factor having a common letter are not significantly different (5% level).

++ Arc sin transformed values.

ns non significant

+ Standard error for May sowing with only one replication.

Table 2.19 Dry matter partitioning in broccoli at curd maturity stage.

FACTOR	PERCENTAGE OF DRY MATTER (%) ++			
	Leaf	Stem	Root	Curd
CULTIVAR				
Premium Crop	40.6 a	35.6 b	15.8 b	23.6 b
Mercedes	38.7 b	34.9 b	17.7 a	25.4 a
Idol	41.4 a	36.3 b	16.6 ab	21.0 c
Fordhook Late	40.5 a	39.2 a	16.2 ab	18.2 d
s. e.	0.55	0.65	0.47	0.58
SOWING DATE				
18 September	40.1	35.5 a	17.1 b	23.3 a
19 November	40.6	37.3 a	15.2 c	21.5 b
17 January	39.2	37.1 ab	15.6 bc	23.7 a
21 March	40.9	34.7 ab	16.4 bc	23.8 a
22 May	40.4	37.5 b	19.9 a	17.5 c
21 July	40.6	36.9 b	15.2 c	22.3 ab
s. e.	0.58 ns	0.69	0.62	0.50
s. e. (SD5) +	1.07	1.28	1.15	0.92

Means for each factor having a common letter are not significantly different (5% level).

++ Arc sin transformed values.

+ Standard error for May sowing with only one replication

ns non significant

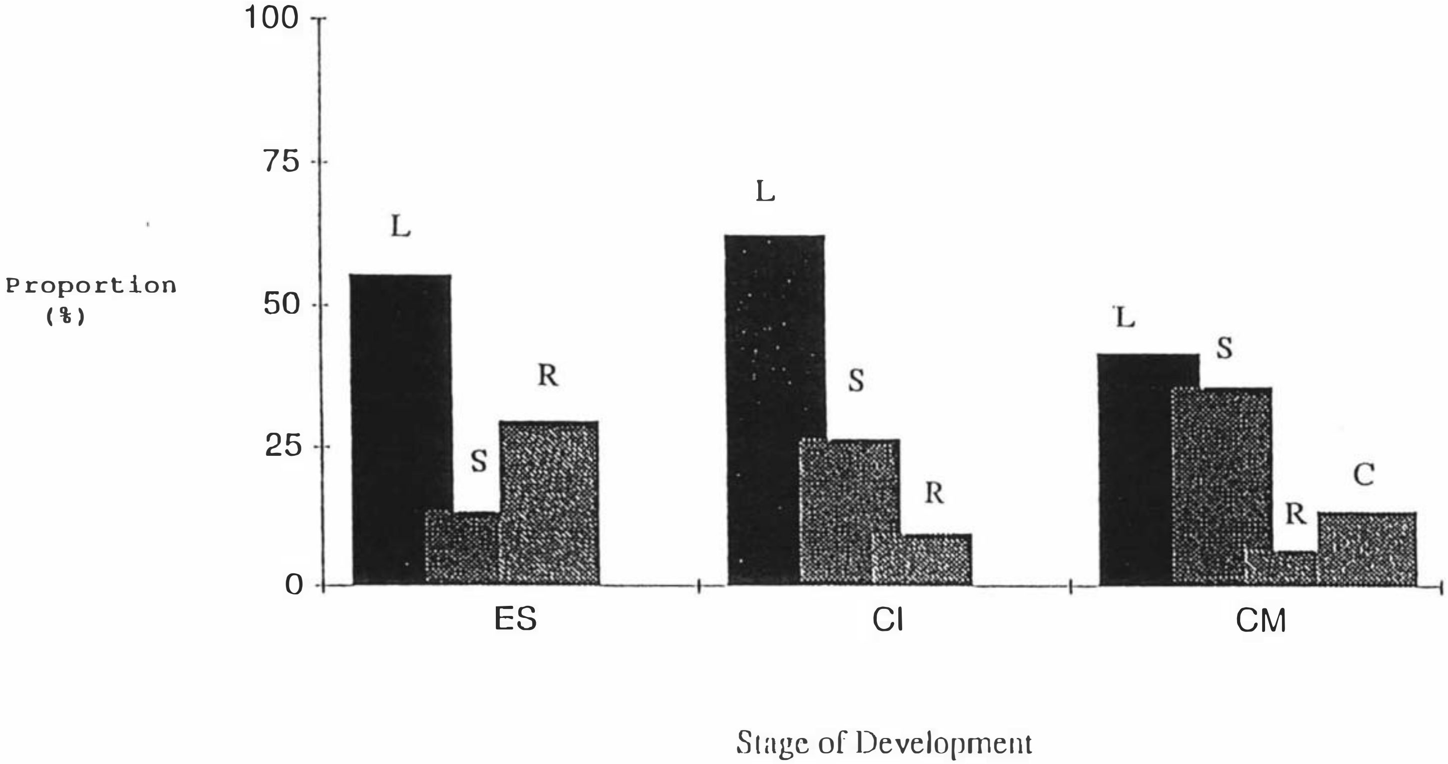


Fig. 2.10 Dry matter partitioning in broccoli (L leaves; S stem; R roots; C curd) at three developmental stages (ES early seedling; CI curd initiation; CM curd maturity) averaged over 4 cultivars and 6 sowing dates.

2.4 Discussion

2.4.1 The Heat Unit System

The use of the heat unit system has been subjected to a number of justifiable criticisms foremost of which are that plant growth and development are not linearly related to temperature and that the use of heat units is not logically sound as they are not a form of available energy for plants (Wang, 1960). Salter (1960), however, stressed that this time scale can be a convenient and simple method of integrating temperature with time and, provided the method is used with caution, it can take into account temperature differences over different periods of time. Moreover, the present use of the heat unit system is more because of its many practical applications rather than for its theoretical soundness.

In the present study, the use of a heat unit time scale reduced the variation between sowing dates in the initial relative rate of dry matter accumulation, rate of curd growth, "time" to curd initiation, "time" to curd maturity and rate of leaf production, relative to a chronological time scale. Temperature accounted for about 79% of the variation in the reciprocal total duration from sowing to curd maturity in broccoli while sunshine hours accounted for an additional 13%. These results highlight the importance of temperature as a major environmental component determining the growth and development of broccoli. Reports from different workers on broccoli and related crops are quite variable. Temperature accounted for most of the variation in the growth of cauliflower (Salter, 1960) or in the duration to crop maturity in crisp lettuce (Wurr and Fellows, 1984; Gray and Morris, 1978). In broccoli, temperature explained 74.3% of the variation in rate of development from sowing to curd maturity while solar radiation explained a further 17.7% (Marshall and Thompson, 1987a). In contrast to the present study, these studies did not fully cover all the seasonal changes throughout the year, i.e., sowing dates were fewer and at narrower intervals. Nevertheless, the fact that the temperature did not fully account for all the variations suggests the possible contribution of other environmental components particularly radiation. Assessing the effects of such other environmental components, however, was beyond the scope of this study.

2.4.2 Plant Growth and Development

The base temperature selected for the computation of heat unit summation against which to relate plant growth and development was the one which resulted in the least variation with sowing dates. It can be considered that this base temperature is also the threshold temperature or the lowest temperature at which growth or development could proceed.

Results suggest that the different growth and development processes in broccoli require different base temperatures. The base temperature for total dry weight production and rate of curd growth appeared to be higher (3C) than for curd initiation and for the rate of leaf production (0C and -2C, respectively). The former are growth processes and the latter are developmental events and may thus proceed at different base temperatures.

In attempting to understand the growth of sets of plants, Elias and Causton (1975) have pointed out the importance of considering the stage of development of the plant. They used plant dry weight as the approximate index of development. However, this approach can be limited by the effect of an environmental component on the plant ontogenetic drift. For instance, plants at the onset of flowering may not necessarily have the same dry weights. Erickson and Michellini (1957), on the other hand, proposed the Leaf Plastochron Index where plant development was equated with leafiness. In the present study, it was possible to identify three distinct, important developmental stages of broccoli, the early seedling (initial), the curd initiation and the curd maturity stage. The growth rate pattern of the plants were then described with reference to these development events.

Theoretically, if temperature were the single cause of variation in the growth rates of plants the use of a heat unit time scale would result in a constant initial relative growth rate for all sowing dates. Results indicate that the initial relative growth rate of broccoli as a function of heat unit summation did not vary in 3 sowing dates (March, May and July) and were variable in the other three. Under a normal time scale the March, May and July sowings would have represented periods of grossly differing growth rates. The unifying effect of heat unit time scale is thus shown. As pointed out, the remaining variation, considering all sowing dates, and after taking account of temperature, suggests the possible contribution of other environmental factors in addition to that due to experimental error.

It should be emphasized that the growth rates are a function of heat unit summation and are thus affected by the base temperature used. A base temperature higher than 3C would "increase" the growth rate during the winter sowings more than it would during the summer sowings. The opposite is true if the base temperature were lower than 3C. With temperature as the single component of the model, 3C was selected as the appropriate base temperature but the inclusion of other environmental factors in the model may have resulted in the selection of a base temperature higher or lower than 3C (Marshall and Thompson, 1987a).

Basically, the relative growth rate of the plant depends upon the net assimilation rate (NAR), which is a measure of the efficiency of the leaves to produce new materials as the assimilatory organ of the plant, and upon leaf area ratio (LAR) which is a measure of the leafiness of the plant (Hunt, 1982). This suggests that the differences in the initial RGR may be due to the instability of its components NAR and LAR with sowing date.

NAR may be affected by the specific leaf weight (SLW) which is indicative of the thickness or density of the leaves. Leaf thickness is a morphological character which has often been correlated with CO_2 exchange rate per unit leaf area (Barnes et. al, 1969; Dornhoff and Shibles, 1976). In this study NAR did show a negative correlation ($r=-0.81^{**}$) with SLW at CI time suggesting that the lower the SLW (thicker leaves) the higher is the NAR. In relation to the sowing dates, it appears that when the temperature regime was lower (May and July sowings) initial NAR was higher due to low SLW. This inter-relationship between NAR and SLW was also shown in lettuce (Nichols, 1972).

LAR in turn is directly proportional to its components SLW and LWR. These three parameters showed almost similar trends with sowing dates. They are independent of the time scale as they are expressed as ratios and are thus unaltered by the use of a heat unit time scale, in contrast to NAR and RGR. Initial trends with sowing dates nevertheless show that they can vary with different temperature regimes.

At the later stages, particularly during the curd maturity stage, there were little variations in the growth parameters with sowing dates. This suggests a greater stability of the growth parameters with different environments after curd initiation.

In the different cultivars, the low NAR of Fordhook Late during curd initiation was balanced by its high LAR so that its RGR was comparable with the other cultivars. Moreover, its low NAR may be due to its high SLW.

The effect of temperature on the different growth parameters have been studied on other crops. There was a general tendency for RGR to increase with increasing temperature in Impatiens parviflora (Elias and Causton, 1975), in sunflower and maize (Warren-Wilson, 1966a), in young tomato (Hurd, 1977) or in cucumber (Milthorpe, 1959, as cited by Warren-Wilson, 1966a). In all these crops NAR also tended to rise slowly with temperature but did not vary within the temperature range of 20C-30C which, presumably, is the optimum temperature range. It is difficult to compare these results with the present study as RGR and NAR were expressed under a normal time scale. In the present study, temperature differences have been accounted for by the use of a heat unit time scale. If a normal time scale were used results should essentially be similar.

The distinct pattern of changes in the different growth parameters of broccoli was also typical of the crops used in the aforementioned studies.

The rate of leaf production of all cultivars showed a good linear fit against heat unit summation above -2C and were similar in all sowing dates except during the May sowing when the rate was much slower. The lower base temperature for leaf production compared to that for dry matter production suggests that leaf initiation in broccoli occurs at a temperature which may be too low for normal growth. This is supported by the findings of Salter (1960) who found that the appropriate base temperature for the initiation of leaves in cauliflower was 0C as compared to 5.5C for curd growth and total dry matter production.

The final number of leaves can be considered as the morphological age of the plant at curd initiation time and this appeared to be fairly constant with sowing dates. Wiebe (1975) found that in some broccoli cultivars leaf number was less influenced by temperature in contrast to that of cauliflower. Wurr, Fellows and Crisp (1982) also showed that the differences in the rate of leaf production and the final number of leaves in cauliflower were largely irrespective of environmental treatments.

In the 4 cultivars in this study, the number of leaves appear to be related to their time to curd initiation, the later the time to curd initiation, the more leaves are formed. This corroborates the findings of Salter (1960), Wiebe (1975) and Wurr et al., (1982). Thus, for a particular cultivar, the number of leaves can be a good developmental index of the curd initiation stage of broccoli.

The growth of the curd from initiation until maturity as a function of heat unit summation above 3C was best described by a quadratic model. Using the method of Wurr et al. (1982) it was possible to estimate the time (or number of heat units) to curd initiation. Considering a normal time scale the variation in the total duration from sowing to maturity is determined by both the number of days from sowing to curd initiation and from curd initiation to curd maturity. The variations in these developmental durations are reflected very well in the temperature differences across different sowing dates. The variation with sowing date in the total HUS from sowing to curd maturity may be acceptably low low

(CV=12.81%). Using the HUS varietal constants to estimate the crop duration of broccoli at any sowing date may be then be valid. However, the predictability of the crop duration based on heat unit summation as tested by the linear regression model was good in only four sowing dates (November, January, March and July sowings). A sounder approach may then be to consider the constant for each sowing date.

The differences in plant potential for curd and total dry matter production with sowing dates was also related to differences in temperature regimes as they showed good correlations with the daily average heat unit summation during each growing period. The lower the temperature regime, the lower is the potential for dry matter accumulation.

Wurr et al. (1982) also stressed the importance of the balance between leaf and curd growth. They cited for instance that "buttoning" in cauliflower which is the premature transition of plants to the generative stage is caused by curd initiation occurring before the leaves have developed sufficiently to support adequate curd growth. Moreover, economic yield almost always showed good correlation with total leaf area per plant (Ho, 1988).

Plant potential for dry matter accumulation is dependent upon RGR and upon how long a high RGR is sustained. Although there was little variation in RGR between cultivars (Table 2.2), dry matter accumulation was higher in Fordhook Late (Table 2.13) as a high RGR was maintained relatively longer (Table 2.12). This, however, did not guarantee a higher yield for Fordhook Late as it had a very low harvest index (Table 2.16). For Mercedes, a higher harvest index did not result in a higher yield as its total dry matter production is low due to an early drop in RGR. In considering yield, therefore, it may be good to consider cultivars with a high harvest index and a high RGR which can be maintained for a long time.

The lower harvest index in Fordhook Late may be associated with its lower NAR during curd initiation (Table 2.3; Fig. 2.5a). A lower NAR during this stage means a lower efficiency of the leaves to produce new materials and hence, a lower harvest index. In the other three cultivars, the curd initiation stage coincided with the peak in NAR.

Sowing date did not show any effect on the pattern of dry matter partitioning in all the cultivars before the development of the curd. At curd maturity the pattern showed slight variations with sowing dates and cultivar mainly because of the differences in the harvest index. Harvest index during the May sowing was considerably lower than the other sowing dates. There was no significant interaction effect between sowing date and cultivar suggesting that the differences in dry matter partitioning between the different cultivars was consistent at all sowing dates.

It should be pointed out that during the May sowing a number of frosts were recorded during the early growing season. Most plants did survive but may have been affected physiologically such that leaf production and rate of curd and total dry matter production no longer proceeded optimally.

2.4.3 Practical Implications

Results of this study point out the applicability of the use of the heat unit system in describing the rate of growth and development of broccoli. Predicting the time to curd initiation and the curd maturity of the plant would provide valuable assistance to the grower. Sowing schedules aimed for any practical purpose such as provision of a continuous supply of fresh crop in the market or synchronizing harvests to reduce harvesting costs could be planned using the HUS model and the historical weather data for the area in consideration.

The differences in yield potential with different sowing dates and cultivar, and estimates of the harvest time are important information for the grower. A cost and return analysis based on this information may aid in deciding whether or not to grow broccoli at a particular time of the year.

