The Effect of Temperature on the Rate of Shoot Development in the Raspberry (Rubus idaeus L.) cultivar "Autumn Bliss"

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ABSTRACT

Temperature effects on the rate of growth and development of cv. "Autumn Bliss" were investigated. The stool and root system are perennial and produce buds which arise annually as populations of shoots. Axillary buds produced sequentially by the apical meristem are hierarchical with respect to their position on the cane. The timing of lateral development, vigour and, consequently, fruiting, depends on the position of the originating axillary bud with respect to the apical meristem. Shoot elongation is determinate on terminal flower bud initiation. Node number was therefore thought to be an important variable with which to model the effect of temperature on shoot development and architecture. Chill-treated stool and root systems of pot-grown plants (5°C for 7, 21 and 35 days and grown on in a glasshouse), when compared with controls showed no absolute requirement for vernalization. Pot-grown plants, graded according to the fresh weight of the mother plant and grown in glasshouse, polytunnel and outside plots, exhibited significant differences in cropping. Temperature determined the rate of shoot development, so that the cropping season was earlier and more contracted for glasshouse plants. Grading affected rate of establishment, initial shoot population and amount of vegetative growth. Pot-grown plants held at constant day/night temperatures of 10, 15, 20 and 25°C up to terminal flower primordia appearance showed significant differences in the rate of node production, but not in the maximum node number attained by shoots. Rate of lateral development and yield of every fifth node was investigated. Suitable functions were fitted to model the changes in the rate of node production at emergence, terminal flower primordia appearance and cessation of shoot elongation, using day degree accumulation. This was in order to predict phenological events in the first shoot to emerge for each plant and its effect on subsequent plant development.

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Abbreviations and Symbols

1) Abbreviations:

Chemical names;

"Benlate" - ICI, contains Benomyl.

"Torque" - ICI, wettable powder containing 50% w/w Fenbutatin Oxide.

NPK - N:P:K ratio of Nitrogen:Phosphorus:Potassium in liquid fertiliser.

NAA - α - Naphthaleneacetic acid.

IAA - Indoleacetic acid.

Others;

LSD - least significant difference.

sed - standard error of the differences of the means.

sed* - standard error of the differences of the means with the maximum and minimum numbers of replicates.

se - standard error of the population sample.

P - probability that the responses resulting from different treatments are not significantly different.

%cv - coefficient of variation.

ns - no significant difference between treatments.

PAR - photosynthetically active radiation (μmol m^{-2} s^{-1}).

f - fraction of incident PAR absorbed by the canopy (μmol m^{-2} s^{-1}).

Stages of development;

P - planting.

E - emergence.

TPC - appearance of the terminal floral primordia complex.

TF - point at which, i) the terminal flower bud is distinct and hence ii) the number of nodes in the TPC is definitive ≡ "green bud" stage.

BR - first berry ripe (≡ TB).

TB - terminal berry ripe.

T_1 - T_4, time to each stage E, TPC, TF and BR respectively (days).

T_1 = P → E, T_2 = P → TPC, T_3 = P → TF, T_4 = P → BR.

H_1 - H_4, temperature-sum for each stage of development (day°C).

H_1 = P → E, H_2 = E → TPC, H_3 = TPC → TF, H_4 = TF → BR.

Symbols for models:

General;

W_0 - fresh weight of mother plant (g).

d_0 - mean cane diameter of mother plant canes (taken at 4cm above soil level) (cm).

LD - lamina dimensions (cm^2 = length (cm) x breadth (cm) of leaf lamina).

L_A - actual leaf area (cm^2).

k_0 - temperature-sum constant.

T_0 - base temperature, T_2 - upper threshold temperature (°C).

ΔN - rate of node production (nodes per day).

N_e - node number of shoot at emergence (nodes).

t_e - time to emergence (days).

Richards model and Logistic model:

t - time (days).

h - temperature-sum from planting (day°C).

N - node number of shoot (nodes).

A - maximum number of nodes produced per shoot (nodes).

n - defines the shape of the curve.

b,k - rate constants of node production (nodes per day/ nodes per day°C).

n_0 - fitted node number at **E.**

n_1 - fitted node number at t_2.

t_1, t_3 - points of maximum rate of change of node production (days).

t_2 - point of maximum rate of node production (days).

h_1, h_3 - temperature-sum for points of maximum rate of change of node production (day°C).

h_2 - temperature-sum for the point of maximum rate of node production (day°C).

CHAPTER 1
THE PHENOLOGY OF CULTIVAR "AUTUMN BLISS"

1.1 INTRODUCTION

The object of this research is to produce a model of shoot development for the autumn-fruiting raspberry cultivar "Autumn Bliss", in order to relate the rate of shoot development to the timing of flower initiation and to study its effect on yield.

To gain an understanding of the steps leading to cane maturity in autumn-fruiting cultivars, the aim of this chapter is to describe and define the phases of shoot development specific to cv. "Autumn Bliss". This cultivar was bred at East Malling Research Station, from complex parentage (including *Rubus articus* L.) and released in 1983 (Jennings, 1988).

The biennial life cycle of raspberry canes (*Rubus idaeus* L.) has been described in detail by Williams and Hudson (1956), Hudson (1959), Williams (1959a) and Hudson and Williams (1961). Williams and Hudson (1956) divided the growth cycle into three major phases:

i) The initiation of buds on raspberry roots and their subsequent elongation to the soil surface, ii) the growth of the vegetative shoot in its first year and iii) the production of flowers on lateral shoots followed by fruit development and death of the cane in the second year.

Hudson and Williams (1961) expanded these into nine phases:

i) Initiation of a root bud; ii) subterranean sucker; iii) emergent sucker; iv) first winter dormancy; v) shoot elongation; vi) cessation of vegetative growth and initiation of flower buds (anomalous phase 6; tip flowering); vii) breaking dormancy of flower buds; viii) flowering and fruiting- (anomalous phases 5 - 8; flowering on new shoots); ix) senescence and death.

Floral initiation in summer-fruiting cultivars begins in late autumn and continues in the following spring. Autumn-fruiting cultivars, in contrast, initiate flowers and fruit in the first year. The timing of flower initiation is genetically

determined and forms the basis for selection of autumn-fruiting cultivars (Jennings, 1988). As cv. "Autumn Bliss" crops earlier than other autumn-fruiters this has two implications:

i) Cropping is completed in the first year, thus canes are annual not biennial.

ii) Cropping occurs in late summer, not autumn. Its classification as an autumn-fruiting cultivar seems inappropriate. This aspect will be studied in Chapter 3.

1.2 BUD FORMATION ON THE MOTHER PLANT

The essential perennating organ in *Rubus* is the stem base or stool and attached root system (composed entirely of juvenile tissue) from which arises annually a population of shoots. Annual growth is initiated by the formation of basal axillary buds on the stem base, at or below the soil surface, in what has been termed the "replacement zone" (Hudson, 1959; Williams, 1959a). In addition root suckers expand from root buds (Figure 1.1A). The shoots formed from these buds have been termed "stool canes" and "spawn canes" (Jennings, 1966).

Little is known about factors influencing the timing and conditions in which these latter buds form. In studies made on shoot production from root cuttings, root buds were shown to arise adventitiously on most roots throughout the year (Hudson, 1954; Hudson, 1959). However, elongation of these buds occurred only during the "on" season (September - April); this applied to summer-fruiting and autumn fruiting cultivars alike (Hudson, 1956).

Basal buds remained unexpanded until the senescence of the parent cane, while root buds expanded throughout shoot development, in plants comprised of a single rooted cutting (Williams, 1959a). They therefore appear to be under the control of the apical meristem (Williams, 1959b), unlike root buds. If the number of root and basal buds was constant for a given area of root and stool tissue, then it can be said that the number of potential sites for these buds increases by a factor of α, where α is equal to the amount of new root tissue and the number of canes produced per annum. This clearly ignores the influence of environmental and physiological factors, which will be investigated and discussed later in this study.

This strategy of shoot production provides the potential for rapid colonisation of available ground area (Williams, 1959a). The ability of *Rubus* to propagate both sexually and vegetatively earns *Rubus* its reputation as an extremely aggressive invading species (Whitney, 1982).

Buds expand in appropriate temperatures (Hudson, 1956) when the proximal internodes elongate (Hudson, 1959) and the juvenile shoot emerges.

1.3 EMERGENCE OF SHOOTS

The point of emergence is important in terms of modelling shoot development as a means of assessing the rate of bud development from its formation to its appearance at the soil surface. Due to the difficulty of evaluating the exact timing of bud formation, it is assumed to occur at planting in this study.

Pre-emergent shoots possess tightly packed scale leaves. As internodes elongate and the shoot emerges, the leaves expand (Jennings, 1988). If environmental conditions are favourable the shoot develops rapidly (Figure 1.1B).

1.4 THE VEGETATIVE PHASE

1.4.1 Bud types

In raspberry, an hierarchy of buds exists according to their position on the shoot. Although Waldo (1934) and MacDaniels (1922) stated that all buds are potentially fruit buds, clearly the apical meristem produces vegetative primordia (leaf and stem tissue) as well as floral primordia.

Braun (in White, 1979) claimed that lateral buds can be considered as new lines of development as they alone produced branches, as opposed to terminal buds, which were only the undeveloped parts of a single axis. In the vegetative shoot, apical dominance ensures that successive axillary (lateral) buds produced are subordinate. However, towards the end of the vegetative period, this dominance weakens and successive daughter buds are released.

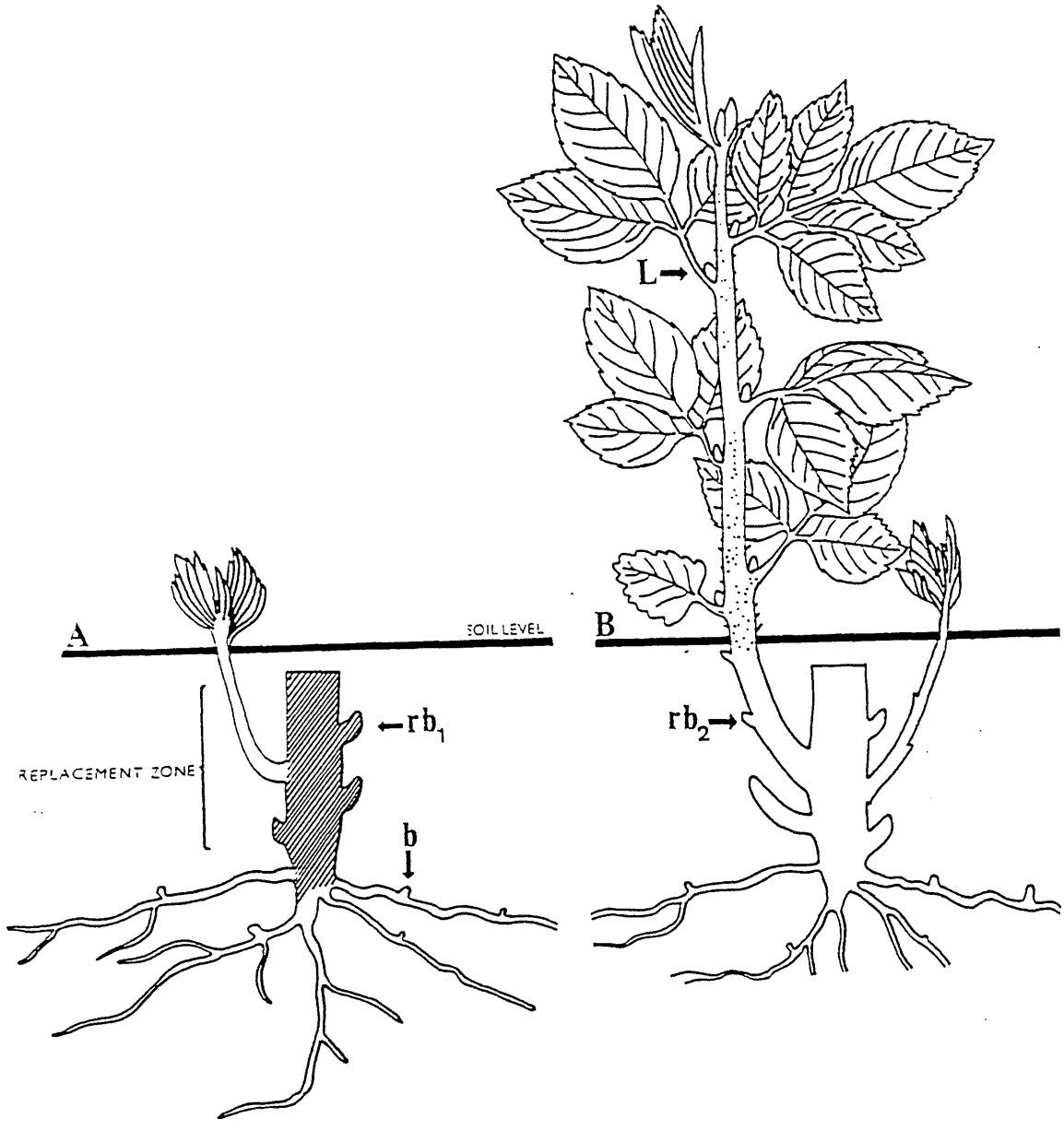


Figure 1.1A Stool and root system of the mother plant. Where basal buds (rb_1) from the "replacement zone" give rise to "stool shoots" and root buds (b) give rise to "spawn shoots".

Figure 1.1B Vegetative shoot, with lateral buds (L) at each leaf axil; vegetative apex; showing basal buds (rb_2) forming part of the next years stool.

Thus, the growth potential of a given lateral bud depends on its position on the shoot axis (White, 1979) with respect to the apex and the roots. All buds initially produce vegetative growth - a mature apex will produce floral primordia (Williams, 1960). Many cultivars, including "Autumn Bliss", possess more than one axillary bud per node or leaf axil. These buds appear to have different growth potentials and are therefore denoted primary and secondary lateral buds (Waldo, 1934; Wood and Robertson, 1957; Jennings, 1979b).

1.4.2 Leaf morphology

Leaves of cv. "Autumn Bliss" are initially very small, simple, lobed and with a high lamina density. Leaflet morphology changes (as the shoot develops) from simple to three leaflet leaves (Williams, 1959a) to four and five leaflet leaves and finally back to three leaflet and simple lanceolate leaves at the shoot apex.

1.4.3 Canopy development

Primary leaf (a leaf produced on the main axis) abscission occurs in stages throughout the life of the shoot. Leaves of the oldest nodes are in competition for light from leaves at nodes in the canopy above. They are lost in the first abscission stage, as the canopy assumes maximum light interception level. The second stage is at floral initiation, when lateral expansion occurs. Lateral leaves (secondary leaves) assume the photosynthetic machinery of the plant, in the place of the primary leaves. Unlike, corn (*Zea mays* L.), for example, where canopy development is restricted to the period between emergence and anthesis (Warrington and Kanemasu, 1983b). Lower lateral leaves are lost by shading from other primocanes within the plant canopy (Wright and Waister, 1982b, 1984, 1986).

1.4.4 Shoot production

Shoots appear to be produced more or less continuously until the population

per plant stabilises. Stabilisation is brought about by shoot mortalities, in a process described by Wright and Waister (1982a) as self-thinning. This is probably due to light becoming a limiting factor for growth and development. Competition among shoots for assimilates may also be a cause which can lead to loss in potential yield (Wright and Waister, 1986).

1.5 FLOWER INITIATION AT THE APEX

1.5.1 Determinate growth

The raspberry, among other species (for example corn, (*Z. mays* L.) Warrington and Kanemasu, 1983a) has a determinate growth habit (Ourecky, 1976; Keep, 1988). Thus, once floral organogenesis is initiated, the apex is "used up" and its growth ceases (Lyndon, 1990). For cv. "Autumn Bliss" the functioning of the apical meristem is terminated as flower primordia are initiated at the apex.

Thus, in terms of producing a model for shoot development, not only does flower initiation mark the transition from juvenility to maturity, it also marks the development of mature architecture as lateral production ensues.

1.5.2 Determination of flower initiation

Many studies have been carried out on flower bud development in *Rubus*: MacDaniels, 1922; Waldo, 1934; Snyder, 1936; Mathers, 1952; Robertson, 1957; Wood and Robertson, 1957; Williams, 1959c; Haltvick and Struckmeyer, 1965; Vasilakakis, Struckmeyer and Dana, 1979; and Dale and Daubeny, 1987.

Mathers (1952) defined the morphological changes occurring at the apex (Table 1.1). The terminal inflorescence first becomes visible to the naked eye at stage I. Prior to this the growing point is ovate (Mathers, 1952) and concealed by developing leaves. The inflorescence is apparent as a "cluster" of buds after stage I. The terminal bud develops first, such that the inflorescence axis lengthens forming a compact pyramid termed "green bud" stage.

Table 1.1 A description of the morphological changes occurring in the terminal inflorescence and terminal flower, from studies on the cultivars "Malling Promise", "Malling Landmark" and "Lloyd George"

STAGE	DESCRIPTION	
I	Growing point of inflorescence axis becomes broad and flat	
II	Terminal flower development	Perianth ring initiated
III		Torus broad and flat, sepal rudiments appear
IV		Torus begins to grow upwards; first cycle of anther rudiments initiated
V		second cycle of anther rudiments initiated
VI		sepals turning upwards; 2 - 3 cycles of anther initials, lowest anthers begin to show lobing

(After Mathers, 1952).

This is composed of 5 - 8 flowers (Mathers, 1952). Once "green bud" stage is reached the maximum number of nodes is determined, each of which, apart from the terminal flower has the potential to produce a lateral (Jennings and Dale, 1982).

1.5.3 Development of flowers in axillary buds

Mathers (1952) and Williams (1959c) studied flower development in the summer-fruiting cultivar "Malling Promise" and the autumn-fruiting cultivar "Lloyd George". They found that flower initiation occurred basipetally. However, buds at nodes 5 - 10 below the apex were more advanced than those at nodes 2 - 4. Initiation occurred progressively later down the shoot.
Buds below soil level remained vegetative (Williams, 1959c).

1.6 FRUITING CANE ARCHITECTURE

The developing shoot becomes progressively woody. For the purposes of this study the developing shoot is termed a cane once flower initiation has occurred.

Once axillary buds are released from correlative inhibition, lateral expansion and development occurs. Lateral expansion is most prevalent in the upper nodes, which are known as the cropping zone (Jennings and Dale, 1982) (Figure 1.1C).

1.6.1 Lateral vigour and morphology

Dale and Topham (1980) carried out a multivariate analysis of lateral characteristics for twelve genotypes. They showed that reproductive vigour was greatest towards the shoot tip and that general lateral vigour was greatest towards the shoot base. Fruiting canes with many laterals tended to have vigorous lower laterals (Dale and Topham, 1980; Jennings and Dale, 1982). Lateral node number and fruit bud number increased down the cane (Dale, 1979).

Prolepsis is exhibited in lateral morphology. As the lateral expands from the bud, there is a transition in leaf morphology and size; beginning with bud scales at the first few lateral nodes. Flower buds are apparent on the apices of upper laterals as they expand; lower laterals have vegetative apices initially (Williams, 1959c). This suggests a certain amount of preformation in upper buds before release and expansion. Lateral growth is determinate on the production of terminal (primary) flower buds (Jennings, 1964a; Dale, 1986). Therefore laterals are a repeat of the main axis morphology. The process of reiteration, that is branching caused by meristems not brought into play in the original architecture of the plant (Tomlinson, 1978), is exhibited in lateral formation and basal bud expansion. This is seen in the basipetal trend towards increasing complexity of lateral morphology. Replacement shoots from basal buds are the ultimate example of this.

1.7 FRUITING AND SENESCENCE

Flowers and fruit form a cyme (not a raceme as stated by Ruxton and Modlibowska, 1954) as each growing point is terminated in an inflorescence. New growth depends on the production of new lateral growing points (Clapham *et al.*, 1968). The flowers and fruit are associated in a similar way to those of *Fragaria ananassa* L., where each lateral branch (like a single truss) bears primary, secondary, tertiary, quaternary and (in cv. "Autumn Bliss") quinary fruit (Anderson and Guttridge, 1982) (Figure 1.2).

Environment and cultivar influence the rate of ripening (average 30 - 45 days after anthesis). Yields, as expected, reach a peak and then decline over the cropping period. However, fruit weight remains constant, only decreasing towards the end of the season (Dale, 1989). Once the upper laterals start to produce fruit there is extensive leaf loss and senescence. This process continues distally down the plant. As cv. "Autumn Bliss" crops early, most of the laterals have fruited prior to unfavourable conditions. This leaves little or no viable above ground nodes to expand in the following season. Thus, the cane dies back to soil level. Basal buds expand in the following year from these stools.

1.8 SUMMARY

In terms of new lines of development (*ie.* active meristems), the life of an individual shoot in a plant population depends on the number of nodes which expand to form laterals. Correspondingly, the life of a plant depends on the ability of reserve buds on the stool and roots to expand and replace the shoot population.

Lateral production and probably shoot production depend on the release from correlative inhibition of successive buds. The assessment of the rate of development and timing of flower initiation will provide information on the architectural dynamics of cv. "Autumn Bliss". Correlative inhibition is an excellent experimental model for the study of spatial organisation of the developmental activities in the plant (Phillips, 1975).

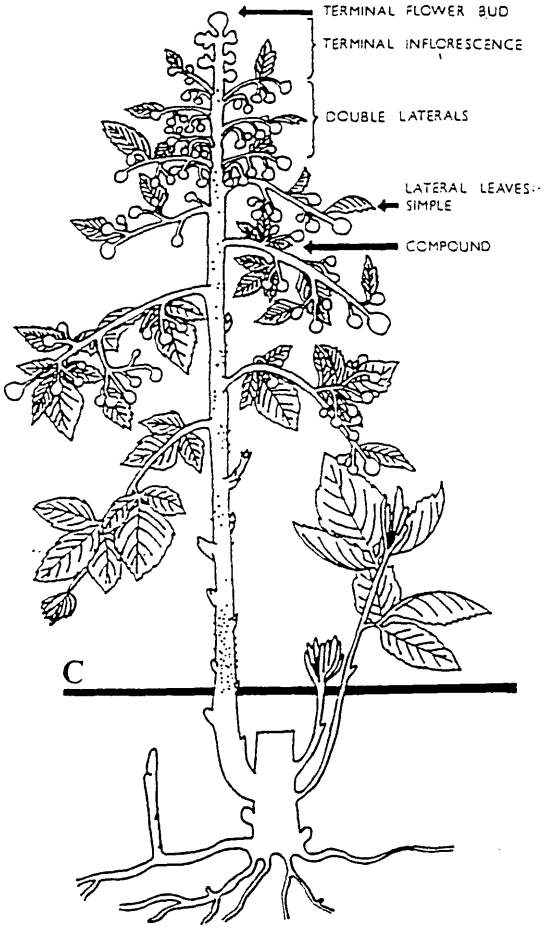


FIGURE 1.2

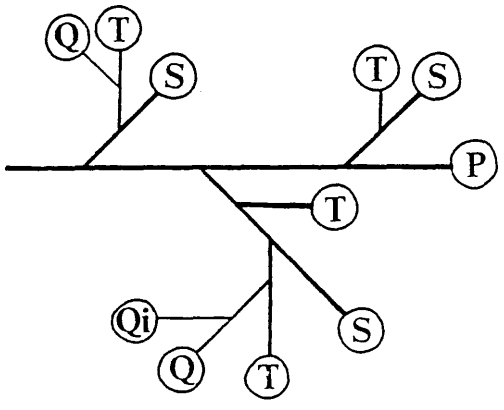


Figure 1.1C Fruiting cane architecture, displaying the change in lateral morphology, terminal inflorescence (deliberately shown unexpanded) and the production of new shoots.

Figure 1.2 Arrangement of berries on the lateral. Rate of ripening relates to location: P - primary, S - secondary, T - tertiary, Q - quaternary and Q_i - quinary fruit (after Anderson and Guttridge, 1982).

CHAPTER 2
MATERIALS AND METHODS

Plants composed of at least one stool and root system (see individual chapters for details) were potted in a peat:grit (4:1) compost, with no nutrients in 25cm diameter pots. All existing shoots were cut back to below soil level.
Plants were watered daily or as required, and were fed with a standard NPK liquid feed from the time of terminal flowering onwards.

Dry weights of plants were assessed for above ground plant material only. This was due to the difficulty in separating roots from the peat mix compost, without the loss of a large proportion of fine roots. Dry weight harvesting was carried out at the end of each experiment, by oven drying plant material at 80°C for a minimum of 48 hours, or until the dry weight remained constant. Sequential harvesting throughout experiments was not possible due to the relatively low numbers of replicates.

Infestations of the spider mite *Panonychus ulmi* Koch. were controlled with natural predators (*Phytoseiulus persimilis* and *Encarsia* parasites) and spraying with "Torque" (applied at a rate of 0.5g/l). Mildew infections (*Sphaerotheca macularis* (Wallr: Fr.) Lind.) were controlled with sprays of "Benlate" (1g/l).