Chapter 3

Greenhouse Experiment: **The Effect of Temperature on the Growth, Development, Curd Quality and Maturity Characteristics of Broccoli.**

3.1 Introduction

The field experiment showed that although temperature had a profound effect on the yield of broccoli, it had no apparent effects on curd quality. In the field experiment the average daily maximum temperature during summer (January) was 22C and the highest recorded was 26C. These maximum temperatures may not have been high enough, however, to affect curd quality.

Aside from its effect on curd quality, high temperature has been reported to delay or prevent curd initiation in both broccoli and cauliflower (Fujime, 1988; Huber, 1926 as cited by Sadik, 1967). Moreover, Wiebe (1975) reported that the morphological development of the curd of tropical cauliflower could vary with different temperature regimes.

Knowing the response of broccoli to high temperature is important as there is an increasing interest in growing the crop in the tropics where daily temperature can average close to 30C.

Quantitative and qualitative cold requirements for flowering in cauliflower have been reported by a number of workers (e.g., Wellington, 1954; Skapski and Oyer, 1964). However, in broccoli, reports are less clear (e.g., Gauss and Taylor, 1967a; Fujime, 1988).

This Greenhouse Experiment was designed to study the effects of both high and low temperature treatments, relative to a near optimum, on the curd quality, yield, dry matter production and time to curd maturity of broccoli. Based on the results of the Field Experiment, the temperature levels of 10C, 20C and 30C can be considered low, near optimal and high, respectively, with respect to their effect on the growth and development of broccoli. The temperature treatments chosen consisted of continuous 20C or interrupted by a 1-week exposure to either 10C or 30C. The low and high temperature treatments were imposed on the plants at different stages of plant growth to determine the relative sensitivity of the different growth stages of the plant to the treatments. In addition to the four cultivars used in the Field Experiment, cv Shogun was used as the curd development of this cultivar was found to be particularly sensitive to high temperature in the field during summer months under commercial cultivation in New Zealand.

This study aimed to:

(1) determine the effect of high and low temperature treatments on curd initiation, curd quality, yield and time to curd maturity of different cultivars of broccoli;

(2) determine the response of the plants to the temperature treatments imposed at different stages of plant growth;

(3) assess varietal differences in growth rates in plants grown under continuous 20C using growth analysis techniques and compare results with those of the Field Experiment.

3.2 Materials and Methods

3.2.1 Experimental Design and Treatments

A three-factor factorial experiment in randomized complete block design (RCBD) with three replications was used in this study. The following were the experimental treatments:

Cultivar
a) Premium Crop
b) Mercedes
c) Idol
d) Fordhook Late
e) Shogun

Temperature
- a) 10C (controlled climate cabinet)
- b) 19C-21C (glasshouse; henceforth called 20C)
- c) 30C (controlled climate cabinet)

Stage of Plant Growth

Temperature treatments were imposed on the plants at different stages of plant growth at weekly intervals (defined in Section 3.1.5)

3.2.2 Production of Seedlings

Seeds of the different cultivars of broccoli were sown in cellular trays. A mixture of 95% fine peat and 5% fine sand with fertilizer additions (Appendix. 1a) was used as the propagation medium. The trays were inside a glasshouse arranged in beds heated at 25C. Supplementary liquid feertilizer at a concentration of 100 ppm N and 200 ppm K_2O was given to the growing seedlings 2-3 times a week.

3.2.3 Preparation of the Medium and Pots

A soilless medium consisting of 50% peat and 50% pumice by volume was prepared. A standard fertilizer mix for vegetables (Appendix 1b) was added. About 4 l of the mixture was put into 14" by 10" polyethylene planter bags. The bags were arranged inside a glasshouse according to the experimental layout.

3.2.4 Transplanting and Irrigation

At the 4-leaf stage (one month after sowing) the seedlings were transplanted into pots. A system of irrigation using alkathene pipes and microtubes was installed. A time clock was used to control irrigation. The glasshouse was heated when the temperature fell below 19C and to keep the temperature close to 20C fan ventilation was used which came into operation when temperature rose above 21C.

3.2.5 Imposition of the Treatment

The growth cabinets were set at either 10 or 30C and 75% RH. A layer of shade cloth was placed directly below the light source in the cabinets to prevent possible occurrence of photobleaching in the plants as this is a potential problem at low temperature. Treatments were imposed starting at transplanting time. Three randomly chosen plants of each cultivar were transferred to each of the growth cabinets. After a week of treatment the plants were moved back to the glasshouse. Succeeding batches of plants were exposed to similar treatments at weekly intervals to cover all the plant growth stages. Control plants were kept inside the glasshouse until maturity.

For the purpose of analysis 3 main developmental stages were identified for the different cultivars based on their earliness to curd initiation:

early (transplanting up to curd initiation stage)
- first 3 weeks for Premium Crop and Mercedes;
  first 4 weeks for the other cultivars

mid (early curd development period)
- fourth to sixth week for P. Crop and Mercedes;
  fifth to seventh week for the other cultivars

late (late curd development period)
- seventh to ninth week for P. Crop and Mercedes;
  eighth to tenth week for the other cultivars

3.2.6 Collection of Data

Growth analysis was carried out on the control plants. Three plants per replicate were harvested at weekly intervals. Data collection procedures for growth analysis used in Study 1 were followed.

At curd maturity, the following data were gathered:

Maturity Period. Curd maturity determination was based on the criteria used in Study 1. The number of days from sowing to maturity was noted for each individual plant.

Curd Quality. Three quality indices namely, head branching, head depth and uniformity of bud maturity were considered. Head branching and depth grading systems (Chowings, 1974) are illustrated in Fig. 3.1. For uniformity of bud maturity the following scale was used:

5 - all buds of similar size
3 - 75% of buds of similar size
1 - 50% of buds of similar size

Curd Fresh Weight and Size. Curd fresh weight was taken and expressed as a ratio of the shoot weight. Curd diameter was used as the size index.

3.3 Results

3.3.1 Growth Analysis

The different sets of growth data were fitted to polynomial models as they cannot be fitted using the modified Richards function presumably because of large error variances. The Richards function was not sufficiently robust to fit the data sets. The second degree polynomial (quadratic) model best described most sets of data and was then used throughout the analysis. This was expressed as:

$$\log_e Y = b_o + b_1 X + b_2 X^2$$

where: Y = total plant dry weight, leaf dry weight, or leaf area per plant
X = number of days from sowing
b_o = Y intercept
b_1 = regression coefficient (linear component)
b_2 = regression coefficient (quadratic component)

Based on the model, predicted values were estimated and the different growth parameters (relative growth rate, net assimilation rate, leaf area ratio, specific leaf weight and leaf weight ratio) were derived (refer to Section 1.3.1).

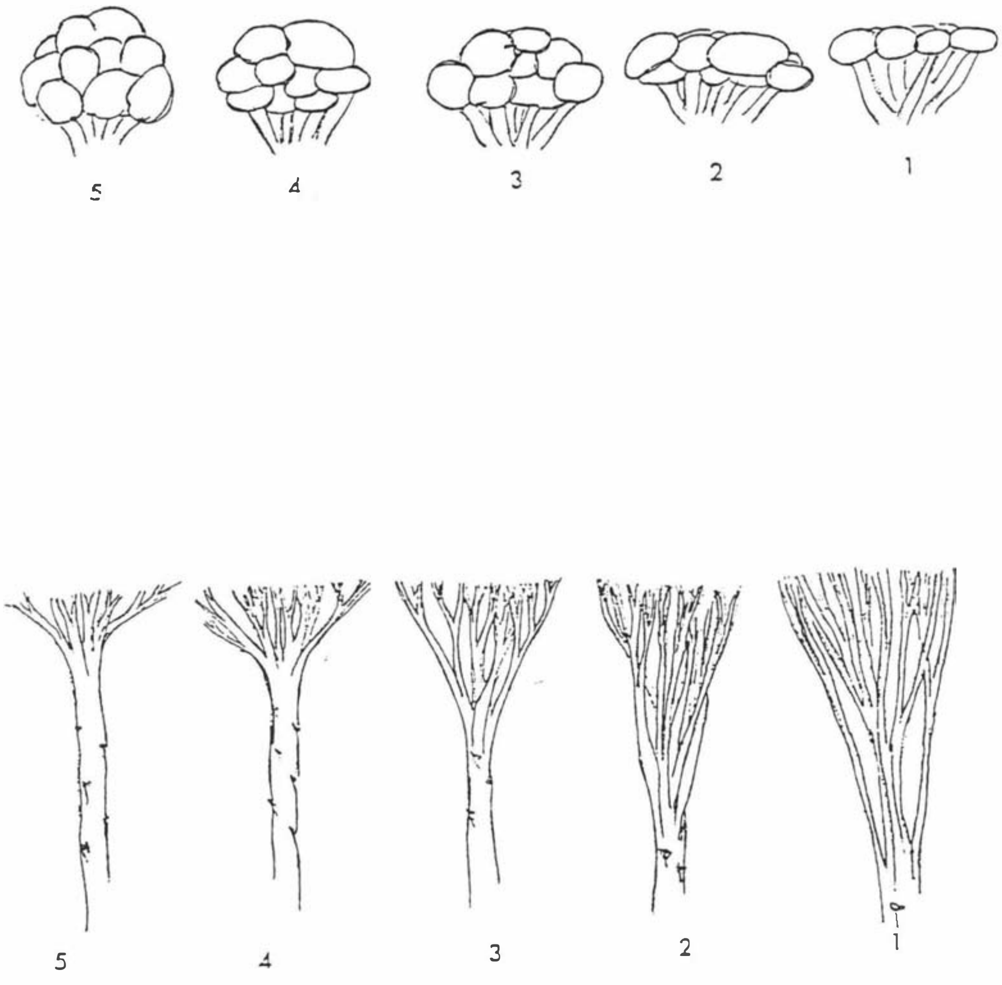


Figure 3.1 Diagrammatic representation of primary heads of broccoli.
Top: deep head (5); shallow head (1)
Bottom: wide angle branching (5); narrow angle branching (1)
Source: Chowings (1974)

Figs. 3.2a and 3.2b show typical curves of the different growth parameters for the different cultivars of broccoli grown continuously at 20C. These figures show the time trends in RGR, NAR, LAR, SLW and LWR from the 4th week after sowing up to the 12th week which was approximately 18, 15, 22, 31 and 28 days before the curd maturity of Premium Crop, Mercedes, Idol, Fordhook Late and Shogun, respectively. The data could not be extended up to curd maturity as there were not enough sample plants for growth analysis. Results of the analysis of variance of the different growth parameters between the five cultivars at different growth stages are shown in Appendix 6. The trends in the different growth curves were very similar between the different cultivars although there were slight differences at certain stages of plant growth particularly in RGR, LAR and SLW. The differences in LAR and SLW between the cultivars appeared to be greater during the earlier growth stages. Although not significantly different, NAR was higher in Shogun early on but droppped faster with time relative to the other cultivars. The opposite was true for Fordhook Late. Initial LAR of Fordhook Late was highest but dropped faster than the other cultivars. SLW, on the other hand, was lower initially in Fordhook Late, becoming similar to the other cultivars at the later stages.

3.3.2 Maturity Period

The number of days from sowing to curd maturity varied among the 5 cultivars (Table 3.1). Mercedes was the earliest maturing cultivar followed by Premium Crop, Idol, Shogun and Fordhook Late. The maturity period of these different cultivars was not affected by any temperature treatment imposed at any stage of plant development.

3.3.3 Curd Quality

Scores for the three quality indices were generally comparable in cultivars Premium Crop, Mercedes, Fordhook Late and Shogun. The scores were significantly lower for Idol (Table 3.1).

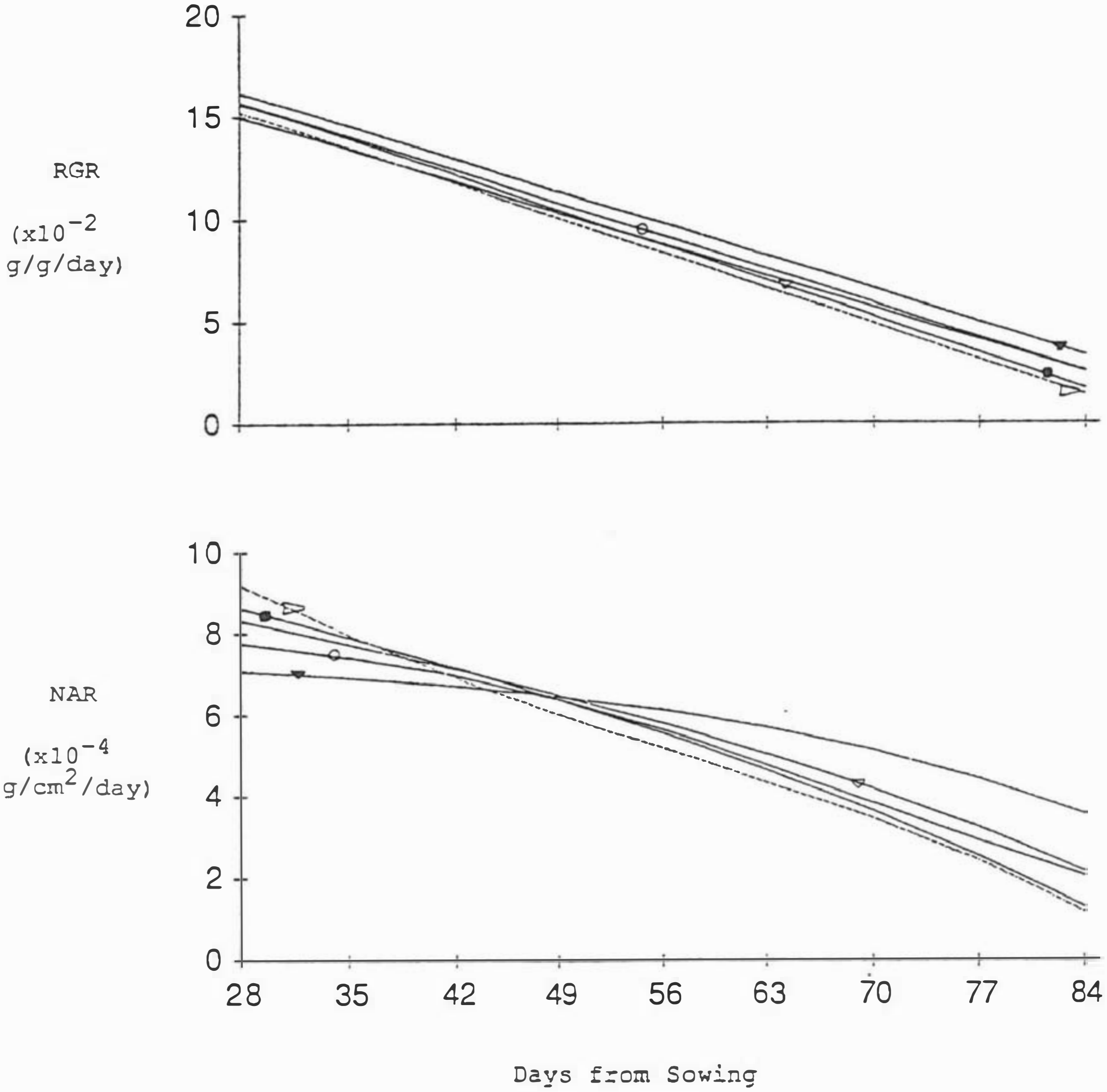


Fig. 3.2a Time trends in relative growth rate (RGR) and net assimilation rate (NAR) of different cultivars of broccoli (-○- Premium Crop; -●- Mercedes; -▽- Idol; -▼- Fordhook Late; ▷ Shogun). Primary data fitted to a quadratic equation.