Leaf area was measured using a Leaf Area Meter (Delta-T Area Meter System, Mark 2[1], fitted with a high resolution camera (model RCA TC 1005); 18mm vidicon with a 16mm manual iris lens). In all experiments, plants were exposed to natural daylength and natural light intensities.

The levels of photosynthetically active radiation (PAR), transmitted in each plot were measured using a Sunfleck Ceptometer[1] (model SF 80). This was equipped with a probe, fitted with 80 sensors at 1cm intervals, along its entire length (all the sensors were scanned by an inbuilt microprocessor, which stored and averaged each sensor reading).

[1] Delta -T Systems, 128, Low Road, Burwell, CAMBRIDGE.

The point of flower initiation in *Rubus* can be assessed in a number of ways. Methods employed successfully on *R. idaeus* L. (Mathers, 1952; Vasilakakis, Struckmeyer and Dana, 1979; Crandall and Garth, 1981; Dale and Daubeny, 1987) and *F. ananassa* L. (Jahn and Dana, 1970; Durner and Poling, 1985) were dissection under a stereoscopic microscope, longitudinal sections of buds using a rotary microtome and non-destructive macroscopic examination of the apex. Macroscopic examination of the apex was most convenient as a means of assessment in this study. In most of the experiments replicate numbers were too low to allow destructive methods of determination.

CHAPTER 3

THE EFFECT OF VERNALIZATION TREATMENTS ON THE RATE OF FLOWERING AND ON PLANT PRODUCTIVITY

3.1 INTRODUCTION

Research carried out by Williams (1960) showed that the summer-fruiting cultivar "Malling Promise" required a minimum inductive treatment (10°C, 9 hour daylength) of three weeks, before the appearance of flower initials in terminal buds, whereas, "Lloyd George" (an autumn-fruiting cultivar) showed no such chilling requirement.

The aim of this chapter is to determine whether cv. "Autumn Bliss" likewise has no chilling requirement for the specific promotion of flowering. For cultivars such as "Malling Promise", where shoot development is biennial, the processes of dormancy and vernalization appear to be connected in the over-wintering cane (Williams, 1960). Because canes of cv. "Autumn Bliss" behave like annuals, flowering and fruiting in the first year of growth (Lawrence, 1981), they can be cultivated as such commercially (Dana, 1983; Keep, 1988). One year old canes are mown down, so that the perennating organ is the only part exposed to winter temperatures. Therefore it is inappropriate to look at chilling in over-wintering dormant lateral buds; but rather at its delayed effect, by chilling basal and root buds.

The vernalized state is not transferred through meiosis, but through mitotic cell divisions (Thomas and Vince-Prue, 1984). The requirement of vernalization is perpetuated in perennials by various means. In *Chrysanthemum morifolium* L. de-vernalization of buds occurs over summer. New perennating shoots are therefore, non-vernalized. Buds are only receptive to chilling at a certain stage of development in *Geum urbanum* L.. Finally, the vernalized state is not transferred indefinitely through cell divisions in some perennial grasses (Thomas and Vince-Prue, 1984).

The age at which plant material is sensitive to vernalization treatment varies from species to species. Williams (1960) showed that there was an increase in the

rate of response to chilling treatment as node number increased in canes of cv. "Malling Promise". Canes of 15 - 30 nodes responded, but canes of fewer than 15 nodes did not respond to any length of inductive treatment. Vasilakakis, M^{c}Cown and Dana (1979) showed that levels of gibberellin-like substances and cytokinin increased in cold-treated (outdoor/over-wintering) canes and as node number increased (10-node compared with 20-node plants).

Generally, the response to chilling treatments may be delayed until higher temperatures are experienced (Wareing and Phillips, 1981). In addition, the effect of temperature increases with the duration of chilling time, until the response is saturated. Optimum vernalizing temperatures lie between 1 - 7°C (Thomas and Vince-Prue, 1984).

It is important therefore to clearly define the age of material treated and the nature (temperature and duration) of the vernalizing treatment. This provides clear information for determining the point of saturation of the response and whether the response is obligate or facultative, delayed or non-delayed.

3.2 METHODS

Two year old mother plants (stem base and root system) were graded according to stem diameter to quantify initial plant mass in order to ensure that all grades were evenly distributed between treatments (see section 4.3.4.2, equation 4.1). They were kept in pots in a glasshouse for 12 months at 15±3°C (natural daylength). Three successive batches of eight plants, with shoots cut back to soil level, were removed to a cold store (5°C, without light) in April 1989 for 35 days, 21 days and 7 days respectively. All three batches were removed at the same time and returned to the glasshouse. A fourth batch remained in the glasshouse during this time to act as a control. Any shoots which elongated during chilling were removed, so that only treated basal and root buds were allowed to develop. Plants were repotted and placed at random in a glasshouse cubicle held at 15±3°C (natural daylength) and repositioned at two week intervals.

The timing of flower primordia appearance at the apical meristem and berry

ripening were recorded for each plant. Shoot number was measured at intervals until fruiting. Total fruit number and fresh weight were recorded per plant. After fruiting each plant was harvested and dry weights and leaf areas determined.

3.3 RESULTS

Some plants died in the control and 7 day chilling treatments therefore, the number of replicates was 5, 6, 8 and 8 plants for chilling times of 0, 7, 21 and 35 days respectively.

The mean rate of terminal flower primordia appearance and mean rate of berry ripening per plant were calculated as the inverse of the time taken from planting. The former was not significant (Figure 3.1a). The linear sum of squares for the rate of berry ripening was significant, indicating that the rate was higher for longer chilling times (Figure 3.1b).

Both the mean total fruit number and fresh weight per plant gave significant linear sums of squares. This also indicated an increase in response with increased chilling time (Figure 3.2a - 3.2b).

Mean total primary leaf dry weight per plant gave a significant quadratic sum of squares. This showed that the lower mean dry weight for plants treated for 21 days was significant (Figure 3.3a). Mean total stem dry weight, mean total dry weight per plant and mean total primary leaf area showed the same trend (Figures 3.3b, 3.3c and 3.4 respectively). Lateral and secondary leaf dry weights, as well as secondary leaf area per plant were not significant for different chilling treatments.

Shoot number was measured throughout the growth period (Figure 3.5a) and at harvest (Figure 3.5b). A significant quadratic sum of squares was also obtained for the latter.

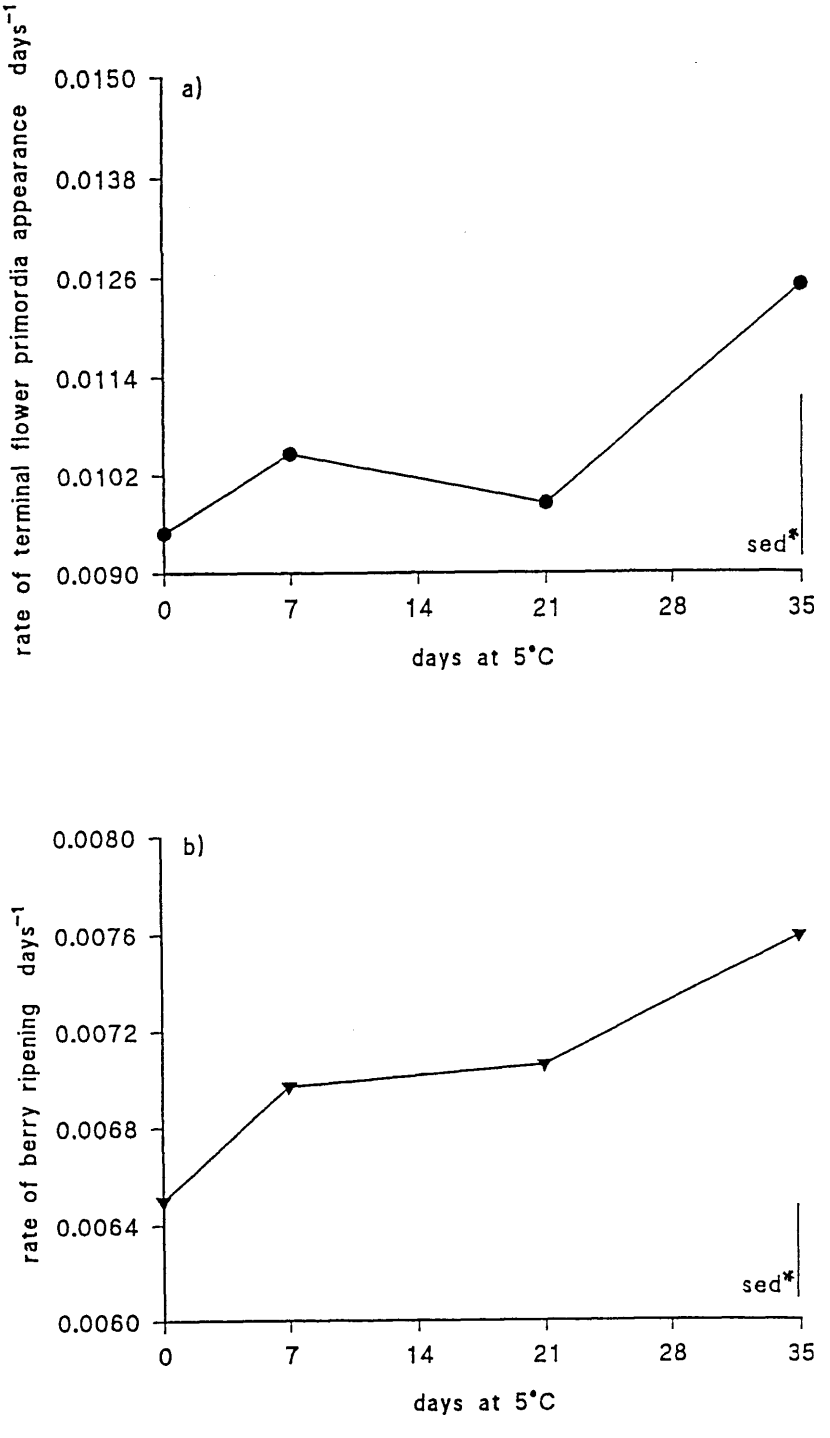


Figure 3.1a The relationship between the mean rate of terminal flower primordia appearance per plant and the length of chilling treatment at 5°C. No significance between treatments.

Figure 3.1b The relationship between the mean rate of berry ripening per plant and the length of chilling treatment at 5°C. Significant linear sum of squares (P=0.011).

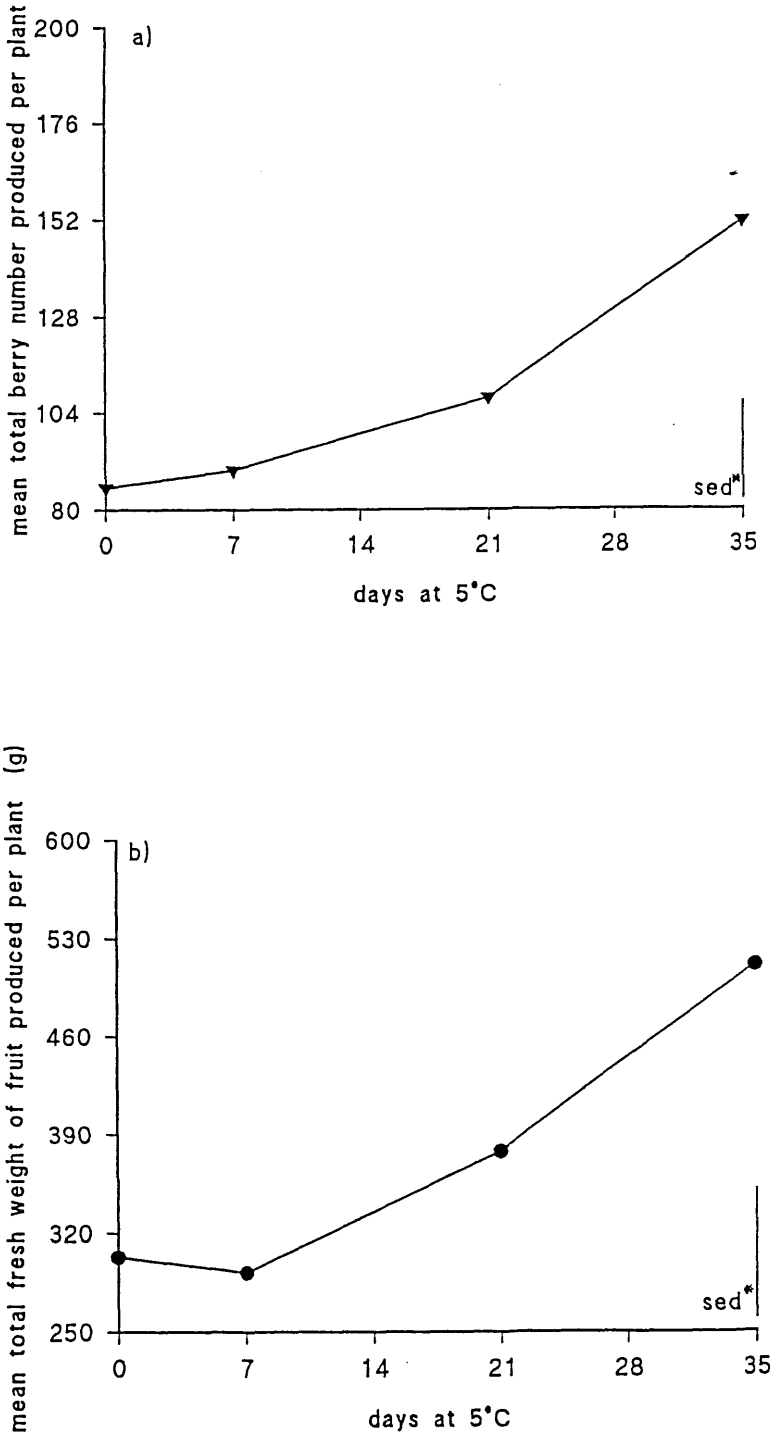


Figure 3.2 The relationship between the mean fruit yield per plant and the length of chilling treatment at 5°C.

a) mean total fruit number per plant. Significant linear sum of squares (P=0.005).

b) Mean total fresh weight of fruit per plant. Significant linear sum of squares (P=0.01)

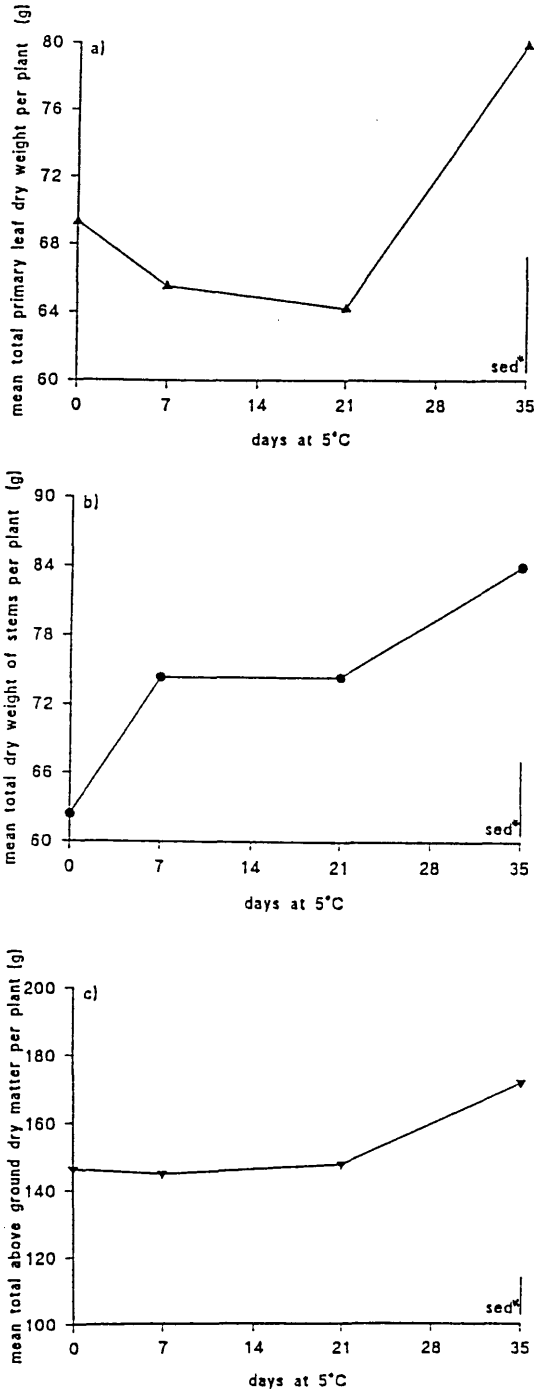


Figure 3.3 The relationship between plant dry weight and the length of chilling treatment at 5°C.

a) Mean total primary leaf dry weight. Significant quadratic sum of squares (P=0.042)

b) Mean total stem dry weight per plant. Significant linear sum of squares (P=0.006)

c) Mean total above ground dry matter per plant (minus fruit weight). Significant linear sum of squares (P=0.016).

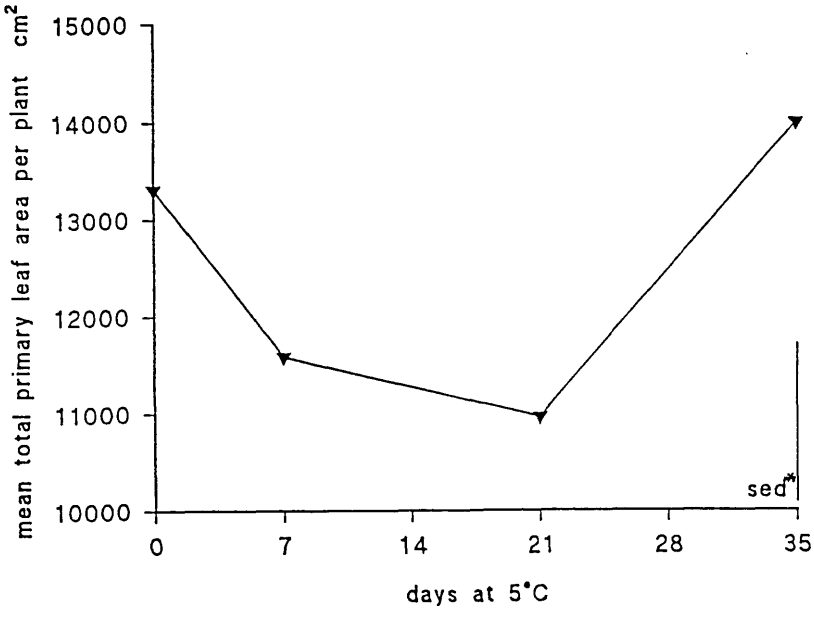
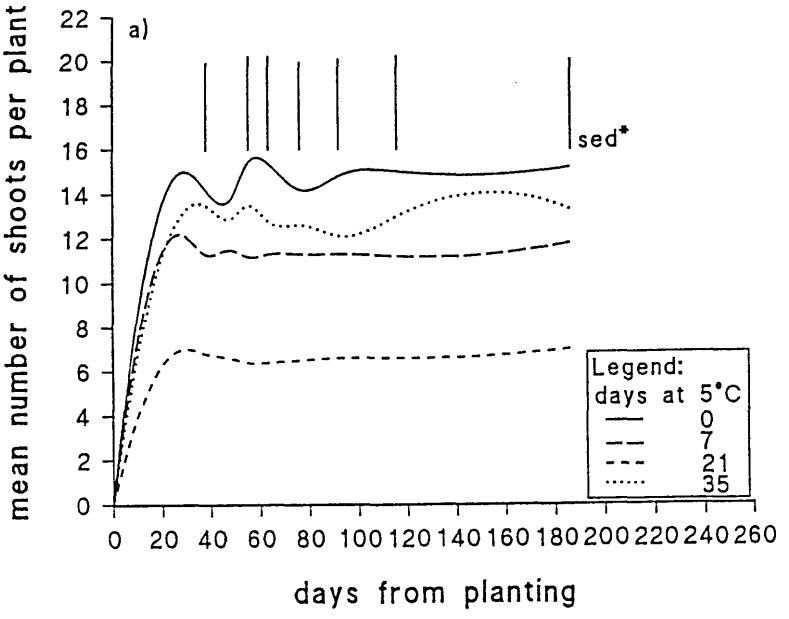


Figure 3.4 The relationship between the mean total primary leaf area per plant and the length of chilling treatment at 5°C. Significant quadratic sum of squares (P=0.037)



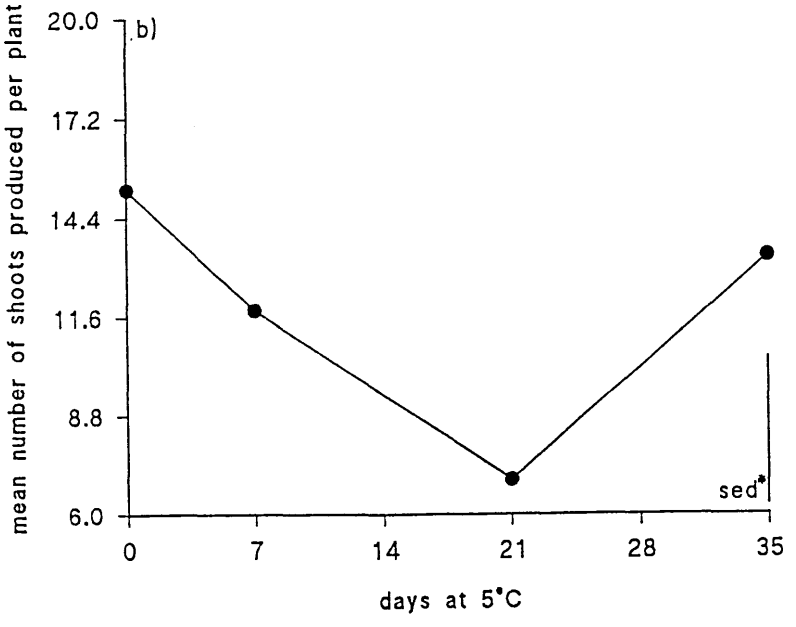


Figure 3.5 The relationship between shoot number per plant and the length of chilling treatment at 5°C. a) Mean shoot number per plant between planting and harvesting. b) Mean shoot number per plant at harvest. Significant quadratic sum of squares (P=0.047)

3.4 DISCUSSION

3.4.1 The effect of chilling on floral induction

From the evidence presented above cv. "Autumn Bliss" does not have an absolute requirement for vernalization as flowering occurred in shoots of chilled and unchilled plants. This agrees with research on the autumn-fruiting cultivars "Heritage" (Vasilakakis, Struckmeyer and Dana, 1979; Vasilakakis *et al.*, 1980) which flowered when held at temperatures not lower than 22°C in a glasshouse and "Lloyd George" (Williams, 1960)(Table 3.1). From the former two papers, it was unclear what temperatures the plants had been exposed to prior to chilling, which may have affected the results obtained.

There were no significant differences between the rates of terminal flower bud appearance for different chilling times. This implies the lack of a facultative requirement for vernalization as well. However, as there were significant differences between rates of berry ripening, this suggests that there should have been a corresponding significance between rates of flower primordia appearance. This lack of significance may have been due to error in the assessment of the timing of this stage.

Assuming that chilling at 5°C speeded up the rate of shoot development as a whole, then chilling root buds and basal buds resulted in a delayed response, which increased with the duration of chilling at 5°C. This temperature appeared to be effective. Williams (1960) successfully employed an inductive temperature of 10°C (with a 9 hour daylength), whereas Jennings (1964b) used 7°C. Vasilakakis, Struckmeyer and Dana (1979) and Vasilakakis *et al.* (1980) also used 7°C with cv. "Heritage" (Table 3.1). Williams (1960) and Vasilakakis *et al.* (1980) showed that, as shoots increased in node number, their response to chilling treatments was more rapid and hence flowering occurred at a lower node number. In the cultivar "Heritage" (Vasilakakis *et al.*, 1980) newly initiated shoot buds on roots (4 - 5 nodes) (Table 3.1) responded to chilling. According to their growth habit, autumn-fruiting cultivars would need to be sensitive to chilling at pre-emergent or early post-emergent shoot development. This would enable them to respond to vernalizing

temperatures, which are prevalent at the beginning of the growing season. This appears to be the case. Although generally young, undifferentiated buds are insensitive to cold, sensitivity develops as they differentiate (Thomas and Vince-Prue, 1984). Further experimental evidence has shown that chilling of the root system itself can accelerate maturity in juvenile plants. Juvenility and vernalization are related in the determination of flowering, the former in terms of ontogenetic development and the latter in terms of season (Thomas and Vince-Prue, 1984).

Vernalization is a physiological effect of chilling rather than a physical effect, as freezing temperatures are not essential in bringing about the necessary changes in the plant (Wareing and Phillips, 1981). It appears to occur solely in meristematic zones (Wareing and Phillips, 1981; Thomas and Vince-Prue, 1984). It is connected to flowering by the production of a "thermo-induced" state, which in theory leads to the formation of a flowering hormone (Wareing and Phillips, 1981).