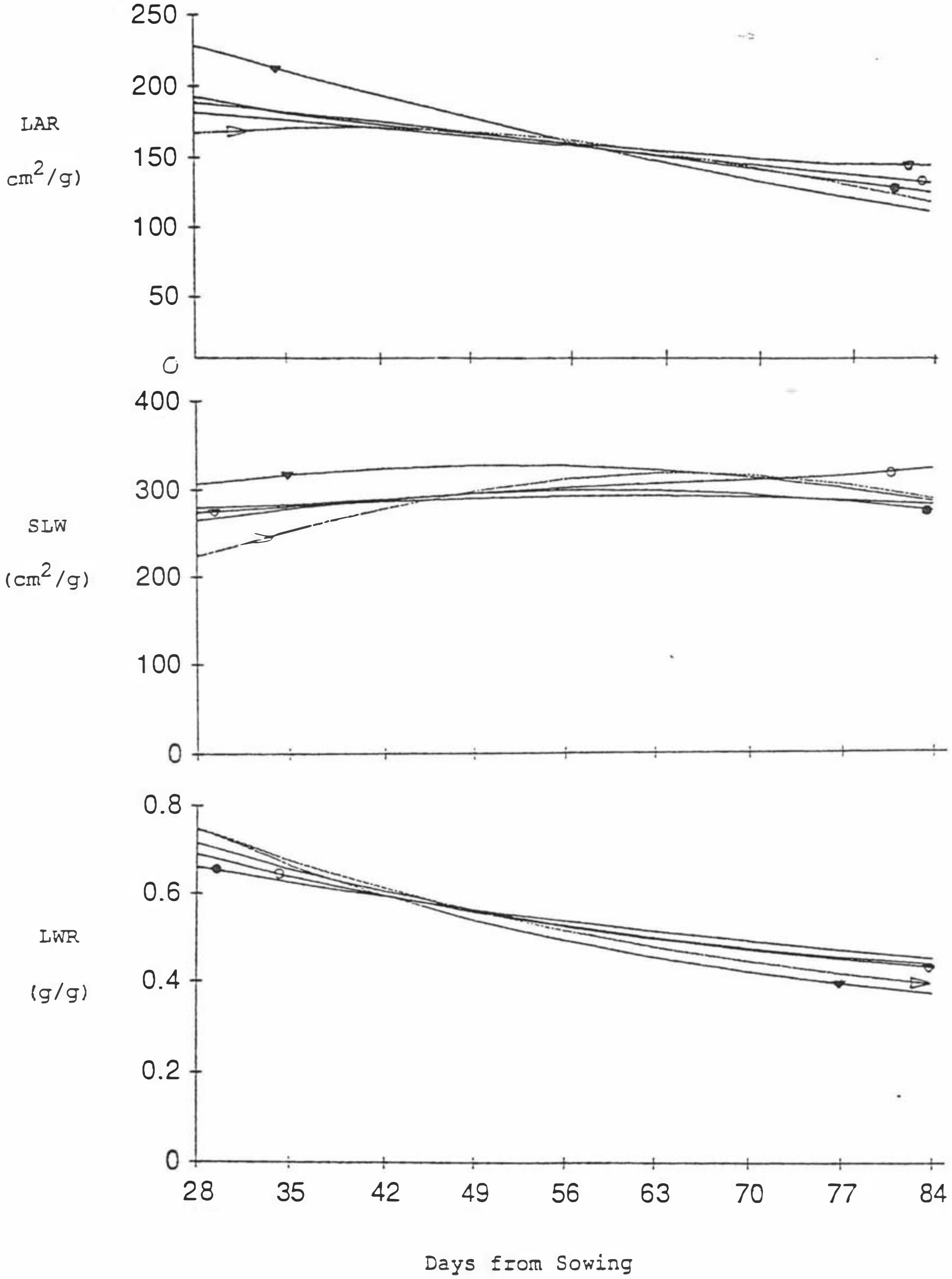


Fig. 3.2b Time trends in leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) of different cultivars of broccoli (-○- Premium Crop; -●- Mercedes; -○- Idol; -▼- Fordhook Late; ▷ Shogun). Primary data fitted to a quadratic equation.

Table 3.1 Number of days to curd maturity and curd quality of broccoli as affected by genotype and temperature treatments.

FACTOR	DAYS TO CURD MATURITY	CURD QUALITY		
		Curd Branching	Curd Depth	Uniformity of Bud Maturity
CULTIVAR				
Prem. Crop	102 d	3.21 a	3.33 bc	3.45 a
Mercedes	99 e	3.08 a	3.09 c	3.34 a
Idol	106 c	2.58 b	2.72 d	3.02 b
Fordhook Late	115 a	3.22 a	3.98 a	3.36 a
Shogun	112 b	3.26 a	3.62 b	3.43 a
s.e.	1.02	0.091	0.098	0.102
TEMPERATURE (C)				
10	106	3.23 a	3.52 a	3.48 a
20	107	3.22 a	3.49 a	3.46 a
30	107	2.75 b	3.03 b	3.02 b
s.e.	0.79 ns	0.071	0.076	0.079

ns non significant

Means with the same letter are not significantly different at 5% level.

Regardless of the other factors, the 30C treatment caused a reduction in curd quality (considering all three criteria) relative to the control (20C treatment). Low temperature had no apparent effects.

When imposed before the curd initiation stage of the plant, high temperature treatment did not affect curd quality. At the early and late curd development stages curd quality was significantly reduced with the reduction being more pronounced at the latter stage (Table 3.2). At the early curd development stage the reduction in quality was associated more with curd branching and decreased uniformity of bud maturity. At the later stage all the three quality indices were affected.

The response of the cultivars to the high temperature treatment appeared to be quite variable. The effect on curd quality was more apparent on Premium Crop, Mercedes and Idol than on Fordhook Late and Shogun (Table 3.3).

3.3.4 Harvest Parameters

Total fresh weight production varied between cultivars (Table 3.4). Fordhook Late had the highest total fresh weight followed by Shogun, Idol, Premium Crop and Mercedes. Curd fresh weight and size were comparable in cultivars Idol, Fordhook Late and Shogun and was considerably lower in Mercedes and Premium Crop. Harvest index varied with cultivars which was consistent with the Field Experiment.

Total fresh weight production was lower for plants under the low temperature treatment but curd fresh weight production was unaffected.

3.4 Discussion

The varietal differences in the growth parameters found in the present study is comparable to that of the field experiment. The lower initial NAR of Fordhook Late was associated with a higher SLW. Conversely, Shogun which

Table 3.2 Temperature by stage of plant growth interaction effect on the curd quality of broccoli.

TEMPERATURE / STAGE	CURD QUALITY		
	Curd Branching	Curd Depth	Uniformity of Bud Maturity
10 C			
Early	3.28	3.45	3.51
Mid	3.04	3.39	3.40
Late	3.38	3.70	3.54
20 C			
Early	3.30	3.57	3.49
Mid	3.21	3.42	3.46
Late	3.16	3.48	3.43
30 C			
Early	3.18	3.54	3.60
Mid	2.76	3.17	2.93
Late	2.31	2.37	2.53
s.e.	0.123**	0.132**	0.137**

** highly significant

Table 3.3 Cultivar by temperature interaction effect on the curd quality of broccoli.

CULTIVAR / TEMPERATURE (C)	CURD QUALITY		
	Curd Branching	Curd Depth	Uniformity of Bud Maturity
Premium Crop			
10	3.42	3.37	3.62
20	3.26	3.50	3.47
30	2.96	3.11	3.25
Mercedes			
10	3.54	3.63	3.67
20	3.22	3.17	3.63
30	2.47	2.48	2.74
Idol			
10	2.67	2.87	3.19
20	2.98	2.98	3.12
30	2.09	2.30	2.76
Fordhook Late			
10	3.23	4.03	3.42
20	3.25	4.14	3.56
30	3.17	3.75	3.10
Shogun			
10	3.31	3.68	3.52
20	3.41	3.67	3.52
30	3.06	3.51	3.26
s.e.	0.158 **	0.160 **	0.177 **

** highly significant

Table 3.4 Total plant weight, curd diameter, curd fresh weight and harvest index of broccoli as affected by genotype and temperature treatments.

FACTOR	TOTAL PLANT FRESH WEIGHT (g)	CURD FRESH WEIGHT (g)	CURD DIAMETER (cm)	HARVEST INDEX (%)^A
CULTIVAR				
P. Crop	210.0 d	26.85 b	6.73 b	20.39 bc (12.34)
Mercedes	171.8 e	29.84 b	6.34 b	22.17 a (14.42)
Idol	382.8 c	50.32 a	8.30 a	21.14 ab (13.05)
F. Late	662.4 a	57.61 a	8.00 a	17.89 d (9.50)
Shogun	473.3 b	53.32 a	7.78 a	19.56 c (11.24)
s.e.	11.7	2.53	0.173	0.44
TEMPERATURE				
10 C	356.9 b	42.04	7.66 a	20.42 (11.77)
20 C	387.2 a	46.81	7.48 a	20.43 (12.08)
30 C	396.1 a	41.92	7.14 b	19.83 (10.58)
s.e.	8.57	1.96	0.134	0.34^{ns}

^{A} Arc sin transformed values
Untransformed values in parenthesis.

Means with the same letter are not significantly different at 5% level.

^{ns} non significant

had an initially higher NAR had a lower SLW. Moreover, the low NAR of Fordhook Late was balanced by its high LAR so that its RGR was comparable with that of the other cultivars.

Results also point out some interesting features of the effect of temperature on the development and curd quality of broccoli. All the cultivars developed curds regardless of the temperature treatments and the treatments did not affect earliness to curd maturity. This suggests that all the cultivars used may not have cold requirements for curd formation. This agrees with Gauss and Taylor (1967a) who claimed that there is no quantitative or qualitative cold requirement for curd formation in broccoli, but not with other workers (Fujime, 1988; Fontes et al. 1967; Miller and Konsler and Lamont, 1985). It may be that in the latter studies low temperature simply favoured early curd initiation but may not necessarily be an absolute requirement for it.

The effects of high temperature on curd quality was manifested only when imposed at a later stage of curd development. It is thus evident that high temperature treatment prior to curd initiation did not elicit any physiological change to hasten or delay curd maturity of the plant or affect the quality of the curd. It appears that high temperature directly affected the morphological development of the curd.

There is little in the literature to explain the effect of high temperature on the abnormal development of the curd. Previous studies on the effect of high temperature on broccoli and cauliflower are limited on finding whether or not curd initiation occurs and on the time to curd initiation. Generally, high temperature treatment prevented or delayed curd initiation in both broccoli and cauliflower (Fujime and Hirose, 1982 and 1988; Huber, 1926 as cited by Sadik, 1967). This was not found to occur in the present study.

The description of the sink development and dry matter distribution in the cauliflower inflorescence by Hardwick (1984) may help in understanding the effect of high temperature on the development of the broccoli curd. He observed that in a curd there are substantial variations in mass between its component florets and that the variations were not simply due to competition for assimilates between the florets. He concluded that the variations originated at the apical meristem as variations in the timing of primordial initiation. In the case of a curd exposed to high temperature, the variation in size and weight per floret appeared to be enhanced. This, presumably, is because of the disruption of the synchrony of the growth of individual florets, the morphologically advanced ones tending to grow faster than the younger ones thus forming an irregular or uneven curd surface.

When imposed during the early curd development period, the effect of high temperature on curd quality was present but less apparent. Only the uniformity of bud maturity was affected. The stage of curd development may have been too early for the high temperature treatment to exert its effect on the whole floret.

There was not much effect of temperature on the harvest parameters of broccoli except that low temperature tended to reduce total dry matter accumulation of plants. Despite this lower dry matter production, curd dry weight production was comparable with that from plants under high temperature treatment. The effect of low temperature on the dry matter accumulation of plants has also been shown in the earlier field experiment.

Results of this experiment suggest that under field conditions quality of broccoli curds can be affected by periods of abnormally high temperatures. It may be good to schedule planting such that the curd development period, particularly that period close to maturity, coincides with a time when conditions of extremely high temperature are unlikely.

Chapter 4

Controlled Climate Experiment: **The Effect of Temperature on the Growth, Development, Curd Quality and Maturity Characteristics of Broccoli.**

4.1 Introduction

This experiment was complementary to the Field and Greenhouse experiments. It was designed to determine further the effects of different and more extreme temperature treatments on the growth and development, maturity characteristics, yield and curd quality of broccoli. Due to space restriction only three of the cultivars used in the Field and Greenhouse Experiments were used. These three cultivars were selected because they represented different periods of maturity. The treatments consisted of continuous high (30C) or near optimal (20C) temperature and a 2-wk treatment at the opposite temperature at different stages of plant growth. A low temperature treatment was not included as it was found in the Glasshouse Experiment to have no effect on the maturity period, yield and curd quality of broccoli. Moreover, the period of exposure to high temperature was increased to two weeks as a one-week exposure before curd initiation time also showed no effect in the Greenhouse Experiment. Plants might show some response to a longer period of exposure to high temperature before the curd initiation stage.

This study aimed to:

(1) compare the growth rates of the different cultivars under the different temperature treatments using growth analysis techniques;

(2) determine the effects of the temperature treatments on the curd quality, yield, dry matter production and times to curd initiation and maturity of the different broccoli cultivars;

(3) determine the relative importance of the different growth stages of the plant to any temperature treatment; and

(4) relate results to those in the Field and Greenhouse Experiment.

4.2 Materials and Methods

4.2.1 Experimental Design and Treatments

A 2-factor factorial experiment using a completely randomized design (CRD) with 2 replications, was used in the study with the following as the treatments:

Cultivar (3)
- a) Premium Crop
- b) Idol
- c) Fordhook Late

Temperature Treatments
- a) 22C/18C day/night
  - - referred as 20C (A)
- b - e) 20C-30C-20C
  - 2 wk at 30C at:
    - - 2 wk from sowing (AB1)
    - - 4 wk from sowing (AB2)
    - - 6 wk from sowing (AB3)
    - - 8 wk from sowing (AB4)
- f) 32C/28C day/night
  - - referred as 30C (B)
- g - j) 30C-20C-30C
  - 2 wk at 20C at:
    - - 2 wk from sowing (BA1)
    - - 4 wk from sowing (BA2)
    - - 6 wk from sowing (BA3)
    - - 8 wk from sowing (BA4)

Due to the limited number of climate rooms the whole procedure was repeated for the second replication.

4.2.2 The Growth Chambers

Two controlled environment chambers were used in the experiment. One chamber was set at day/night temperature of 32/28C and the other at 22/18C. The chambers were equipped with a combination of white fluorescent and incandescent lamps to supply 12-hr 150 w/m^2 photoperiod lights daily. Relative humidity was maintained at about 85% in both chambers. Details about the climate rooms are given in Appendix 7.

4.2.3 Seedling Production and Potting

Seeds of the different cultivars were sown in cellular trays filled with a mixture of 50% sand and 50% peat. The seedlings were raised inside each growth chamber. Half strength Hoagland solution (Appendix 11) was supplied to the growing seedlings daily.

Sixteen days after sowing the seedlings were potted into 1-gallon pots filled with the same soilless mixture. The pots were labelled according to the different treatments and were randomly arranged on trolleys inside the growth chambers. Automatic liquid feeding using full strength Hoagland solution was henceforth used.

4.2.4 Imposition of the Treatments

The different temperature treatments were imposed on the plants following the schedule as outlined. The treatments consisted of raising plants under continuous 20C or 30C, or a treatment of the opposite temperature for 2 weeks at different stages of plant growth.

4.2.5 Growth Analysis

Growth analysis was carried out on the plants under the different temperature treatments using the same procedure used in the previous studies. Due to limited space in the chambers only one plant per treatment per sampling date was harvested for growth analysis. Because of the limited number of sample plants it was not possible to statistically analyse the temperature treatment by cultivar interaction effect on the different growth analysis parameters. Only the main factor effects were considered for statistical analysis.

4.2.6 Final Harvest and Data Analysis

At final harvest the same set of data in the greenhouse experiment were gathered and similar data analysis procedures were carried out.

4.3 Results

4.3.1 Growth Analysis

Figures 4.1a and 4.1b show the time trends in relative growth rate (RGR) net assimilation rate (NAR), leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) with time of broccoli grown at 30C or 20C. Results of the statistical analysis are shown in Appendix 8. The RGR and NAR of plants grown at the lower temperature regime were higher earlier on, becoming similar to the plants grown at higher temperature towards maturity. At the seedling stage LAR and SLW were not affected by the temperature regime but at the later stages these two parameters were higher at the higher temperature regime. LWR was generally unaffected by temperature. The 2-wk treatment at the opposite temperature at different stages of plant growth did not have any consistently significant effects on these different growth parameters (Tables 4.1 - 4.5).

Figures 4.2a and 4.2b show the time trends in the different growth parameters for the different cultivars. No statistical differences in all parameters were noted between the cultivars (Appendix 8) although Fordhook Late showed a slightly higher LAR and SLW during the early phases of growth than the other two cultivars (Fig. 42b), consistent with the earlier field and greenhouse experiment.

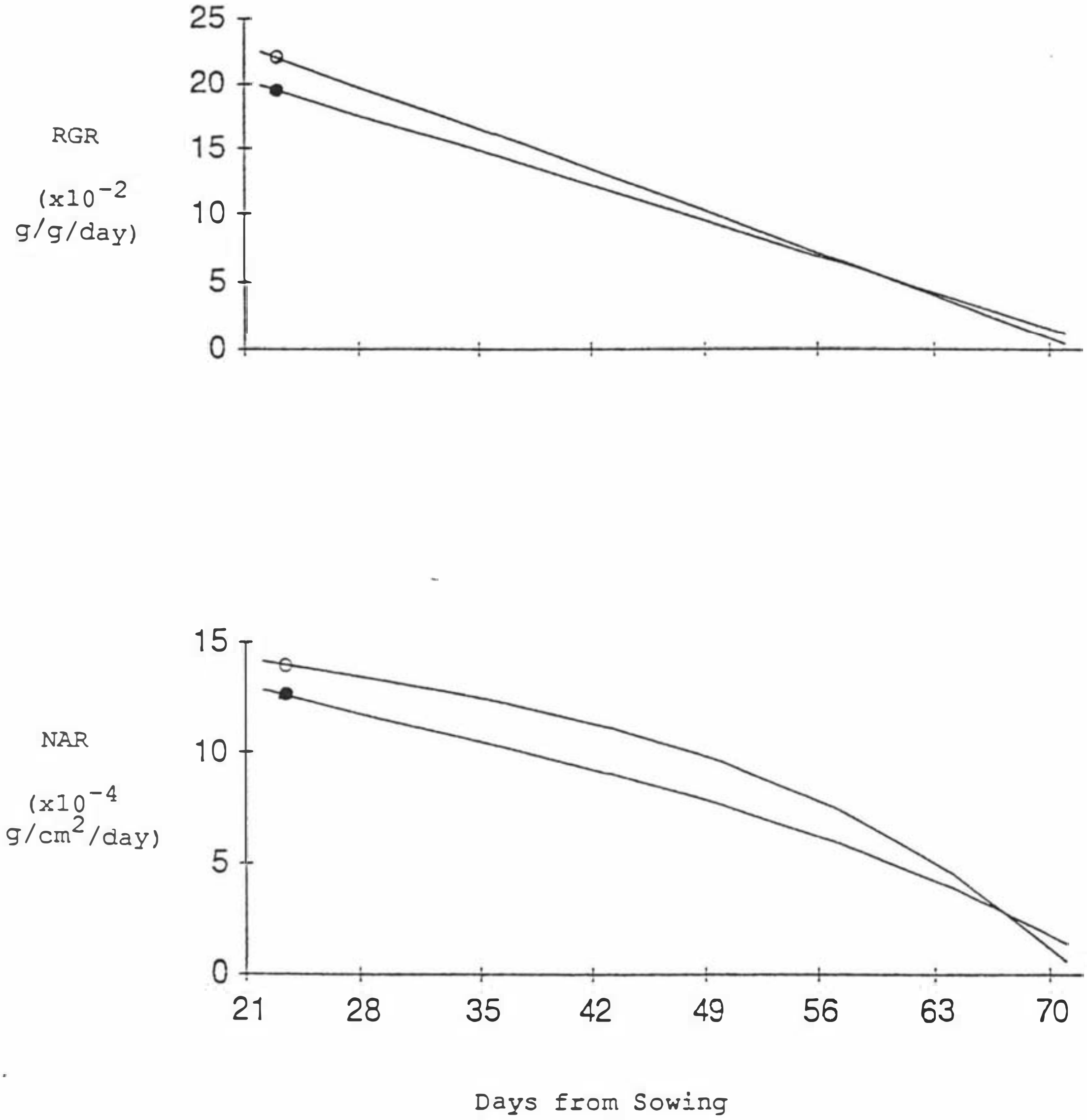


Fig. 4.1a Time trends in relative growth rate (RGR) and net assimilation rate (NAR) of broccoli grown at 30C (-●-) and at 20C (-○-). Primary data fitted to a quadratic equation.

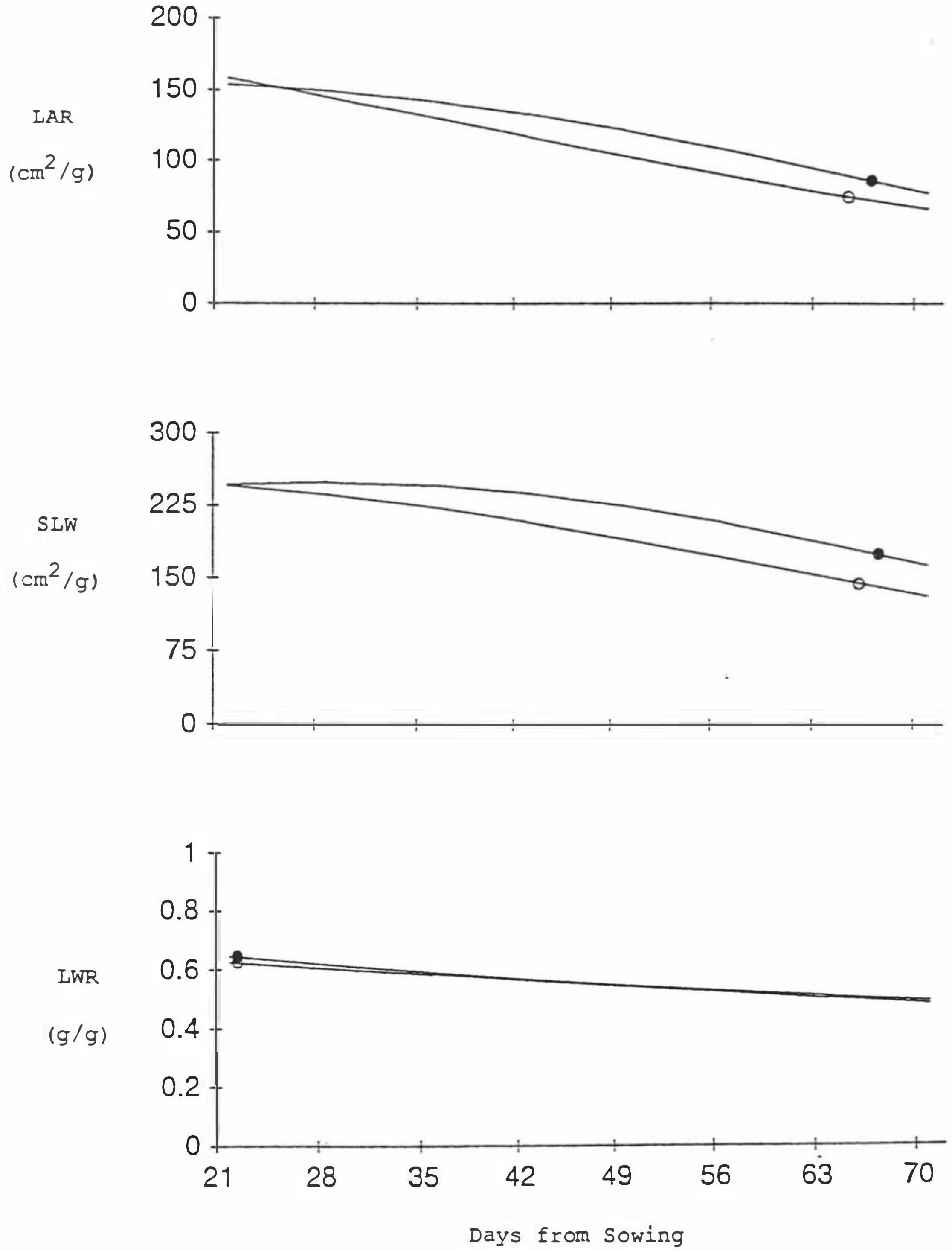


Fig. 4.1b Time trends in leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) of broccoli grown at 30C (-●-) and at 20C (-○-). Primary data fitted to a quadratic equation.

Table 4.1 Relative growth rate (RGR) of broccoli as affected by different temperature treatments (means of 3 cultivars).

TEMPERATURE TREATMENT ++	RGR ($\times 10^{-2}$ g/g/day) Days from Sowing 21	35	49	63
A	23.1 a	16.6 a	10.1 a	3.6
AB1	21.4 ab	15.4 ab	9.5 b	3.5
AB2	22.9 a	16.3 a	9.8 a	3.3
AB3	22.3 ab	16.2 a	10.1 a	4.0
AB4	23.0 a	16.5 a	10.0 a	3.5
B	19.9 ab	14.4 b	9.0 b	3.5
BA1	21.2 ab	15.3 ab	9.5 b	3.0
BA2	19.6 b	14.4 b	9.2 b	4.0
BA3	19.8 a	14.5 b	9.2 b	3.8
BA4	19.2 b	14.2 b	9.2 b	4.3
s.e.	1.04	0.45	0.15	0.73 ns

++ refer to section 4.1.1

Means with the same letter are not significantly different (5% level).

ns non significant

Table 4.2 Net assimilation rate (NAR) of broccoli as affected by different temperature treatments (means of 4 cultivars).

++ TEMPERATURE TREATMENT	NAR (x 10^{-4} g/cm^2 /day) Days from Sowing			
	21	35	49	63
A	14.7 a	13.1 a	10.2 a	4.8
AB1	13.2 ab	10.6 ab	8.2 ab	4.3
AB2	14.2 a	12.2 ab	9.2 a	3.8
AB3	14.3 a	13.0 a	10.2 a	5.1
AB4	14.5 a	13.0 a	10.3 a	4.8
B	12.8 ab	10.2 b	7.5 ab	3.7
BA1	14.2 ab	11.4 ab	8.2 b	4.1
BA2	12.5 b	10.0 ab	7.6 b	4.2
BA3	12.7 b	10.3 b	7.6 b	3.6
BA4	12.2 b	10.0 b	7.4 b	3.9
s.e.	0.64	0.84	0.48	0.62 ^{ns}

Means with the same letter are not significantly different (5% level)

^{ns} non significant

$^{++}$ refer to section 4.1.1

Table 4.3 Leaf area ratio (LAR) of broccoli as affected by different temperature treatments (means of 4 cultivars).

++ TEMPERATURE TREATMENT	LAR (cm^2/g) Days from Sowing			
	21	35	42	63
A	156.3	127.4	99.6	74.4 b
AB1	162.3	144.9	114.8	80.7 b
AB2	161.2	133.3	105.9	80.9 b
AB3	155.7	124.5	98.9	78.2 b
AB4	157.9	127.9	97.4	69.4 b
B	153.7	143.9	120.1	88.1 ab
BA1	148.3	136.4	115.2	89.4 a
BA2	156.3	145.0	121.4	95.2 a
BA3	155.4	144.8	122.9	92.8 a
BA4	155.5	147.8	128.9	100.5 a
s.e.	3.25 ^{ns}	7.82 ^{ns}	9.08 ^{ns}	5.9

Means with the same letter are not significantly different (5%level).

^{ns} non significant

$^{++}$ refer to section 4.1.1

Table 4.4 Specific leaf weight (SLW) of broccoli as affected by different temperature treatments (means of 4 cultivars).

++ TEMPERATURE TREATMENT	SLW (cm^2/g)			
	Days from Sowing			
	21	35	42	63
A	244.5	220.8	185.9 b	145.8 b
AB1	241.7	226.4	194.0 ab	152.2 b
AB2	254.1	231.1	199.9 ab	164.4 b
AB3	243.0	212.6	183.6 b	156.5 b
AB4	246.0	226.2	187.8 b	140.8 b
B	249.3	242.0	211.0 ab	164.8 b
BA1	238.4	244.3	224.4 ab	186.2 a
BA2	247.3	246.4	226.0 ab	190.6 a
BA3	245.0	252.0	239.1 a	207.9 a
BA4	253.1	246.7	222.8 ab	183.6 a
s.e.	5.08 ^{ns}	12.0 ^{ns}	14.58	13.22

Means with a common letter are not significantly different (5% level).

^{ns} non significant

$^{++}$ refer to section 4.1.1

Table 4.5 Leaf weight ratio (LWR) of broccoli as affected by different temperature treatments (means of 4 cultivars).

++ TEMPERATURE TREATMENT	LWR (g/g) Days from Sowing			
	21	35	42	63
A	0.68 a	0.60	0.55	0.52
AB1	0.68 a	0.66	0.62	0.56
AB2	0.67 ab	0.60	0.55	0.51
AB3	0.67 ab	0.61	0.56	0.52
AB4	0.69 a	0.60	0.54	0.50
B	0.63 b	0.60	0.58	0.55
BA1	0.66 ab	0.60	0.54	0.48
BA2	0.65 ab	0.61	0.56	0.51
BA3	0.66 ab	0.60	0.54	0.48
BA4	0.62 b	0.60	0.59	0.56
s.e.	0.016	0.014 ^{ns}	0.016 ^{ns}	0.018 ^{ns}

^{ns} non significant

Means with the same letter are not significantly different at 5% level.

$^{++}$ refer to section 4.1.1

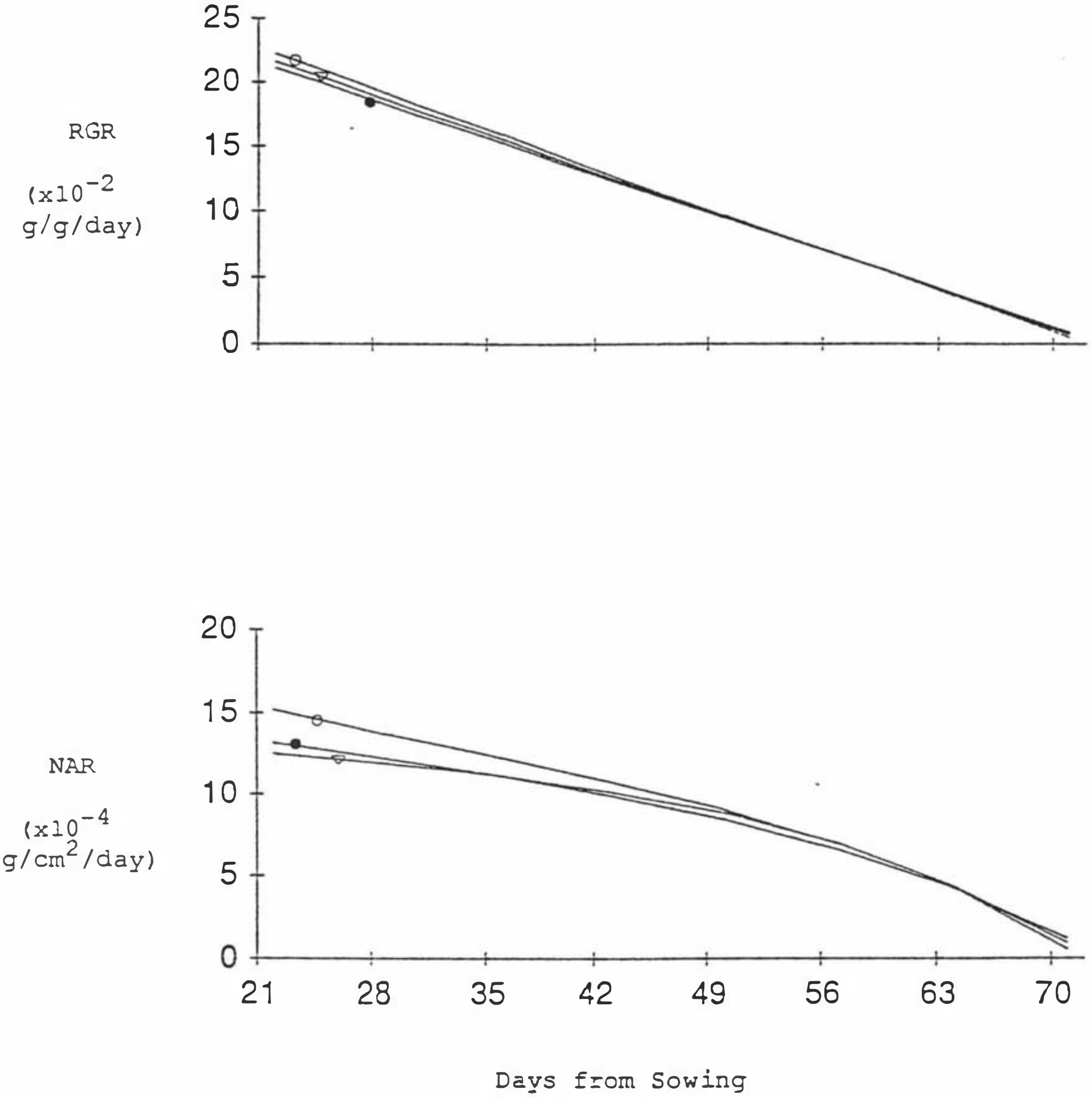


Fig. 4.2a Time trends in relative growth rate (RGR) and net assimilation rate (NAR) of different cultivars of broccoli (-○- Premium Crop; -●- Idol; -▽- Fordhook Late). Primary data fitted to a quadratic equation.