Jennings (1988) claimed that autumn-fruiting cultivars are daylength- and temperature-neutral, since they initiate flowers in long days and high temperatures, compared with summer-fruiting cultivars, which initiate flowers in short days and low temperatures. He stated that the only limiting factor in flower initiation is a growth factor. These facts provide insufficient evidence concerning flower initiation, however the above results support this claim with respect to vernalization.

3.4.2 The effect of chilling on plant growth and yield

Fruit yield, total above ground dry matter and stem dry weight increased with chilling time at 5°C. Thus, chilling appeared to promote the storage and mobilisation of reserves to fruiting. Non-structural carbohydrate accumulates in the stem and root system after fruiting in the mature cane (Whitney, 1982).

However, primary leaf dry weight, area and total shoot number displayed a non-linear relationship with chilling treatment. The response to chilling reached a minimum at 21 days. It can be said that periods of chilling up to 21 days cause a reduction in these variables compared with control plants. Chilling for longer than 21 days induced a positive response.

Table 3.1 Summary of research on flower induction in *Rubus idaeus* L.

reference	cultivar	treatment	details	time/stage to flowering	age of shoot treated (nodes)	type of plant material used
Williams (1960) 1)	"Malling Promise"	induction	10°C/9hr dl	3wks	20	RC, GH, 16hr dl
2)	-"-	induction (1-13wks) & LT	-"- 3°C,6wks, no light	2wks	-"-	-"-
3i)	-"-	-"-	-"-	-	25	-"-
3ii)	-"-	-"-	-"-	5wks & LT	15	
3iii)	-"-	-"-	-"-	2wks & LT	20	
3iv)	-"-	-"-	-"-	LT only	30	
4)	-"-	control	GH, 16hr dl	-	?	-"-
	"Lloyd George"			28wks		
Jennings (1964b)	"Malling Jewel"	combined inductive/ LT	7°C/9hr dl	6wks	25	apex removed (at approx 30 nodes)
Vasilakakis, Struckmeyer and Dana (1979)	"Latham"	induction	22-24°C/nat dl	24-28wks	?	over-wintering canes
-"-	"Heritage"	-"-	-"-	5-7wks	?	-"-
		-"-	outside/nat dl	earlier		
Vasilakakis, *et al.* (1980)	"Heritage"	-"-	GH (>22°C)/nat dl	80*	4-5	22-24°C 16hr dl
			outside/nat dl	41*	4-5	
			7°C,25 days/16hr dl	32*	10-12	
			-"-	28*	14-16	

LT low temperature treatment (to break dormancy), GH glasshouse, RC root cuttings, wk week, dl daylength (nat dl natural daylength), * refers to node number, ? not qualified.

The change in primary leaf dry weight and area with chilling treatment reflected the changes in shoot number. The mature cane variables of lateral dry weight, secondary leaf dry weight and area appeared to be unaffected by chilling.

In conclusion, such chilling treatments have important implications in commercial cultivation, in glasshouse cultivation (Goulart, 1989a) and in subtropical cultivation (Snir, 1986). Chilling improves yield in cv. "Autumn Bliss" by "forcing" earlier development of shoots and increasing the yield per plant. However, as previous work has shown, the shoot becomes more sensitive to chilling as it matures. Thus, application of chilling at a later stage of development should result in an enhanced response.

There is a need for the classification of raspberry cultivars according to their chilling requirements for flowering. Goulart (1989a) classifies autumn-fruiters as everbearers. Jennings (1988) argues that there is a wide range of response even among autumn-fruiting cultivars. Therefore, there should be no division between summer and autumn-fruiting cultivars; they represent two ends of a constant temperature/daylength response.

CHAPTER 4
THE EFFECT OF ENVIRONMENT ON THE GROWTH AND DEVELOPMENT OF CV. "AUTUMN BLISS"

4.1 INTRODUCTION

Much research has been put into developing autumn-fruiting cultivars that will crop up to the first hard winter frosts, which cause crop loss and prevent further fruit development (Braun and Garth, 1984a). This has been the reasoning behind the production and release of "Autumn Bliss" as a new, early autumn-fruiting variety (Keep *et al.*, 1984; Gibson, 1987; Jennings, 1988; Lovelidge, 1988).

The increase in consumer demand for late season red raspberries has promoted research to develop new cultural practices (Goulart, 1989a). Work has been carried out on the American variety "Heritage" to study the effect of protected cropping under glass (Vasilakakis, Struckmeyer and Dana, 1979; Vasilakakis *et al.*, 1980; Dale, 1986; Goulart, 1989a) and the application of chemical growth regulators to advance the timing of terminal flower initiation (Redalen, 1980; Braun and Garth, 1984a; Braun and Garth, 1986; Goulart, 1989a). Lockshin and Elfving (1981), Keep (1988) and Hoover *et al.* (1989) suggested the use of plastic tunnels to cover canes during the cropping period. This has been followed up by growers in the United Kingdom for the cropping period only (Burgess, 1986; Partis, 1987; Lovelidge, 1988) and in Holland for the whole season (Geense, 1983; Verwijs, 1983; Dijkstra and Van Oosten, 1984). This work indicates that protection increases productivity, varies the timing and length of cropping period and reduces wastage.

The purpose of this experiment was to investigate and quantify the effect of different environments (glasshouse and polytunnel) on plant development and yield, compared with control plants grown in outdoor conditions, and in addition to this, to study the interaction between grading and environmental treatments.

4.2 DEFINITION OF TREATMENTS AND METHODS

Two protected plots (glasshouse and polytunnel) were selected and compared with an outdoor plot. Their environments were defined by continuous assessment of temperature (using thermohygrographs).

One year old plants (single stem base and root system) were graded and divided into four groups, according to their fresh weights (weights ranged from 3 - 114.5g; grading A to D; lowest fresh weights to highest fresh weights). Five plants from each grade were randomly selected for each plot and potted up in April 1988. Each plot was fully randomised at two week intervals throughout the experiment.

The times from planting to emergence, terminal bud appearance, terminal anthesis and terminal berry ripening were recorded for the first plant to reach that stage per treatment. Measurements for shoot height, shoot number and leaf number were recorded at two week intervals. Fruit was picked daily from each plant and all plants were harvested for the assessment of leaf area and canopy dry weight at the end of the cropping period. Light intensity was measured at each plot. An average of ten samples was taken at 14.00hr on a bright summer day, with the sensors of the Ceptometer held at 1.5m above ground level.

Treatments were statistically replicated, such that five randomly selected plants from each grade were exposed to every environment. The design of the experiment was essentially factorial. However, although each grade of mother plant was represented in every environment, the environments (plots) themselves were not truly replicated and can be considered as blocks. Values of seds were quoted in figures only where there were significant differences between treatments.

4.3 RESULTS

4.3.1 Description of treatments

4.3.1.1 Environmental treatments

Canes of cv. "Autumn Bliss" attain a maximum height of approximately 1.0m. As it is the development of the canopy, in particular the apex, that is of interest, the

ambient air temperature, rather than the soil or ground level temperature was monitored.

The three environments can be described (Table 4.1) as regulated, protected (glasshouse), unregulated, protected (polytunnel) and unregulated, unprotected (outside plot). Temperatures were the least variable and on average higher in the glasshouse than in the polytunnel. High fluctuations and freezing temperatures were experienced among plants in the outside plot (Figure 4.1a - d). Light levels were lowest in the polytunnel, and highest in the outside plot (Table 4.2), although PAR levels transmitted in all three plots were low compared with levels recorded at the meteorological station. All plots were partially shaded by glasshouse structures.

Table 4.1 Description of environmental treatments

ENVIRONMENT	MAX/MIN AIR TEMPERATURE (°C)	REGULATION OF AMBIENT TEMPERATURE	PROTECTION AFFORDED FROM	
			FROST	WIND
glasshouse	38/13	regulated (thermostatically controlled)	protected	protected
polytunnel	38/1	not regulated	some	protected
outside	33/-4	not regulated	none	some

Table 4.2 Differences in the levels of photosynthetically active radiation (PAR) transmitted in each plot

PAR (μmol $m^{-2}s^{-1}$)	PLOT LOCATION			
	GLASSHOUSE	POLYTUNNEL	OUTSIDE	MET. STATION
Mean of 10 samples	840	783	1241	1454
% PAR received at meteorological station	57.77	53.85	85.35	100