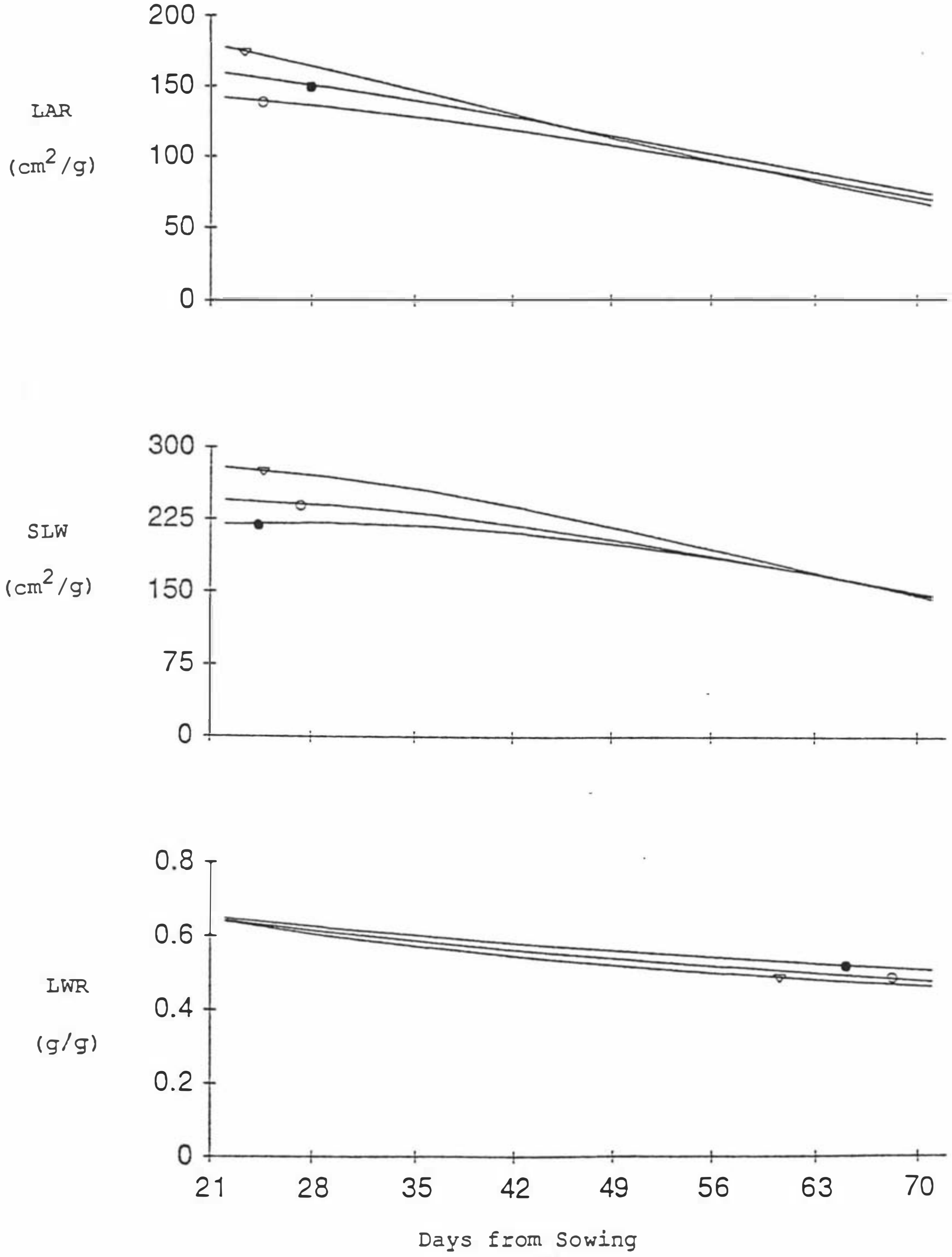


Fig. 4.2b Time trends in leaf area ratio (LAR), specific leaf weight (SLW) and leaf weight ratio (LWR) of different cultivars of broccoli (-○- Premium Crop; -●- Idol; -▽- Fordhook Late). Primary data fitted to a quadratic equation.

4.3.2 Leaf Production

Time trends in leaf production (Fig 4.3) and final number of leaves did not vary with the two temperature regimes. With cultivars the rate of leaf production were similar but the final number of leaves varied as in the earlier experiments.

4.3.3 Curd Initiation and Growth

Due to the limited number of sample plants for growth analysis it was not possible to study time trends in curd growth and to estimate the time to curd initiation by the methods used in the field experiment. Examination of shoot apices during the weekly samplings suggested no differences in the time to curd initiation between plants under the 2 temperature regimes. This occurred about 6 weeks from sowing for Premium Crop and Idol and two weeks later for Fordhook Late.

4.3.4 Curd Quality and Harvest Parameters

An estimate of the time to curd maturity of the plants was taken based on the compactness of the curd. Data on curd quality and for some harvest parameters were also recorded at this time. Table 4.6 shows the maturity period and the curd quality of broccoli as affected by genotype and temperature treatments. Fordhook Late failed to reach maturity at the termination of the experiment so data could only be summarized for cultivars Idol and Premium Crop. It took a longer time for Idol to develop mature curds than Premium Crop. The quality of the curds of the two cultivars was comparable.

All the plants under the different treatment treatments initiated curds but those under 30C failed to develop normal mature curds similar to those found under the 20C treatment. Typical curds formed under the high temperature regime are shown in Plate 4.2a while a normal curd formed at 20C is shown in Plate 4.2b. In the former plate, bracts are present throughout the surface

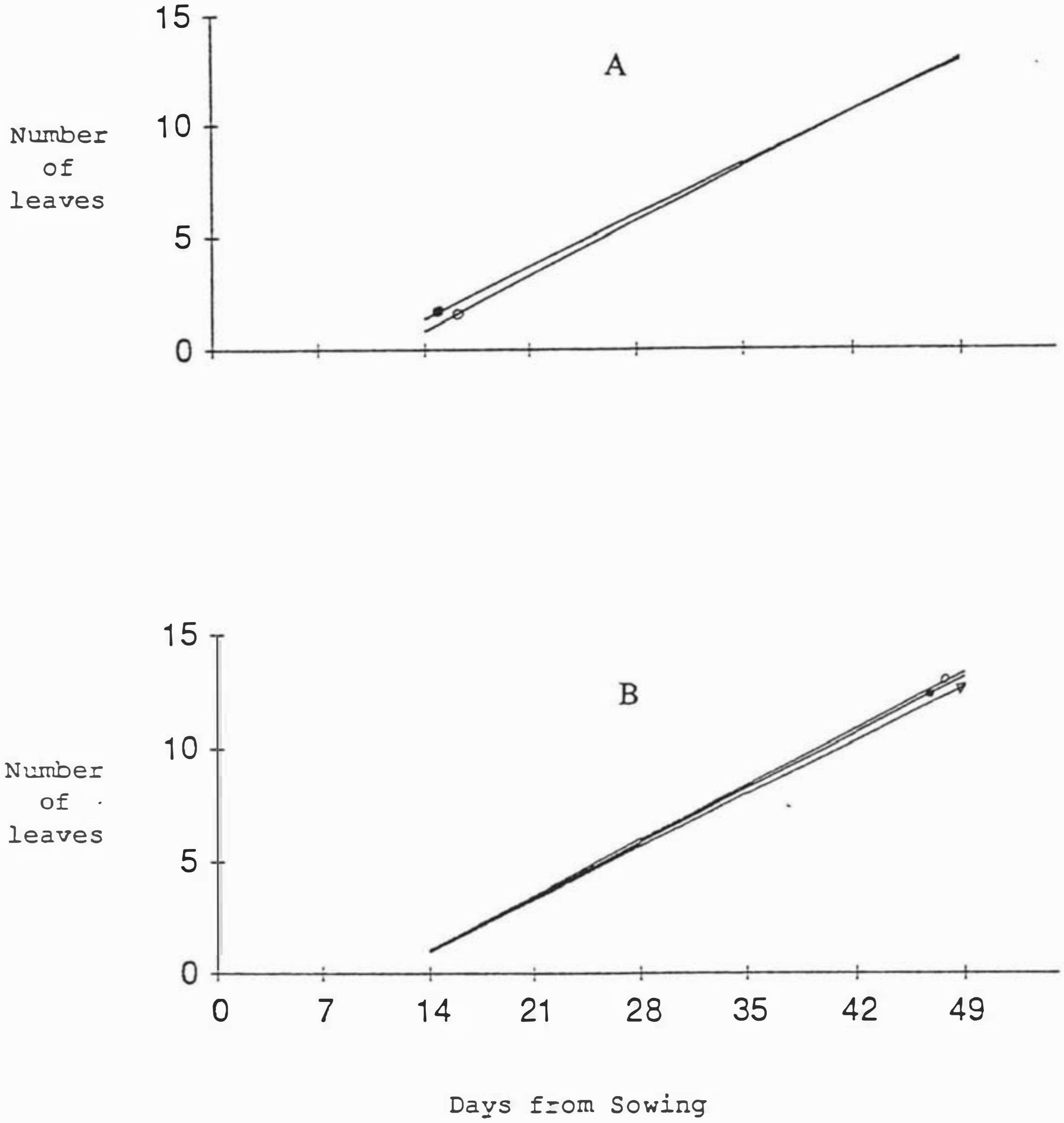


Fig. 4.3 Rate of leaf production in broccoli.
a) Temperature regime means (-○- 20C; -●- 30C)
b) Cultivar means (-○- Premium Crop; -●- Idol; -▽- Fordhook Late)

Table 4.6 Number of days to curd maturity and curd quality of broccoli (cultivar and temperature treatment means).

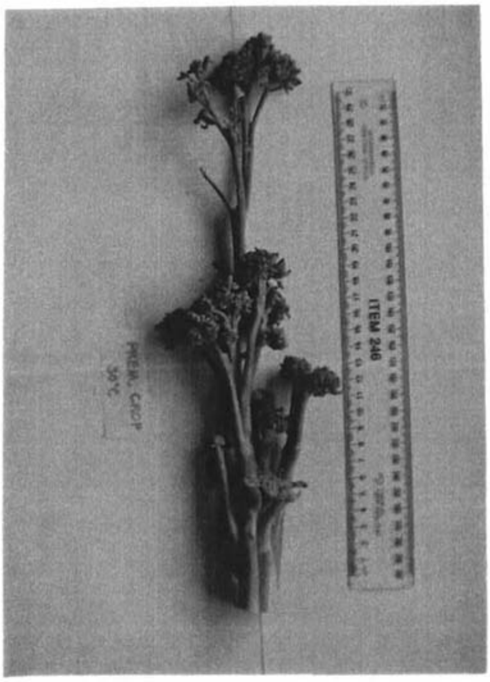
FACTOR	DAYS TO CURD MATURITY	CURD QUALITY		
		Curd Branching	Curd Depth	Uniformity of Bud Maturity
CULTIVAR				
P. Crop	87 b	2.32	2.24	2.34
Idol	98 a	2.29	2.40	2.18
s.e.	1.21	0.09 ^{ns}	0.12 ^{ns}	0.10 ^{ns}
TEMP. TRMT.				
A	87 b	3.67 a	3.71 a	3.46 a
AB1	88 b	3.79 a	3.62 a	3.67 a
AB2	87 b	3.75 a	3.83 a	3.37 a
AB3	85 b	2.83 b	3.08 ab	3.16 ab
AB4	89 b	2.70 b	2.54 b	2.58 b
B	99 a	1.37 c	1.50 c	1.38 c
BA1	100 a	1.12 c	1.12 c	1.12 c
BA2	93 ab	1.08 c	1.08 c	1.08 c
BA3	98 a	1.29 c	1.37 c	1.46 c
BA4	98 a	1.42 c	1.33 c	1.33 c
s.e.	2.72	0.20	0.27	0.23

Means for each factor with the same letter are not significantly different at 5% level.

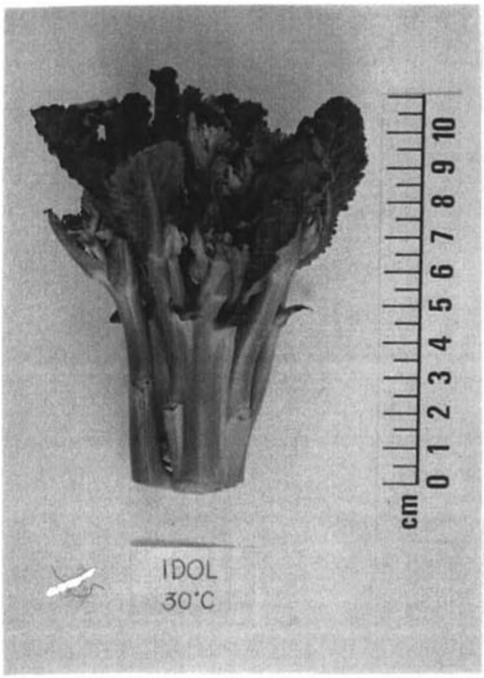
^{ns} non significant

BA4

BA2

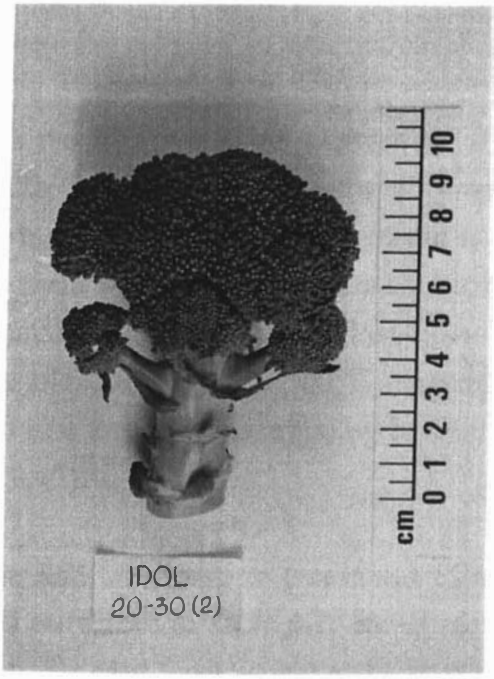


B

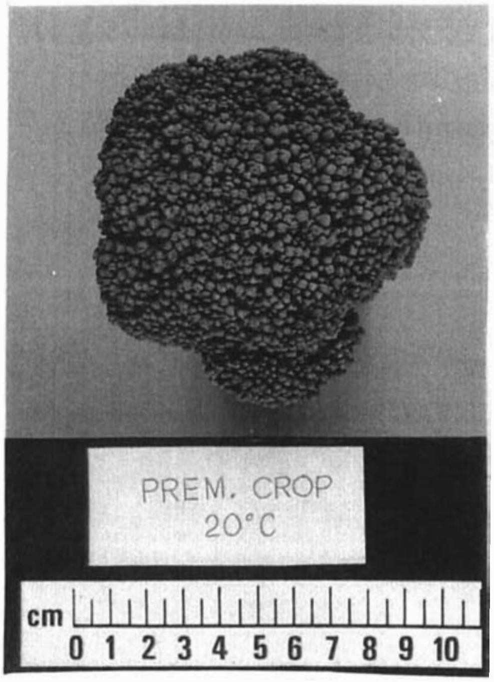


B

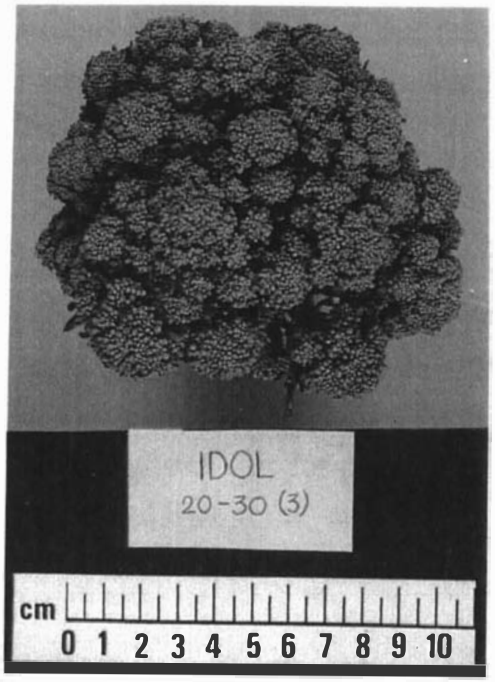
Plate 4.2a Curds produced from plants under different temperature treatments. For treatment codes refer to Section 4.1.1.