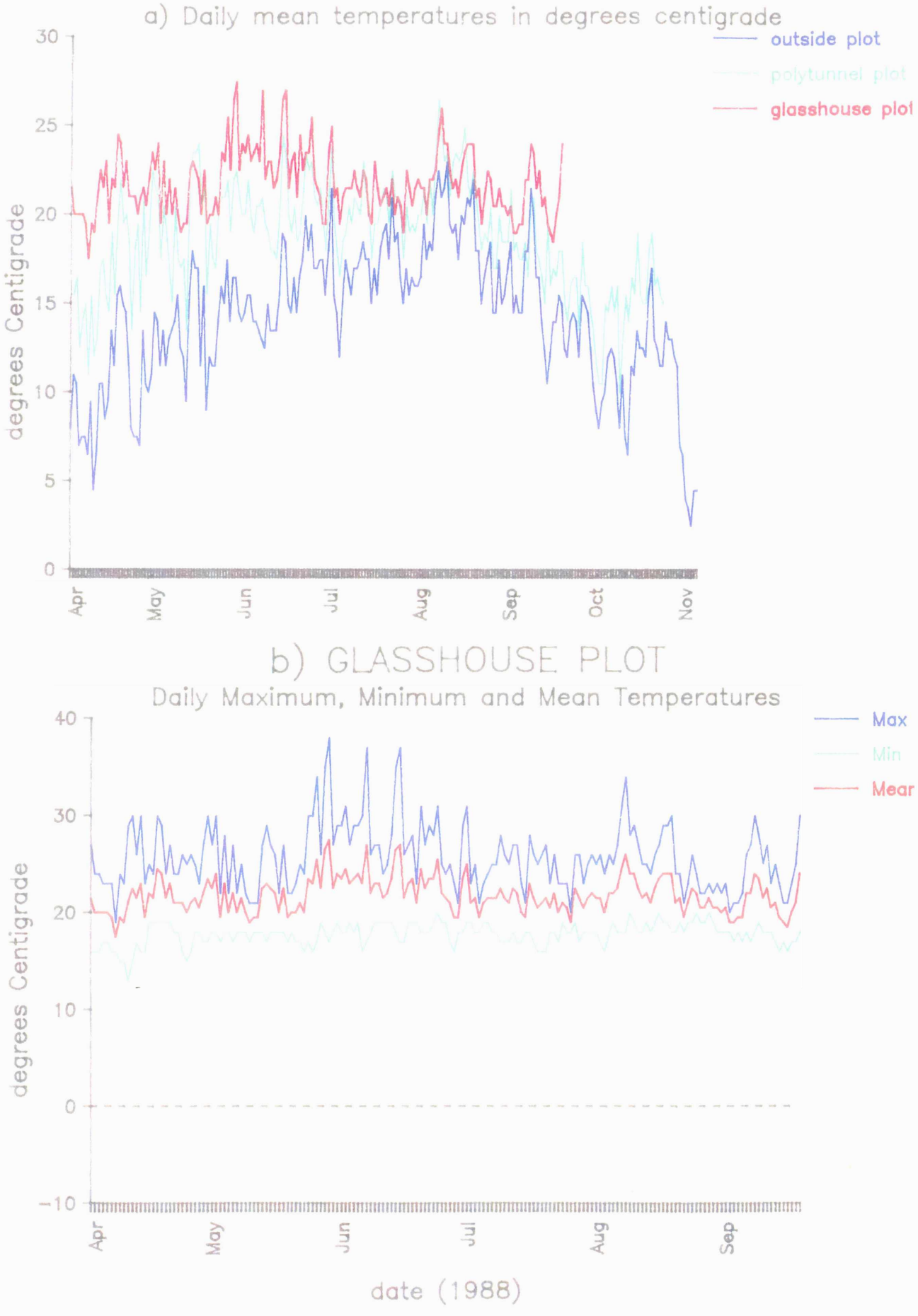
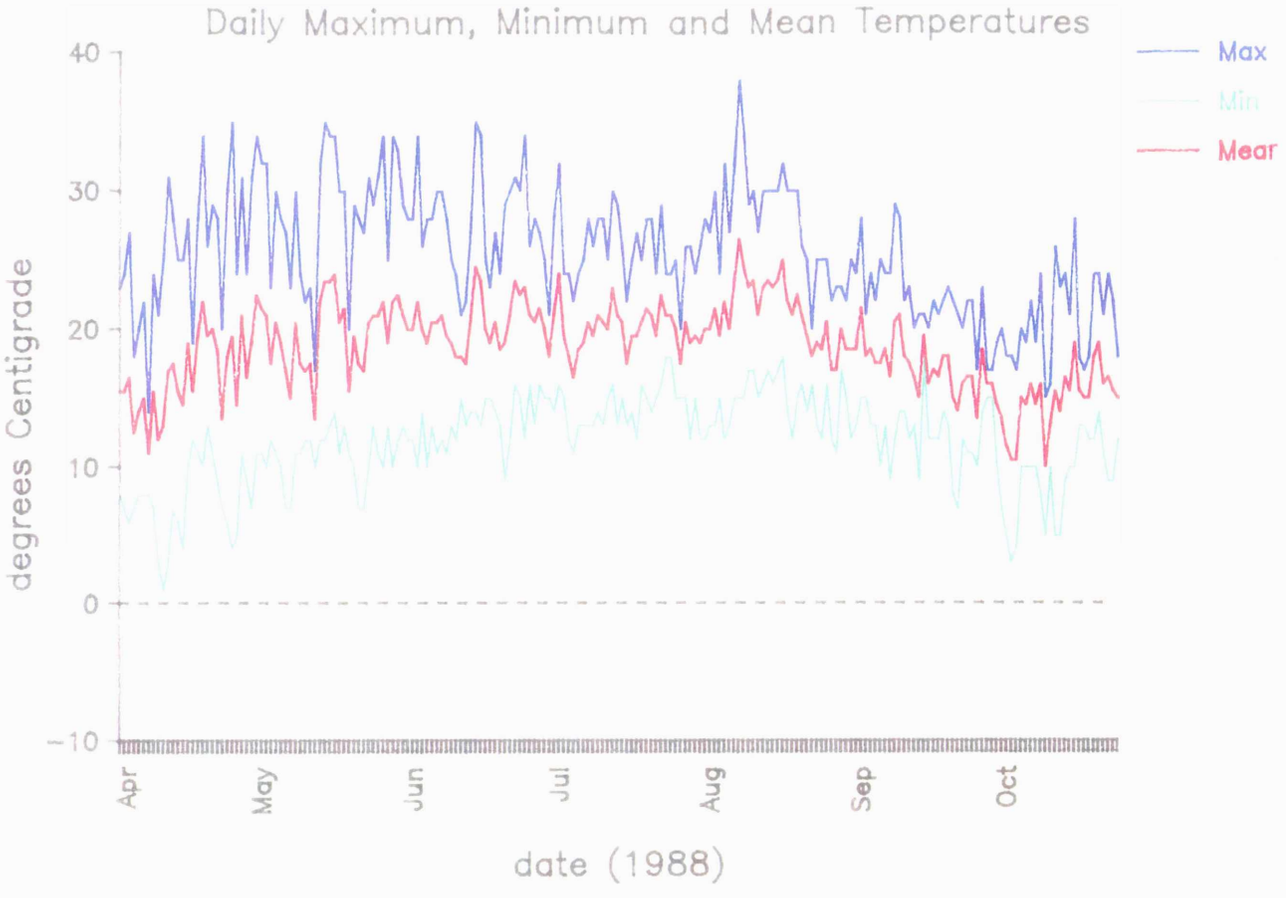
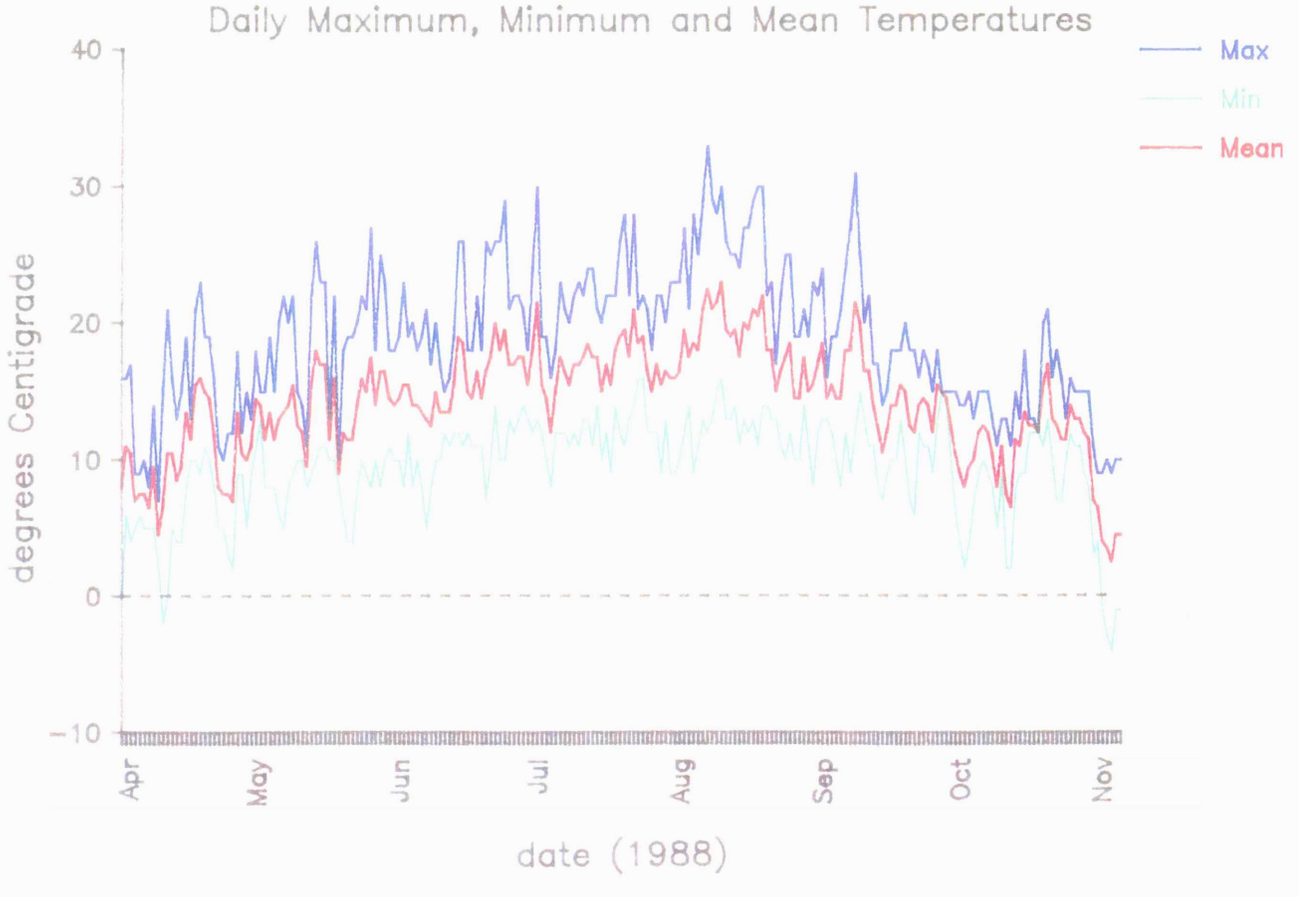


Figure 4.1 a - d Temperature ranges experienced by plants in each environmental treatment during development: a) mean daily temperatures for each treatment, b) glasshouse plot, c) polytunnel plot, d) outside plot

c) POLYTUNNEL PLOT



d) OUTSIDE PLOT



4.3.1.2 Grading treatments

Grading was effective (Table 4.3) as each treatment was highly significant. Differences were most marked between grades of A - C and grade D mother plants. Largest weights, diameters and shoot numbers were exhibited in grade D plants.

Table 4.3 Significant differences among graded mother plants (measurements taken prior to planting)

components (per plant)	grading treatment means				significance	
	A	**B**	**C**	**D**	P	$LSD_{0.05}$
shoot number	1.93	2.35	3.75	4.87	0.003	1.63
shoot diameter (4cm above soil level) (cm)	0.527	0.595	0.800	1.060	<0.001	0.14
fresh weight (g)	5.6	9.1	16.8	45.8	<0.001	11.03

4.3.2 The effect of environment and grading on plant phenology

Table 4.4 summarises the main phenological events in shoot development in each treatment. Fruits were tagged according to the date that they were picked. Typically the terminal fruit ripened first on each shoot, followed immediately (basipetally) by the primary fruit on each lateral, and finally by the secondary and tertiary fruit, *etc.* The mean rate of ripening (days to terminal berry ripe (TB))$^{-1}$ of the first shoot to emerge per plant was significantly higher in plants treated in glasshouse and polytunnel plots compared with those in the outside plot (Figure 4.2)(Appendix 4.1, Table 4.1.1).

The sequence differed notably where ties supporting canes often induced lateral expansion in the axillary bud below the tie. This expansion occurred at an earlier stage than the basipetal expansion exhibited generally in all shoots.

Table 4.4 Summary of phenological stages of development in cv. "Autumn Bliss" for plants in glasshouse (G), polytunnel (P) and outside (O) plots.

STAGE OF DEVELOPMENT	TIME TAKEN FOR FIRST PLANT TO REACH STAGE OF DEVELOPMENT (days from planting)		
	G[2]	P	O
VEGETATIVE GROWTH			
Shoot emergence	15	15	8
Shoot elongation Production of leaves and lateral buds in leaf axils			
REPRODUCTIVE GROWTH			
Terminal flower primordia formation	73	79	99
Anthesis of terminal bud	99	102	112
Release of lateral buds from inhibition Primary flower primordia formation Secondary and tertiary flower primordia formation			
FRUITING PHASE			
Terminal berry ripe	114	120	129
Primary fruit ripening on upper laterals Remaining fruit ripened			
HARVEST AND COMPLETION OF FRUITING	161	189	219

[2]Where: G - glasshouse, P - polytunnel and O - outside.

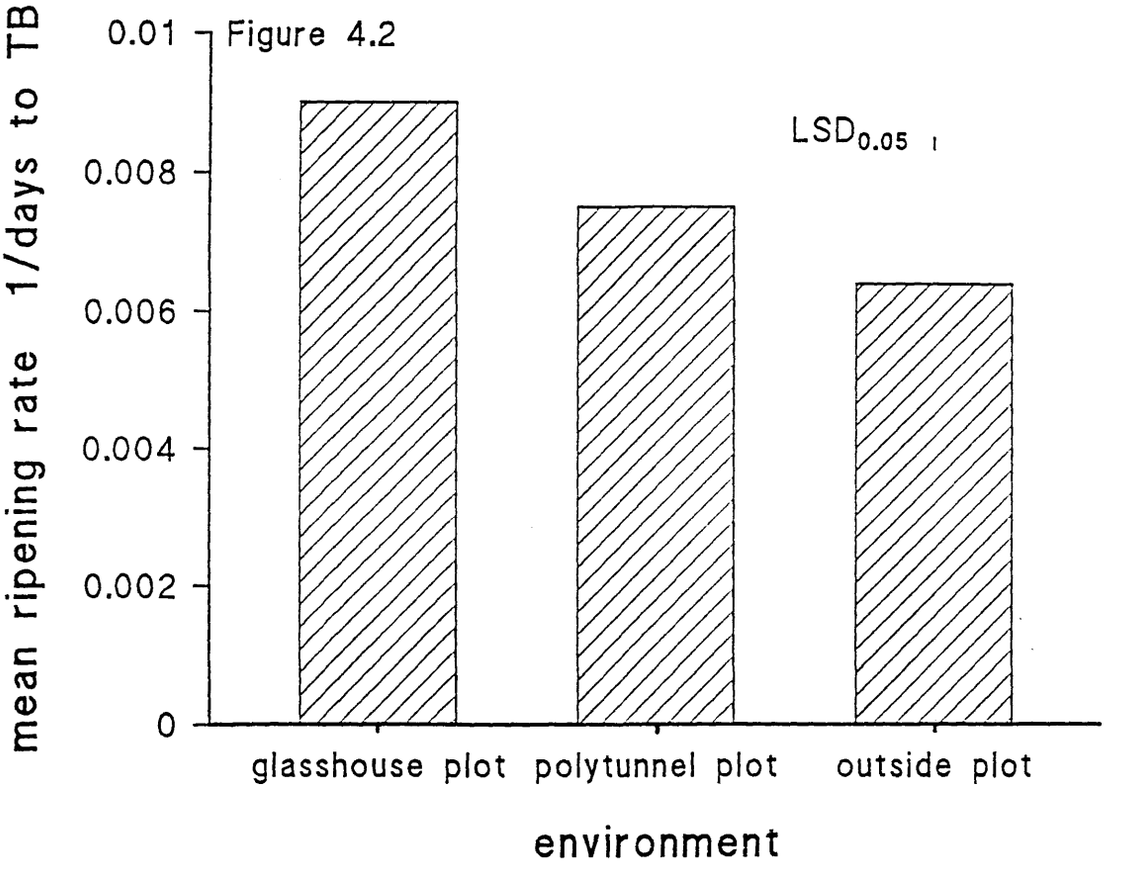


Figure 4.2 The relationship between the mean ripening rate of the terminal fruit (TB) of the first shoot to emerge per plant and environmental treatment,($P < 0.001$).