AB2



A



AB3

Plate 4.2b Curds produced from plants under different temperature treatments. For treatment codes refer to Section 4.1.1.

of the curd, the internodes subtending the primary florets are elongated and the buds present in the florets did not grow to their normal size

In plants under the 20C regime but exposed to 30C at the later stage of plant growth (Plate 4.2b; Treatment AB4) curd quality was lower. Exposure to high temperature during the early growth stages did not affect curd quality. These results are consistent with those of the Greenhouse experiment. Exposure to 20C of the plants under 30C temperature regime did not improve curd quality regardless of the stage of plant growth that the lower temperature treatment was imposed, but resulted in a a range of morphological abnormalities (Plate 4.2a; Treatments B A4 and B A2).

The genotype and temperature treatment effects on some harvest parameters of broccoli are shown in Table 4.7. Idol produced higher shoot fresh weight but had comparable curd fresh weight and size with Premium Crop. The different temperature treatments did not affect shoot fresh weight but affected curd fresh weight and size. Plants grown under 20C produced heavier and bigger curds than those under 30C and, consequently, their harvest index (ratio of curd fresh weight to shoot fresh weight) was higher. The 2-wk treatment at the opposite temperature had no apparent effects on these parameters.

4.4 Discussion

The two temperature regimes brought about some variations in the different growth parameters. The lower RGR and NAR in plants under 30C suggests that 30C may already be beyond the optimum temperature for the growth of broccoli. Warren-Wilson (1966b) suggested that for plants under natural climate the effect of temperature on NAR and RGR must vary according to whether the prevailing temperature lies above or below the optimum for the species under consideration.

Despite the lower LAR of the plants at 20C, RGR was higher mainly because of a high NAR. As in the field and greenhouse experiment the high NAR was associated with a lower SLW (Nichols, 1972; Barnes et. al, 1969;

Table 4.7 Shoot fresh weight, curd fresh weight and size, and harvest index of broccoli (cultivar and temperature treatment means).

FACTOR	SHOOT FRESH WT (g)	CURD FRESH WT (g)	CURD DIAMETER (cm)	HARVEST INDEX (%)[A]
CULTIVAR				
P. Crop	575.9	61.5	6.68	31.41
Idol	684.6	77.9	7.21	32.42
s.e.	23.8	7.7	0.34	1.55
TEMP. TRMT.				
A	625.9	106.2 a	9.58 a	40.30 ab
AB1	595.4	96.7 ab	8.83 a	41.20 a
AB2	607.2	106.2 a	8.66 a	40.20 ab
AB3	806.6	115.2 a	9.83 a	37.70 ab
AB4	681.0	78.6 abc	8.33 a	33.60 abc
B	529.1	26.9 c	4.04 b	22.30 c
BA1	645.5	34.8 c	4.69 b	21.50 c
BA2	566.2	50.6 bc	4.75 b	30.10 abc
BA3	601.3	40.5 c	5.29 b	26.50 bc
BA4	643.9	41.6 c	5.46 b	25.10 bc
s.e.	53.2 ns	17.1	0.77	3.48

[A] Arc sin transformed values

Means for each factor with the same letter are not significantly different (5% level).

ns non significant

Dornhoff and Shibles, 1976). Ragan (1983) attributed a low NAR in peas grown under high temperature to high respiration rate. This may well be true in the present experiment.

The increase in LAR and SLW of the plants with temperature supports the findings of Warren-Wilson (1966a) in rape, sunflower and maize.

Rate of leaf production and final leaf number did not vary between the two temperature regimes suggesting a wide optimum temperature range for this particular phase of development.

All the plants regardless of the temperature treatments initiated curds and time to curd initiation was unaffected. This supports the findings of the earlier greenhouse experiment that the different cultivars studied have no cold requirement for curd initiation.

Temperature may have affected the overall growth of the plant but its more important effect was on the morphological development of the curd. A temperature regime of 30C proved too high for the normal development of the curd. Wiebe (1975) also found some interesting effects of temperature on the morphological development of the curds of tropical cauliflower (cultivars Tropical Snow 55 and Patna Main Crop). He found that under low temperature (12-17C) the plants formed curds similar to broccoli while at high temperature (27C) they formed curds similar to cauliflower. At an intermediate temperature variously distinct riciness (premature initiation of foral buds) was found as a transition stage. Moreover, high temperature led to strong bract growth in temperate cauliflower (cv Aristokrat) and occasionally in broccoli (cv Gem).

There has not been any attempt to explain the exact mechanism by which temperature affects the morphological development of the curd. As earlier discussed, Hardwick (1984) attributed the variation in size between florets of a normal curd to the variation in the timing of primordial initiation. Brief exposure to high temperature may increase the variation in the size between individual florets by affecting the growth rate of older and younger florets.

Growing the plants under a high temperature regime throughout most of their growth, however, possibly induced a major change in the course of curd development. There seemed to be a preferential growth of bracts and internodes and a suppression of the growth and development of the floral buds. Clearly, this developmental response to high temperature is a result of complex biochemical and physiological changes and should be studied in more detail.

The present study also corroborates the earlier findings that, in plants grown under optimum temperature, brief exposure to high temperature affects curd quality only when imposed after the curd has been initiated. Thus far, it appears that curd development is the only critical stage as far as the effect of high temperature on curd quality is concerned. This may be important to note from a practical point of view.

Chapter 5

Summary

A field, greenhouse and controlled climate experiments were conducted to investigate the effects of temperature on the growth and development of broccoli. In the field experiment, six bimonthly sowings of four cultivars of broccoli were made. Various aspects of growth and development were studied including dry matter accumulation, leaf production, curd initiation and curd maturity. The heat unit concept was applied to determine the contribution of temperature to the variation in the different growth and development parameters with sowing dates. As follow-up studies, the greenhouse and controlled climate experiments were conducted to determine the independent effect of temperature on the growth and development of broccoli with emphases on the development, maturity characteristics and quality of the curds. In all these studies growth analysis was done using the functional approach.

In the field experiment total dry matter accumulation from all sowing dates was seen to be a logistic function of heat unit summation above a base temperature of 3C. This time scale was chosen since it resulted in the least error variance when a common regression for all sowing dates and cultivars was derived. With a chronological time scale (i.e., number of days) the function could not be fitted presumably because of too large an error variance, the rate of dry matter accumulation being so variable with sowing dates.

Based on the regression equations of the primary data, growth analysis parameters were derived. This resulted in typical growth curves. The unifying effect of the use of a heat unit time scale on the initial relative growth rate at different sowing dates was clearly shown although there was a certain degree of variation left. That of March, May and July sowings did not vary significantly although these would have represented periods of grossly differing growth rates under a normal time scale. The variations in the initial RGR may have been partly due to the instability of its components leaf area ratio (LAR) and net assimilation rate (NAR) with sowing dates (Causton, 1983) which may be related to the prevailing temperature regime. Initial LAR was lower during the

May and July sowings which may be due to low temperature (Warren-Wilson, 1966a). NAR was relatively higher, which was in turn associated with a lower SLW. The lower the SLW, the thicker the leaves are and the more efficient they are in producing new matter. This relationship between NAR and SLW was also shown in lettuce (Nichols, 1972) and, indeed, Barnes et. al. (1969) and Dornhoff and Shibles (1976) found that SLW correlated well with CO_2 exchange rate.

In the controlled climate experiment, RGR was found to be lower in the plants under the 30C temperature regime compared with those at 20C. This suggests that 30C may be beyond the optimum temperature range for the growth of broccoli. Other workers have found that there was a general tendency for RGR to increase with temperature up to a maximum and fall with further increase in temperature (Elias and Causton, 1975 on Impatiens parviflora; Warren-Wilson 1966a on sunflower and maize; Hurd 1977 on young tomato).

This low RGR at 30C may be attributed mainly to a drop in NAR as its other component LAR did not vary with the 2 temperature regimes. Ragan (1983) also observed a lower NAR in pea subjected to high temperature and he attributed it to temperature stress which could be associated with high respiration rate.

The varietal differences in the different growth parameters was generally consistent in the three experiments . Fordhook Late had a slightly lower NAR which was also associated with a lower SLW. Its high LAR balanced its low NAR so that its RGR was comparable with the other cultivars.

In the field experiment, the rate of leaf production of all cultivars showed a good linear fit against heat unit summation above a base temperature of -2C and was almost constant with sowing dates. The lower base temperature for leaf production compared to that for dry matter production suggests that leaf initiation in broccoli possibly occurs at a temperature which may be too low for normal growth.

Considering a normal time scale, it was evident that the rate of leaf production varied with sowing dates, the higher the temperature regime the faster was the rate of leaf production. However, in the controlled climate experiment rate of leaf production did not differ with the temperature regimes of 20C and 30C. These presumably are within the optimum temperature range for leaf production in broccoli.

The final number of leaves at curd initiation time showed very little variations with sowing dates and, consequently, with temperature regimes. The controlled climate experiment had the same result. This suggests, that in the different cultivars used, the final number of leaves can be a good index of the morphological age of the plant at curd initiation time as it showed good stability with changes in temperature regime. This was also observed in cv Gem (Wiebe, 1975) and in cv Coastal (Gauss and Taylor, 1969a).

In the cultivars, the final number of leaves appeared to be related to the time to curd initiation, the later the time to curd initiation, the more leaves were formed. This agrees with the findings of Salter (1960), Wiebe (1975) and Wurr et al., (1982).

The initiation of the curd was another development event which was found to be strongly influenced by temperature. The variation in the number of days to curd initiation with sowing dates was greatly reduced when number of days was expressed as heat unit summation above a base temperature of 0C.

The growth of the curd from initiation until maturity was best described by a quadratic model as a function of heat unit summation above a base temperature of 3C.

Considering a normal time scale the variation in the total duration from sowing to curd maturity with sowing dates was due to the variation in the two developmental stages: (1) sowing to curd initiation; and (2) curd initiation to maturity. It took more than twice as long for the plants to initiate curd during winter than during summer. The time from curd initiation to maturity was also longest when it coincided with winter. When time was expressed in heat unit summation, variation in the duration of the two developmental events was reduced by about 53 and 52%, respectively. Overall the remaining variation in the total HUS from sowing to curd maturity appeared to be acceptably low (CV = 12.81%). The varietal constants (total number of heat units from sowing to curd maturity for each cultivar) estimated using the HUS model may then be considered acceptable. However, the HUS model did not give good predictability of the crop duration for all sowing dates. Thus, it might be good to consider the constant for each sowing date.

Plant potential for dry matter production varied with sowing dates. Both curd and total dry matter production showed positive correlations with the average heat unit summation per day during each sowing date which suggests that the lower the temperature regime the lower is the potential for dry matter production.

The potential also varied with cultivars. It can be seen that the total amount of dry matter accumulation was dependent upon RGR and upon how long a high RGR could be sustained. Within the cultivars, there was little variation in RGR, however, a high RGR was maintained relatively longer in Fordhook Late so that it produced the most dry matter.

Another important attribute which was found to vary with cultivars was the harvest index. The higher total dry matter production in Fordhook Late did not guarantee a higher yield as it had a low harvest index. Conversely, the higher harvest index of Mercedes did not result to a higher yield as its total dry matter production was lower which may be due to an early drop in RGR. The low harvest index of Fordhook Late may be due to its low NAR during the curd initiation stage relative to that of other cultivars. Curd initiation may represent a critical stage as it is during this time that rapid synthesis of new materials is necessary for the subsequent development of the curd. In the other cultivars a peak in NAR did coincide with the curd initiation stage. This coincidence was, however, less clear in the greenhouse and controlled climate experiment.

It is suggested that in considering yield, it may be desirable to use cultivars with both a high harvest index and a high RGR which can be maintained for a long time.

Dry matter partitioning showed stability with sowing dates and cultivars particularly during the seedling and curd initiation stage. At the curd maturity stage dry matter partitioning varied between cultivars which was mainly due to differences in harvest index.

The greenhouse experiment showed that curd quality (curd depth, curd branching and uniformity of bud maturity) of the different cultivars of broccoli could be affected by high temperature depending upon the stage of plant growth when the treatment was imposed. When imposed before the curd initiation stage, a 1-wk period at 30C did not affect curd quality. When this high temperature was imposed at the early and late curd developmental stages, curd quality was significantly reduced with the reduction being more pronounced at the latter stage. A low temperature treatment of 10C did not affect curd quality regardless of when it was imposed. The different cultivars responded similarly to the treatments although the effect of high temperature was more apparent on Premium Crop, Mercedes and Idol than on Fordhook Late and Shogun.

These effects of high temperature on curd quality were confirmed in the controlled climate experiment. Although the duration of the high temperature treatment was increased to 2 weeks, it still manifested its effects only when imposed after the curd initiation stage. When plants were grown under a continuous high temperature regime, a range of curd morphological abnormalities were observed such as the presence of bracts throughout the surface of the curd, suppression of the growth of the buds and/or irregular elongation of the curd internodes.

It is interesting to note that the effects of high temperature may be confined only on the growth and morphological development of the curd. All the plants, regardless of the temperature treatments, initiated curds and the time to curd initiation was not affected. This suggests that high temperature treatment did not elicit any physiological trigger to hasten, delay or prevent curd initiation in broccoli. Results from other studies are not clear. Gauss and Taylor (1967b) argued that there is no quantitative nor qualitative cold requirement for curd initiation in broccoli while Fujime (1988), Fontes et. al (1967) and Miller et. al (1985) suggested otherwise.

Hardwick (1984) presented evidences that the variations in mass between the component florets in a curd originated at the apical meristem as variations in the timing of primordial initiation. In the present study, high temperature treatment appeared to enhance these variations in the size and weight per floret. The synchrony of the growth of individual florets may have been disrupted, the morphologically-advanced ones tending to grow faster than the younger ones thus forming an irregular or uneven curd surface. Growing the plants under a high temperature regime throughout most of their growth, however, not only enhanced the variation in size of florets but also induced a number of morphological abnormalities. At present, there is nothing in the literature to explain the physiological and biochemical bases of these responses to high temperature.

Chapter 6

Conclusions, General Discussion and Recommendation

6.1 Conclusions and General Discussions

Some basic and practical applications can be considered from the following highlights of the results of the three experiments:

(1) Models to describe growth and development. The modified Richards Function (or the generalized logistic equation) proved satisfactory in fitting primary growth data. The functions fitted enabled the derivation of secondary growth functions or the growth parameters RGR, NAR, LAR, SLW and LWR which were found to be biologically interpretable. In cases where the function could not be used, e.g., in the greenhouse and controlled climate experiment growth data, where the error variance was large and there was not enough curvature towards the end, the second degree polynomial model proved adequate. Varietal differences in the growth parameters were quite consistent regardless of the 2 models (i.e., field experiment vs greenhouse and controlled climate experiment). For a set of treatments in a particular study, however, it is recommended that a single model should be used as the use of more than one model may result in the derivation of secondary functions having different time trends and may no longer be biologically meaningful (Causton et al., 1978; Hurd, 1977). A quadratic polynomial model also best described the growth of the curd (increase in diameter) while a linear model was applicable for the rate of leaf production.

(2) Temperature as a major environmental component determining the growth and development of broccoli. The use of heat unit system, which takes account of the temperature differences over different sowing dates, reduced a major proportion of the variation in the growth and development processes in broccoli including rate of dry matter accumulation, leaf production, time to curd initiation, curd growth and time to curd maturity. This may justify the use of the heat unit system in formulating predictive models for the maturity period of broccoli.

(3) Growth and development in relation to the threshold temperature. Growth as opposed to developmental events in broccoli may proceed at different base temperatures. Rate of total dry matter accumulation and curd expansion which can be classified simply as growth processes appeared to be dependent on a heat unit summation above a base temperature of 3C while leaf and curd initiation which are developmental events required lower base temperatures (-2C and 0C, respectively). This was supported by Salter (1960). However, the theoretical soundness of relating heat units to growth and development appear questionable as, for instance, heat units are not a form of available energy for plants (Wang, 1960).

(4) The growth parameters as indicators of crop performance. The relative growth rate parameter provided a good index of the growth rates of the plants as affected by sowing dates and cultivar. In the field experiment RGR was expressed as a function of heat units and not ordinary time. As this takes account of the temperature differences over different sowing dates, the remaining variation in RGR, which was more evident at the early developmental state, could then be due to other external factors but may include the effect of temperature regime per se (daily average temperature as opposed to accumulated heat units). This variation may also be explained by the changes in the other growth parameters as the different growth parameters are interrelated. RGR is dependent upon NAR and LAR, NAR on SLW, and LAR on SLW and LWR. The trends of these individual parameters with sowing dates were not very clear although there were some tendencies for winter grown plants to have lower initial LAR and SLW and a higher NAR. The effects that the environment has directly on each growth parameter thus contributes to the variation in RGR. Generally, however, there were very little differences in RGR with sowing dates particularly during curd initiation and maturity stages. It may be more meaningful then to express RGR on a heat unit basis as this may enable comparisons of the growth rates of a set of plants grown at different times of the year.

In the controlled climate experiment the low RGR and NAR of plants under 30C regime suggests that 30C may already be beyond the optimum temperature range for the normal growth of broccoli.

Moreover, the three experiments showed that the different growth parameters were also good indicators of the growth performance of the different cultivars.

(5) Curd initiation and maturity. The period from sowing to curd initiation and from curd initiation to maturity are two important developmental stages in broccoli which are temperature dependent. The duration of these stages progressively becomes shorter with increasing temperature regime, but up to a maximum as demonstrated in the controlled climate experiment.

The different cultivars used may not have any cold requirement for curd formation as all the plants developed curd regardless of any temperature treatment.

(6) The use of the heat unit system in predicting time to curd maturity. The applicability of the use of the heat unit system in predicting the time to curd initiation and maturity of broccoli has been pointed out. The data (HUS varietal constants) alone may be of direct value to the growers or it may form part of bigger and more complex models such as that formulated by Marshall and Thompson (1987b).

(7) Temperature and curd quality. Along with yield, curd quality is a very important attribute in broccoli as it determines the value of the crop in the market. Results show that at least one week exposure of the plants to high temperature during the curd developmental period can reduce the quality of the curds. Before initiation, exposure to high temperature had no effect. In the field experiment there was no apparent reduction in curd quality as temperature In some places where temperature can be very high during certain times of the year scheduling of sowing can be critical. Early spring or late summer sowings may be advantageous.

(8) The effect of temperature and genotype on the economic yield in relation to harvest index and the growth parameters. The observed variation in the economic yield with sowing dates may be related largely to differences in plant potential for dry matter accumulation as harvest index was quite stable. In the different cultivars the differences in harvest index was as important. Plant potential for dry matter accumulation may be determined by RGR and upon how long a reasonably high RGR is maintained. In the case of the different cultivars variation in total dry matter accumulation was due more to the latter as variation in RGR was not very apparent. There was not any clear association either, between yield and the other growth parameters, although a low NAR during curd initiation may be related to a low harvest index as was found in Fordhook Late.

Future improvements in yield potential may be brought about by increasing growth or photosynthetic rates or by further increasing the harvest index (Gifford and Evans, 1981). The specific leaf weight might be a good character to consider in breeding for high photosynthetic rates as it has been shown to correlate well with CO_2 exchange rate (Barnes et. al, 1969 and Dornhoff and Shibles, 1976). Intergenotypic variations in SLW at a particular developmental stage can show stability of ranking from season to season as was found in the field experiment and by Lugg and Sinclair (1979). Moreover, Song and Walton (1975) showed that SLW can be heritable. In relation to leaf area development, Gifford and Evans (1981) proposed that a sound strategy might be to select cultivars which expand large thin leaves (high SLW) early in the season and then thick leaves (low SLW) after the canopy intercepts all the light. However, past attempts in breeding for high CO_2 exchange rate or improving it by selection for its component processes have been generally disappointing (Wilson, 1978). In the absence of genetic improvements in photosynthetic and growth rates, it may be good to aim for further increases in harvest index. Varietal differences in harvest index have been shown in the present experiments and appeared to be quite stable with environmental changes.

6.2 Recommendations

The three experiments raise a number of points important for future research in broccoli. These are summarised as follows:

(1) Although temperature was seen as the dominant environmental factor affecting different aspects of growth and development of broccoli, results of the experiments also suggest the possible contribution of other environmental components. In the field, there is little that can be done to modify the environment to suit research needs. Thus, a study of the independent and the interactive effects of different environmental factors can only be done using several controlled climate experiments. Given the necessary facilities, a host of questions concerning the physiological and morphological responses of broccoli to temperature, to other environmental components and to their interaction may be answered. In particular, a detailed study on the pattern of dry matter accumulation, earliness to curd initiation and maturity, leaf production, and yield potential as they relate to environment factors may be important considerations.

(2) The different growth parameters calculated on the basis of temperature (cumulative heat unit summation) may be improved by incorporating the additive effect of other environmental factors particularly solar radiation. This should, however, entail complex mathematical and statistical analysis (e.g., multiple non-linear regression).

(3) The effect of high temperature on the curd quality of broccoli needs to be studied further. The present study simply indicates that high temperature reduces curd quality of broccoli. It may be useful to determine the temperature level and treatment duration at which curd quality starts to be affected.

(4) Information on the mechanism by which high temperature affects the morphological development of the curd may also be important. Clearly, this needs detailed anatomical, physiological or biochemical studies.

(5) To determine the validity of the HUS-model to predict the curd maturity of broccoli several time or location trials should be done. The model formulated and applied by Marshall and Thompson (1987a, 1987b) involved only one cultivar. The present study reveals some varietal differences, thus, future models should include as many important cultivars as possible.

Literature Cited

Anon. (1954). Tables for the evaluation of accumulated temperature. (Form 3300). Air Ministry, London.

Arnold C.Y. (1959). The determination and significance of the base temperature in a linear heat unit system. J. Amer. Soc. Hort. Sci. 74,430-45.

Austin R.B. (1964). A study of the growth and yield of red beet from a long-term manurial experiment. Ann. Bot. 28, 638-46.

Austin R.B., Nelder, J.A. and Berry G. (1964). The use of a mathematical model for the analysis of manurial and weather effects on the growth of carrots. Ann. Bot. 28, 153-61.

Barnes, D.K., Pearce, R.B., Carlson, G.E., Hart, R.H. and Hanson, C.H. (1969). Specific leaf weight differences in alfalfa associated with variety and plant age. Crop Sci. 9, 421-23.

Bernier, G. (1988). The control of floral evocation and morphogenesis. Ann. Rev. Plant Physiol. 39, 175-219.

Brown, D.M. (1975). Ontario Heat Units, AGDEX, 111/31, Ontario Min. of Agric. and Food, Canada.

Bussell, W.T. (1984). Green sprouting broccoli cultivar testing. N.Z. Commercial Grower. Jan-Feb. pp 33.

Causton, D.R. (1983). A Biologist's Basic Mathematics. Ed. Arnold Ltd., London. 216 p.

Causton, D.R., Elias, C.O. and Hadley, P. (1978). Biometrical Studies of Plant Growth. I. The Richards Function and its application in analysing the effects of temperature on leaf growth. Plant, Cell and Environ. 1, 163-84.

Chowings, J.W. (1974). Vegetable variety performance trials technique - Brassica crops. J. Instit. Agric. Bot. 13, 168-85.

Coligado, M.C. and Brown, D.M. (1975). A bio-photo-thermal model to predict tassel-initiation-time in corn (Zea mays L.). Agric. Meteorol. 15, 11-31.

Dornhoff, G.M. and Shibles, R.M. (1976). Leaf morphology and anatomy in relation to CO2 exchange rate of soybean leaves. Crop Sci. 16, 377-81.

Eguchi, T. (1947). A study of flower bud differentiation in cauliflower. J. Hort. Assoc. Japan. 16, 249-50

Elias, C.O. and Causton, D.R. (1975). Temperature and the growth of Impatiens parviflora DC. New Phytol. 75, 495-505.

Erickson, R.O. and Michellini, F.J. (1957). The plastochron index Amer. J. Bot. 44, 297-3

Evans, L.T. (1975). The physiological basis of crop yield. In: Crop Physiology, Some Case Histories (L.T. Evans, ed.) pp 327-550. Camb. Univ. Press.

Evans, L.T. (1969). The Induction of Flowering. Melbourne: Macmillan

Evans, L.T. and Dunstone, R.L. (1970). Some physiological aspects of evolution in wheat. Aust. J. Biol. Sci. 23, 725-41

Evans, G.C. and Hughes, A.P. (1961). Plant growth and the aerial environment. Effect of artificial shading on Impatiens parviflora. New Phytol. 60, 150-60.

Feher, P.K. (1986). The role of broccoli in nutrition. Hort Abs. 56(12), 1030.

Ferguson, H., Eslick, R.F., and Aase, J.K. (1973). Canopy temperature of barley as influenced by morphological characteristics. Agron. J. 65, 425-28

Fontes, M.R. and Ozbun, J.L. (1972). Relationship between carbohydrate level and floral initiation in broccoli. J. Amer. Soc. Hort. Sci. 97(3), 346-48.

Fontes, M.R., Ozbun, J.L. and Sadik, S. (1967). Influence of temperature on initiation of floral primordia in green sprouting broccoli. Proc. Amer. Soc. Hort. Sci. 91, 315-320.

Friend, D.J.C. (1965). Interaction of red and far-red light with the vernalization process in winter rye. Can. J. Bot. 43, 161-70.

Friis, E., Jensen, J. and Mikkelsen, S.A. (1986). Temperature sum models for predicting the date of harvest of vining peas. Acta Hort. 198, 227-33.

Fujime, Y. (1988). A difference of Response to low temperature between cauliflower and broccoli. Acta Hort. 218, 141-52.

Fujime, Y. and Hirose T. (1981). Studies on thermal conditions of curd formation and development in cauliflower and broccoli. I. Effects of low temperature treatment of seeds. Hort. Abst.

Fujime, Y. and Hirose T. (1982). Studies on the thermal requirements for curd formation and development in cauliflower and broccoli. II. Effects of diurnal variation of temperature on curd formation. Hort. Abst. 52(6), 361.

Gasser, C.S., Smith, A.G., Sachs, K., B. McCormick S., and Hinchee, M.A. (1987). Isolation and characteristization of developmentally regulated sequences from tomato flowers. J. Cell Biochem. Suppl. IIB, 2.

Gauss, J.F. and Taylor G.A. (1969a). Environmental factors influencing reproductive differentiation and the subsequent formation of the inflorescence of Brassica oleraceae L. var Italica Plenck, cv Coastal. J. Amer. Soc. Hort. Sci. 94, 105-08.

Gauss, J.F. and Taylor G.A. (1969b). A morphological study on the time of reproductive initiation and subsequent formation of the inflorescence of B. oleraceae L. var Italica Plenck, cv Coastal. J. Amer. Soc. Hort. Sci. 94, 105-8.

Geelen, J.A. and Greaves, L.A. (1984). Broccoli variety evaluation. N.Z. Commercial Grower. Jan-Feb. pp 33.

Gifford, R.M. and Evans L.T. (1981). Photosynthesis, carbon partitioning and yield. Ann. Rev. Plant Phys. 32, 485-509.

Gott, M.B., Gregory F.G. and Purvis O.N. (1955). Studies on the vernalization of cereals. XIII. Photoperiodic control of stages of flowering between initiation and ear formation in vernalized and unvernalized Petkus winter rye. Ann. Bot. N.S. 19, 87-126.

Gray, D. and Morris, G.E.L. (1978). Seasonal effects on the growth and time to maturity of lettuce. J. Agric Sci. Camb. 91, 523-9.

Hanson, W.D., and Grier, R.E. (1973). Rates of electron transfer and of non cyclic photophosphorylation for chloroplasts isolated from maize populations selected for juvenile productivity and in leaf widths. Genetics. 75, 247-37.

Hardwick, R.C. (1984). Sink development, phyllotaxy and dry matter distribution in a large infloresence. Plant Growth Regulation. 2, 393-405.

Hart, R.H., Pearce, R.B., Chatterton, N.J., Carlson, G.E., Barnes, D.K. and Hanson C.H. (1978). Alfalfa yield specific leaf weight, CO_2 exchange rate and morphology. Crop Sci. 18, 649-53.

Ho, L.C. (1979). Regulation of assimilate translocation between the leaves and fruits in the tomato. Ann. Bot. 41, 779-87.

Ho, L.C. (1988). Metabolism and compartmentation of imported sugars in relation to sink strength. Ann. Rev. Plant Physiol. 39, 355-78.

Hughes, A.P. (1965). Plant growth and the aerial environment. VIII. The effects of (a) blue light and (b) low temperature on Impatiens parviflora. New Phytol. 64, 323.

Hunt, R. (1982). Plant Growth Curves. The Functional Approach to Growth Analysis. Ed. Arnold Ltd., London.

Hunt, R. and Lloyd, P.S. (1987). Growth and partitioning. New Phytol. 106, 235-49.

Hunt, R. and Nicholls A.O. (1986). Stress and the coarse control of root-shoot partitioning in herbaceous plants. Oikos 47, 149-58.

Hurd, R.G. (1977). Vegetative plant growth analysis in controlled environments. Ann. Bot. 41, 779-87.

Kamalay, J.C. and Goldberg, R.B. (1980). Regulation of structural gene expression in tobacco. Cell. 19, 935-46.

Kaplan, S.L. and Koller, H.R. (1977). Leaf area and CO_2 exchange rate as determinants of the rate of vegetative growth in soybean plants. Crop Sci. 17, 35-38.

Kato, T. (1964). On flower head formation and development in cauliflower. I. Ecological studies on flower head formation and development. J. Jap. Soc. Hort. Sci. 33, 316-26.

Kish, A.J., Ogle, W.L. and Loadholt, C.B. (1972). A prediction technique for snap bean maturity incorporating soil moisture with the heat unit system. Agric. Meteorol. 10, 203-210.

Kristensen, S., Friis, E., Henrikssen K. and Mikkelsen, S.A. (1986). Application of temperature sums in the timing of crisp lettuce. Acta Hort. 198, 217-25.