The rates of development of shoots differed significantly from the evidence of the following data.

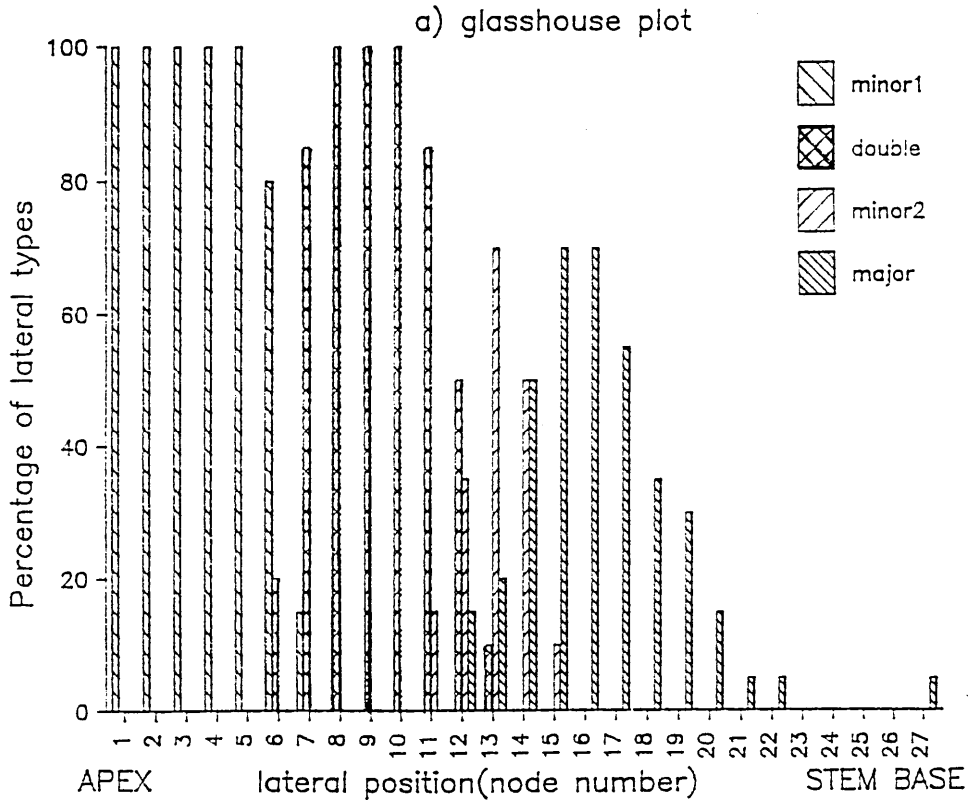
4.3.3 Architecture of canes

Lateral morphology changed with node position. Leaflet number on laterals, as with the main axis, reflects the level of juvenility. From observations on canes in these growing conditions, laterals were divided into four categories according to their leaf morphology and location on the cane. Minor laterals were defined as those which possessed simple or bifoliate leaves. They were formed on the upper 7 nodes, closest to the apex and the lower 11 - 15 nodes (Plate 4.1a). Lateral buds at nodes 6 - 13, produced double laterals with simple or bifoliate leaves (Plate 4.1b). This trait is inherited genetically (Jennings, 1988). Major laterals possessed simple, bifoliate and trifoliate leaves (Plate 4.1c) and were located on the lower nodes. The location of laterals on the cane was similar for each environmental treatment (Figures 4.3a - c). Chi-square tests for lateral numbers of each type, taken at the midpoint of their range of location, were not significant. However, greater numbers of major laterals were found on canes from the polytunnel plot ($0.02 < P < 0.01$). This was due to the lack of lateral formation on the lower nodes of canes from plants grown in the glasshouse and outside plots. Figure 4.4 summarises lateral morphology in this cultivar.

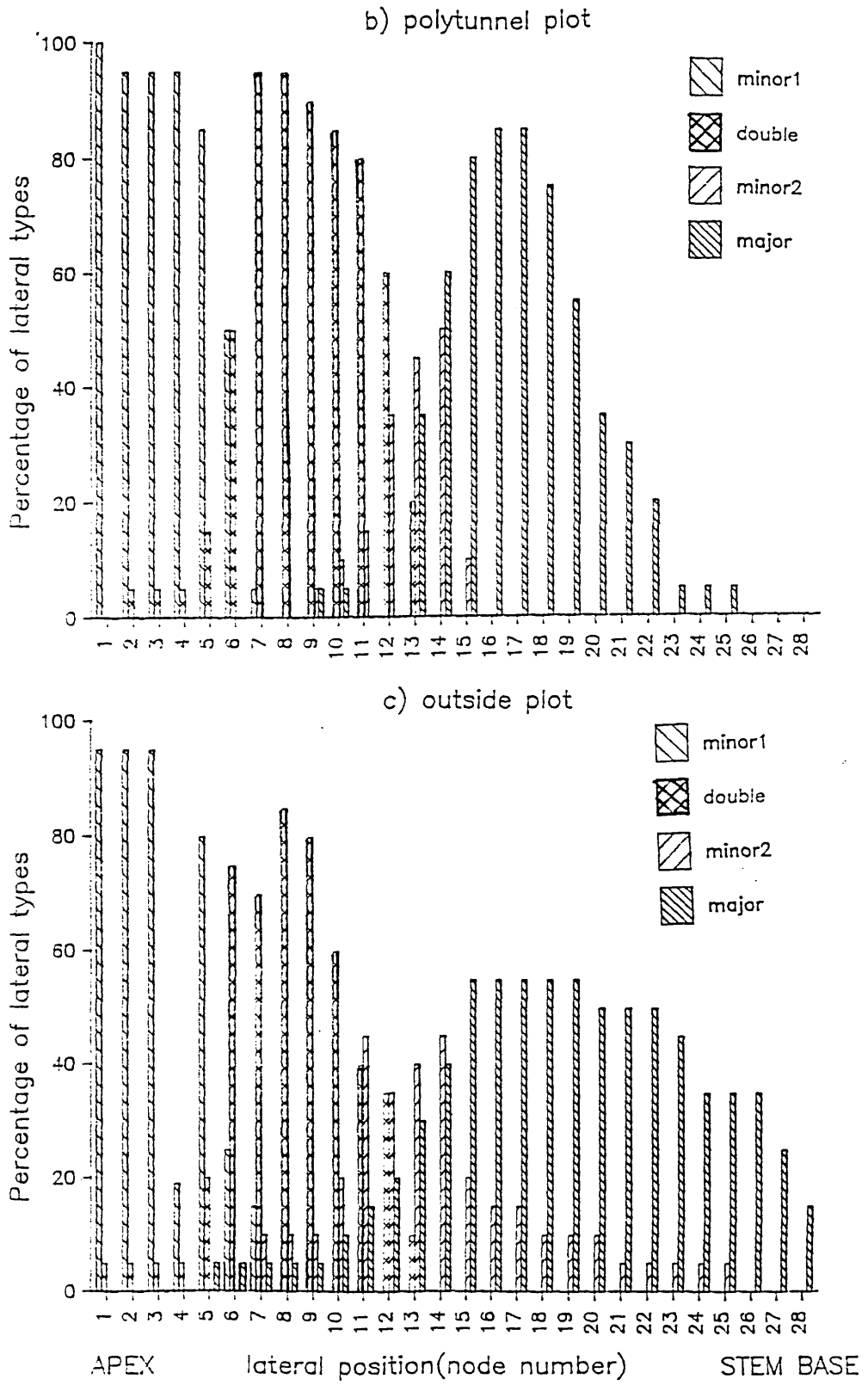
There was a significant difference in the number of laterals per plant, which was due to both treatments and their interaction. Outdoor and Grade D mother plants produced the most laterals and the largest shoot diameters. In contrast, lower weight mother plants produced canes with higher bud numbers (per lateral) (Tables 4.5, 4.6 and 4.7).

Plate 4.1 Lateral morphology at different lateral positions on the cane. a) minor lateral, b) double lateral.

Plate 4.1 Lateral morphology at different lateral positions on the cane. c) major lateral.



4.3a Distribution of lateral types with respect to lateral position on the cane for the: a) glasshouse plot, (see text for definitions and statistical analysis).



4.3b - c Distribution of lateral types with respect to lateral position on the cane for the: b) polytunnel plot, c) outside plot. (see text for definitions and statistical analysis).

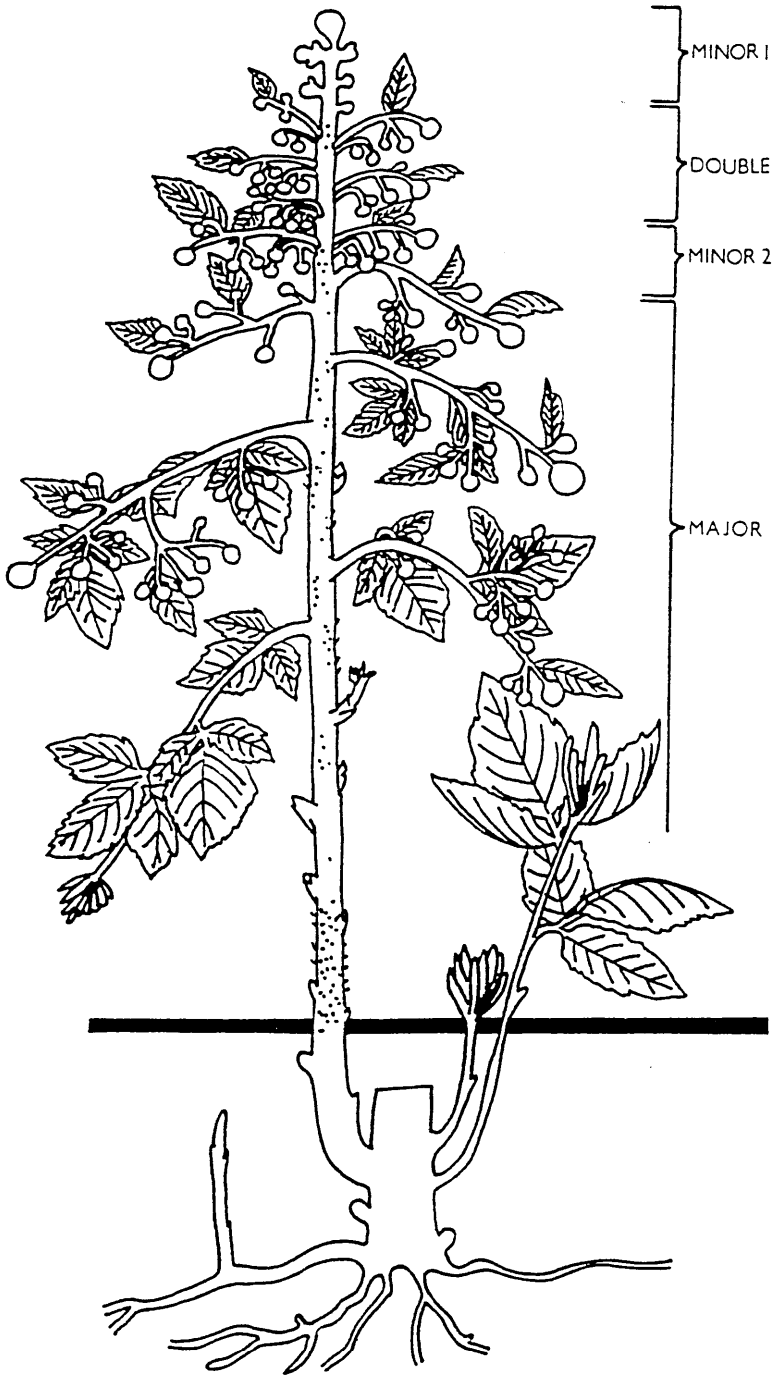


Figure 4.4 Mature cane architecture to show the relationship between lateral morphology and lateral position on the cane.

Table 4.5 Summary of environmental treatment effects on yield components

components (per plant)	environmental treatment means			significance	
	G[3]	P	O	P	$LSD_{0.05}$
shoot number at harvest	3.65	3.80	9.21	<0.001	2.31
number of laterals (number of fruitful nodes)	28.8	37.6	50.3	<0.001	8.83
number of berries per lateral	5.03	5.66	3.21	0.006	1.50
fruit weight (g)	93.3	154.2	157.2	<0.001	19.42
fruit number	127.3	184.2	120.0	<0.001	21.07
number of fruit buds set	175.9	236.6	172.4	<0.001	31.31
% fruit set	54.23	59.10	48.02	<0.001	4.65
number of buds/lateral	10.45	9.79	7.96	ns[4]	ns
mean berry weight (g)	0.747	0.865	1.362	<0.001	0.15
mean fruit weight per lateral (g)	3.80	4.57	4.46	ns	ns

[3]Where; G - glasshouse, P - polytunnel and O - outside plot.