Leshem, Y., and Steiner, S. (1968). Effect of gibberellic acid and cold treatment on flower differentiation and stem elongation of cauliflower (B. oleraceae var botrytis). Israel J. Agric. Res. 18,133-34.

Lintilhac, P.M. (1974). Differentiation, organogenesis and the tectonics of cell wall orientation. II. Separation of stresses in a two dimensional model. Amer. J. Bot. 61(2), 230-37.

Lugg, D.G. and Sinclair, T.R. (1979). A survey of soybean cultivars for variability in specific leaf weight. Crop Sci. 19, 867-92.

McCown, R.L. and Peterson, M.L. (1964). Effect of temperature and age of plants on flowering in Lolium perenne. Crop Sci. 4, 388-91.

McErlich, A.F. (1984). Broccoli varieties. N.Z. Commercial grower. Jan.-Feb., pp 83.

Magnifico, V., Lattanzio, V and Sarli, G. (1979). Growth and nutrient removal by broccoli. J. Amer. Soc. Hort. Sci. 104(2), 201-03.

Marshall, B. and Thompson, R. (1987a). Model of the influence of temperature and solar radiation on the time to maturity of calabrese, Brassica oleraceae var. Italica. Ann. Bot. 60, 513-19.

Marshall, B. and Thompson, R., (1987b). Application of a model to predict the time to maturity of calabrese (Brassica oleraceae). Ann. Bot. 60, 521-29.

Miller, C.H., Konsler, T.R. and Lamont W.J. (1985). Cold stress influence on premature flowering of broccoli. Hort. Sci. 20(2), 193-95.

Morelock, T.E., Peerson, M. and Motes, D. (1982). Broccoli trials in Arkansas. Arkansas Farm Research 1(31), 12-13.

Murthy, K.K. and Singh, M. (1979). Photosynthesis, chlorophyll content and ribulose diphosphate carboxylase in relation to yield in wheat genotypes. J. Agric. Sci. Camb.93, 7-11.

Nelder, J.A. (1961). The fitting of a generalization of the logistic curve. Biometrics 17, 89-110.

Nelder, J.A., Austin, R.B., Bleasdale, J.A. and Salter, P.J. (1960). An approach to the study of yearly and other variations in crop yields. J. Hort. Sci. 35, 73.

Nichols, M.A. (1970). Growth Studies with Lettuce. PhD Thesis. Massey University.

Nichols, M.A. (1972). The effects of fertilizers on the growth of lettuce in New Zealand. Hort. Res. 12, 107-18.

Ragan, P. (1983). The effect of temperature on the growth and development of peas. PhD thesis. Massey U., New Zealand.

Rajan, A.K., Betteridge, B. and Blackman, G.E. (1973). Differences in the interacting effects of light and temperature on growth of four species in the vegetative phase. Ann. Bot. 37, 287-316.

Richards, F.J. (1959). A flexible growth function for empirical use. J. Exp. Bot. 10, 290-300.

Richards, F.J. (1969). The quantitative analysis of growth. In: Plant Physiology - A Treatise. VA. Analysis of growth behaviour of Plants and their organs. Ed. F.C. Steward. pp 1-76. Acad.Press, London.

Sadik, S. (1962). Morphology of the curd of cauliflower. Amer. J. Bot. 49, 90-297.

Sadik, S. (1967). Factors involved in curd and flower formation in cauliflower. Amer. J. Bot. 49, 252-59.

Sadik, S. and Ozbun, J.L. (1967). Histochemical changes in the shoot tip of cauliflower during floral induction. Can. J. Bot. 45(7), 955-60.

Sadik, S. and J.L. Ozbun. (1968). The association of carbohydrate changes in the shoot tip of cauliflower with flowering. Plant Physiol. 43, 1696-1698.

Salter, P.J. (1969). Studies in crop maturity in cauliflower. I. Relationship between the times of curd initiation and curd maturity of plants within a cauliflower crop. J. Hort. Sci. 44, 129-40.

Salter, P.J. (1960). The growth and development of early summer cauliflower in relation to environmental factors. J. Hort. Sci. 35, 239-48.

Salter, P.J. and James, J.M. (1974). Further studies on the effects of cold treatment of transplants on crop maturity characteristics of cauliflower crop. J. Hort. Sci. 49, 329-342.

Salter, P.J. and Ward, R.J. (1972). Studies on crop maturity in cauliflowers. III. Effects of cold treatment and certain growth regulators on crop maturity characteristics and yield. J. Hort. Sci. 47, 57-65.

Skapski, A. and Oyer, E.B. (1964). Influence of pre transplanting variables on the growth and development of cauliflower plants. Proc. Amer. Soc. Hort. Sci. 85, 374-85.

Snyder, F.W. and Carlson, G.E. (1984). Selecting for partitioning of photosynthetic products in crops. Adv. Agron. 37, 147-72.

Song, S.P. and Walton, P.D. (1975). Inheritance of leaflet size and specific leaf weight in alfalfa. Crop Sci. 15, 649-52.

Swarrup, W. and Chatterjee, S.S. (1972). Origin and genetic improvement of Italian cauliflower. Econ. Bot. 26, 381-93.

Tanaka, A., Kawano, K., and Yamaguchi, J. (1966). Photosynthesis respiration and plant type of the tropical rice plant. IRRI. Tech. Bull. No. 7.

Thomas, F.H., Lester, J.N. and Salter, P.J. (1972). Hormonal changes in the stem apex of the cauliflower plant in relation to curd development. J. Hort. Sci. 47, 449-55.

Treharne, K.J. (1972). Biochemical limitation to photosynthetic rates. In: Crop Processes in Controlled Environments. Ed. A.R. Rees. pp 285-303. New York. Acad. 391 pp.

Venus, J.C. and Causton, D.R. (1979). Plant growth analysis: The use of the Richard's function as an alternative to polynomial exponentials. Ann. Bot. 43, 623-32.

Wang, J.Y. (1960). A critique of the heat unit approach to plant response studies. Ecology. 41(4), 785-90.

Wareing, P.F. and Patrick J. (1975). In: Photosynthesis and Productivity in Different Environments. (J.P. Cooper, ed.), London, Camb. Univ. Press., pp 481-99.

Warren-Wilson, J. (1966a). High net assimilation rates of sunflower plants in an arid climate. Ann. Bot. 30, 745-51.

Warren-Wilson, J. (1966b). Effect of temperature on net assimilation rate. Ann. Bot. 30, 745-51.

Wellington, P.S. (1954). The handling of broccoli - factors affecting quality and time. Agr. (London). 61, 431-34.

Wiebe, H.J. (1975). The morphological development of cauliflower and broccoli cultivars depending on temperature. Scientia Hort. 3, 95-101.

Wills, R.B.H., Lim, J.S.K. and Greenfield H. (1984). Composition of Australian Foods. 23 Brassica vegetables. Hort. Abst. 55(3), 192.

Wilson, D. (1978). Dark respiration. Welsh Plant Breed. Stn. (Aberystwyth) 1977. Ann. Rep. pp 157-58.

Wurr, D.C.E., Akehurst, J.M., and Thomas, T.H. (1981). A hypothesis to explain the relationship between low temperature treatment, gibberellin activity, curd initiation and maturity of cauliflower. Scientia Hort. 15, 321-30.

Wurr, D.C.E. and Fellows, J.R. (1984). The growth of three crisp lettuce varieties from different sowing dates. J. Agric. Sci. Camb. 102, 733-45.

Wurr, D.C.E. and Kay, R.H. (1981). Studies of the growth and development of winter heading cauliflowers. J. Agric. Sci. Camb. 97, 409-19.

Wurr, D.C.E., Fellows, J.R. and Crisp, P. (1982). Leaf and curd production in cauliflower varieties cold treated before transplanting. J. Agric. Sci., Camb. 99, 425-32.

Zeevart, J.A.D., Brede, J.M. and Cetas, C.B. (1977). Translocation patterns in Xanthium in relation to long day inhibition of flowering. Plant Physiol. 60, 747-53.

Appendix 1

A. Compost ingredients for the germination medium (all experiments)

Ingredient	Amount (kg/m^3)
Potassium nitrate	1.00
Single superphosphate	2.25
Ground chalk or limestone	2.25
Ground magnesium limestone	1.25
Fritted trace elements [a]	0.40

B. Fertilizer mix for the growing medium (greenhouse experiment).

Ingredient	Amount (kg/m^3)
Osmocote^R (3-4 mo)	2.20
superphosphate	1.50
lime	1.50
dolomite	3.00
fritted trace elements [a]	0.60

[a] comprising Fe (8%), Mn (7.5%), Zn (7.0%), Cu (3.0%), B (3.0%), Mo (0.2%)

Appendix 2

Soil Classification: Manawatu fine sandy loam

Some soil properties (0 - 20 cm) prior to fertilizer application:

organic matter content - 3.7%

total N - 0.13%

pH - 6.4

cation exchange capacity (1 M NH_4OAC, pH 7) - 20.12 meq./ 100 g soil

K (NH_4OAC extractable) - 65 ug/g soil

P (Olsen) - 65 ug/g soil

NH - N (2M KCl extractable) - 70 ug/g soil

NO - N (2M KCl extractable) - 42 ug/g soil

Mineralizable N (aerobic incubation) - 2ug/g soil

Source: Bonoan, R.R. (1989). Unpublished Research, Dept. of Soil Science, Massey U.

Appendix 3

Spray Programme Used in the Field Experiment

Use	Pesticide	Amount/Frequency of Appn.
Caterpillars/ Aphids	Orthene^R	100 g/100 l H_2O; 2-wk intervals after transplanting
	Lannate^R	1.5 - 2.0 l/ha; 2-wk intervals after transplanting
Downy mildew	Ridomil^R	2 kg/100 l H_2O; 2-wk intervals before transplanting
	Euparen^R	2 kg/600 l H_2O; 2-wk intervals after transplanting
Black Rot	Copper oxychloride (Recop^R)	400-500 g/l H_2O; 2-wk intervals after transplanting

Appendix 4

The error mean square and the parameters of the logistic regression of total dry matter accumulation (common to all sowing dates and cultivars) against heat unit summation at different base temperatures.

Base Temp. (^{o}C)	EMS	Regression Parameters			
		a	b	k	d
0	0.512	5.55	-10.31	0.0073	0.729
1	0.476	5.56	-10.30	0.0079	0.731
2	0.442	5.61	-10.34	0.0088	0.684
3	0.393	5.59	-10.31	0.0096	0.693
4	0.458	5.55	-10.24	0.0107	0.694
5	0.542	5.49	-10.14	0.0121	0.667

Appendix 5

Heat unit summation at curd initiation time for the different sowing dates calculated at different base temperatures.

Sowing Date	Heat Unit Summation						
	Base temp. (^{O}C)						
	-2	-1	0	1	2	3	4
18 Sept	994	927	866	792	725	658	593
19 Nov	1311	1267	1186	1136	1071	1006	926
17 Jan	1262	1199	1121	1070	1007	944	882
21 March	1055	982	914	840	767	700	626
22 May	1480	1347	1189	1092	967	834	713
21 July	1200	1104	1010	915	825	728	638
CV (%)	14.52	14.39	13.28	14.80	15.72	17.32	19.37

Appendix 6

Standard errors derived from the analysis of variance of the different growth parameters between the different broccoli cultivars (Greenhouse Experiment).

PARAMETER	STANDARD ERROR				
	Days from Sowing				
	28	42	56	70	84
RGR	1.18 ^{ns}	0.80 ^{ns}	0.43 ^{ns}	0.12 *	0.38 ^{ns}
NAR	0.80 ^{ns}	0.38 ^{ns}	0.35 ^{ns}	0.29 ^{ns}	0.52 ^{ns}
LAR	28.51 ^{ns}	6.90 *	5.28 ^{ns}	8.05 ^{ns}	10.36 ^{ns}
SLW	29.69 ^{ns}	12.88 *	11.51 ^{ns}	8.47 *	11.63 ^{ns}
LWR	0.04 ^{ns}	0.01 ^{ns}	0.01 ^{ns}	0.02 ^{ns}	0.03 ^{ns}

^{ns} non significant

* significant (5%level)

Appendix 7

The Climate Room

The climate room measured 2.75 x 2.75 meters, with an effective growing area of 2 x 2 meters. Conditioned air from ducting along the top of each side wall was passed over the plant trolleys and was recycled via a false floor to the machinery chamber at the rear of each room. The artificial light was supplied from each source in the light rig located in the loft region above each room. Radiation from the rig was passed through a temperature controlled 2.5 cm waterscreen heat-barrier supported on a sheet of plate glass. Mirroring on the walls of each room gave a more even spread of light over the plant growing area and decreased the light gradient from the light loft.

Appendix 8

Standard errors derived from the analysis of variance of the different growth parameters as influenced by temperature regime and cultivars.

FACTOR/ PARAMETER	STANDARD ERROR			
	Days from Sowing			
	21	35	47	63
Temperature Regime				
RGR	0.40 **	0.20 **	0.09 **	0.25 ns
NAR	0.29 *	0.37 **	0.21 **	0.28 ns
LAR	1.46 ns	3.50 *	4.06 *	2.64 **
SLW	2.29 ns	5.37 **	6.52 **	5.91 **
LWR	0.007 ns	0.006 ns	0.007 ns	0.007 ns
Cultivar				
RGR	0.70 ns	0.40 ns	0.11 ns	0.37 ns
NAR	0.81 ns	0.38 ns	0.13 ns	0.24 ns
LAR	9.02 ns	3.97 ns	1.01 ns	0.69 ns
SLW	11.94 ns	7.41 ns	4.52 ns	0.98 ns
LWR	0.009 ns	0.013 ns	0.012 ns	0.005 ns

Appendix 9

A model to predict curd maturity in broccoli
(Marshall and Thompson, 1987a).

The model assumes that the crop progresses towards maturity when air temperature is above a base temperature. This period is referred to as the active duration. Considering this active duration, a multiple linear regression model

$$R_a - \bar{\bar{R}}_a = a(\bar{T}_e - \bar{\bar{T}}_e) + b(\bar{S} - \bar{\bar{S}}) + E$$

is used where R_a is the average rate of progress towards maturity (reciprocal of total crop duration), $\bar{T}_e$ and $\bar{S}$ are the effective temperature difference and solar radiation averaged over the active duration of the crop, a and b are the corresponding regression coefficients, and E is the error term. $\bar{\bar{R}}_a$, $\bar{\bar{T}}_e$ and $\bar{\bar{S}}$ are the grand means of the variates R_a, $\bar{T}_e$, and $\bar{S}$, respectively. The regression is first fitted using temperature alone and then solar radiation is added as a further explanatory variate.

Appendix 10

Proportion of variance in reciprocal total duration from sowing to curd maturity in broccoli accounted for by temperature (HUS; Tb=3C) and sunshine hours using Model B[1].

CULTIVAR	PROPORTION OF VARIANCE (%)[2]	
	Temperature	Sunshine Hours
Premium Crop	82.17	11.32
Mercedes	79.87	13.55
Idol	77.66	13.91
Fordhook Late	78.74	12.58

[1] refer to Section 2.1.11

[2] variance proportion = sum of squares due to the factor / total sum of squares

Appendix 11

Modified Hoagland's Solution

Stock Solution A:	Amount (g/100 l)
Calcium nitrate $Ca(NO_3)_2 \times 4H_2O$	14,759.5
Sequestrene 10% DTPA NaFe	520.0
Stock Solution B:	
Potassium dihydrogen phosphate KH_2PO_4	1,701.0
Potassium nitrate KNO_3	6,319.5
Magnesium sulfate $MgSO_4 \times 7H_2O$	6,162.0
Micronutrients:	
Boric Acid H_3BO_3	35.75
Manganese chloride $MnCl_2 \times 4H_2O$	22.62
Zinc sulphate $ZnSO_4 \times 7H_2O$	2.75
Cupric sulphate $CuSO_4 \times 5H_2O$	1.00
Sodium molybdate $Na_2MoO_4 \times {}_2H_2O$	0.335
Potassium chloride KCl	78.75

pH of final solution = 6.5 - 7.5   Full strength: 8ml/100 l of stock solution

Source: Climate Laboratory, Plant Physiology Division, DSIR, Palmerston North.