[4]ns - no significance between treatments

Table 4.6 Summary of grading treatment effects on yield components

components (per plant)	grading treatment means				significance	
	A	**B**	**C**	**D**	**P**	$LSD_{0.05}$
shoot number at harvest	4.27	4.48	6.47	7.00	ns	ns
number of laterals (number of fruitful nodes)	26.3	36.4	46.3	46.4	<0.001 (0.005 E x G)[5]	10.21 (17.67)
number of berries per lateral	5.83	5.06	4.01	3.63	ns[6]	ns
fruit weight (g)	129.2	140.3	131.2	138.9	ns	ns
fruit number	136.1	145.9	147.2	146.0	ns	ns
number of fruit buds set	177.8	202.3	197.8	201.8	ns	ns
% fruit set	52.53	52.95	54.04	55.61	ns	ns
number of buds/lateral	12.16	10.25	7.71	7.48	0.001	2.53
mean berry weight (g)	1.04	0.998	0.926	0.997	ns	ns
mean fruit weight/lateral (g)	5.74	4.74	3.19	3.44	0.028	1.85

[5] ExG - significant interaction between environment and grading treatments.

[6]ns - no significance between treatments.

Table 4.7 Summary of environmental treatment effects on mature canopy structure

components (per plant)	environmental treatment means			significance	
	G[7]	P	O	P	$LSD_{0.05}$
total fresh weight (g)*	249.6	378.1	451.6	<0.001	47.20
total dry weight (g)*	77.2	125.5	139.6	<0.001	13.44
dry weight of leaves (g)	43.5	59.6	68.3	<0.001	7.06
dry weight of stems (g)	18.01	38.17	46.54	<0.001	4.78
dry weight of laterals (g)	18.7	24.7	27.7	0.029	6.62
shoot diameter (at 5cm above soil level) (cm)	0.622	0.714	0.815	0.001 (<0.001 E x G)[8]	0.09 0.19
total shoot height (cm) at harvest	235	333	455	<0.001	78.70
maximum leaf number	105.6	95.4	41.4	<0.001	14.39
total leaf area (cm^2)	8232	8318	10225	0.026	1608.83

* total does not include fruit weight.

Leaf number was greatest in glasshouse and grade D plants. Total leaf area, total dry weight (also fresh weights) for above ground plant parts and total shoot height were all significantly greater for outside-plot plants. Overall, leaf area, total dry weight, shoot diameter, lateral number and total shoot height were greater in outside-plot plants (Tables 4.7 and 4.8).

[7]Where; G - glasshouse, P - polytunnel and O - outside plots.

[8]ExG - significant interaction between environment and grading treatments.

outside-plot plants (Tables 4.7 and 4.8).

Table 4.8 Grading treatment effects on cane structure

components (per plant)	grading treatment means				significance	
	A	**B**	**C**	**D**	P	$LSD_{0.05}$
total shoot height (cm) at harvest	269	326	324	444	0.003	90.98
maximum leaf number	70.4	75.8	78.1	98.9	0.007	16.62

4.3.4 The effect of treatments on the rate of shoot development

4.3.4.1 Rate of shoot maturity

The variables chosen to measure the development of the plant shoot population and canopy were total shoot height (and mean shoot height), leaf number and shoot number.

Total shoot height (Figure 4.5)(Appendix 4.1, Table 4.1.2) for glasshouse and polytunnel plants showed a clear "plateau" (sudden slowing down and cessation in shoot elongation). Neither "plateau" appeared to coincide with any specific phenological stage. Outside plants showed a continuous increase in shoot height throughout the growth period. Shoot height was significant initially between grades (grade D plants always significantly taller)(Appendix 4.1, Table 4.1.3) and finally between environments.

The rate of shoot elongation (expressed in centimetres of total shoot height produced per day) (Figure 4.6)(Appendix 4.1, Table 4.1.3) displayed a period of rapid elongation, which reached a peak at about the same time as the appearance of terminal flower primordia (approximately 79 days) in glasshouse and polytunnel plants. This dropped nearly to zero and then rose again. Outside plants peaked initially at about 100 days and again at 129 days from planting, but the overall rate did not drop as low as for plants in the other two plots. Glasshouse and polytunnel

outside-plot plants. Rates among grades were significantly higher for grade D plants (Appendix 4.1, Table 4.1.5).

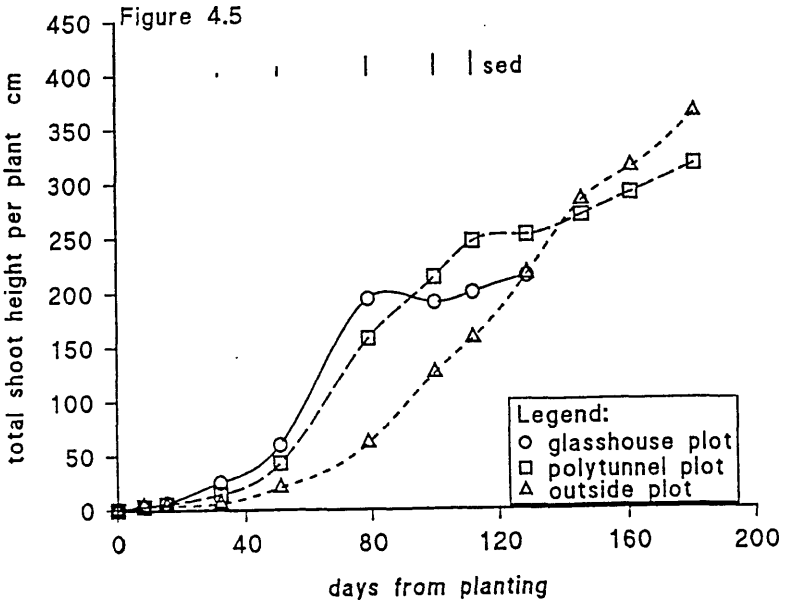
Mean shoot height (Figure 4.7)(Appendix 4.1, Table 4.1.6) reached a maximum for all plots at about the same time as terminal bud anthesis. It was significantly lower in plants treated in the outside plot. There were few significant differences between grades (Appendix 4.1, Table 4.1.7).

Shoot numbers (Figure 4.8a)(Appendix 4.1, Table 4.1.8) were not significantly different between environments until 129 days after planting. This coincided approximately with terminal berry ripening. In contrast to this, shoot numbers were significantly different between grades throughout the experiment (Figure 4.8b)(Appendix 4.1, Table 4.1.9). Therefore, the same number of shoots must have been smaller in height in the outside plot, maturing over a longer period of time and gradually increasing in number over the whole growth period.

Leaf number (Figure 4.9)(Appendix 4.1, Table 4.1.10) continued to increase after terminal flowering, reaching a maximum at about the same time as cropping for all plots. The total leaf number per plant was significantly higher for glasshouse plants. The lower number of leaves on outside plot plants indicates a lower number of nodes per shoot. Grade D plants produced the highest number of leaves throughout the experiment (Appendix 4.1, Table 4.1.11). Total leaf number counts gave no distinction between primary leaves on the main shoot axis and secondary leaf production on the laterals.

4.3.4.2 Shoot population establishment

Grading had a significant effect on shoot number, except towards the end of the cropping period, grade D plants producing and sustaining the greatest number of shoots and grade A the least. The population of shoots per plant was dependent on the grading system.



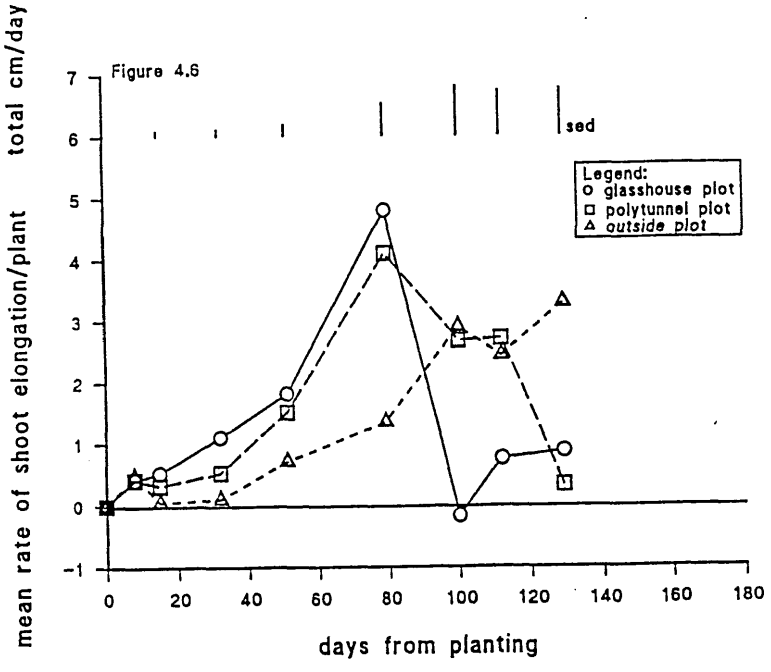


Figure 4.5 Total shoot height (sum of total shoots) per plant for each environmental treatment

Figure 4.6 Mean rate of shoot elongation (centimetres of total shoot height per plant per day) for each environmental treatment

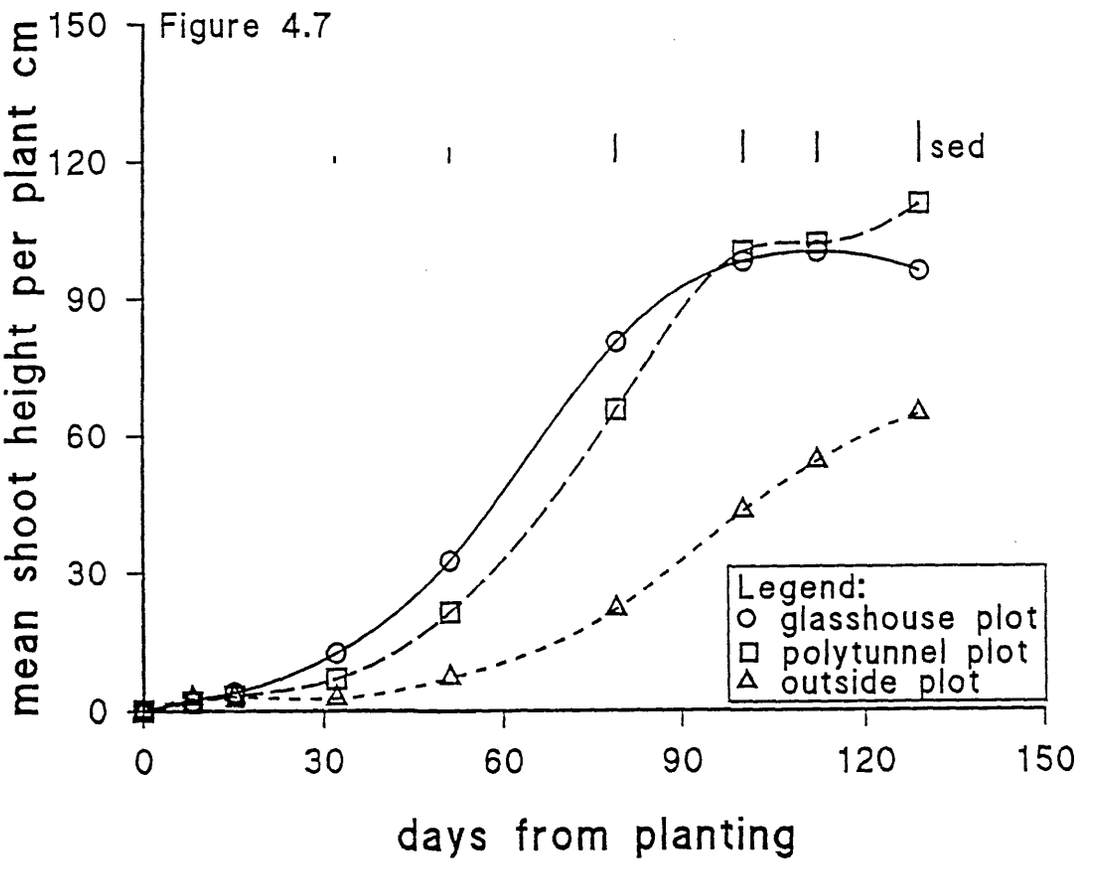
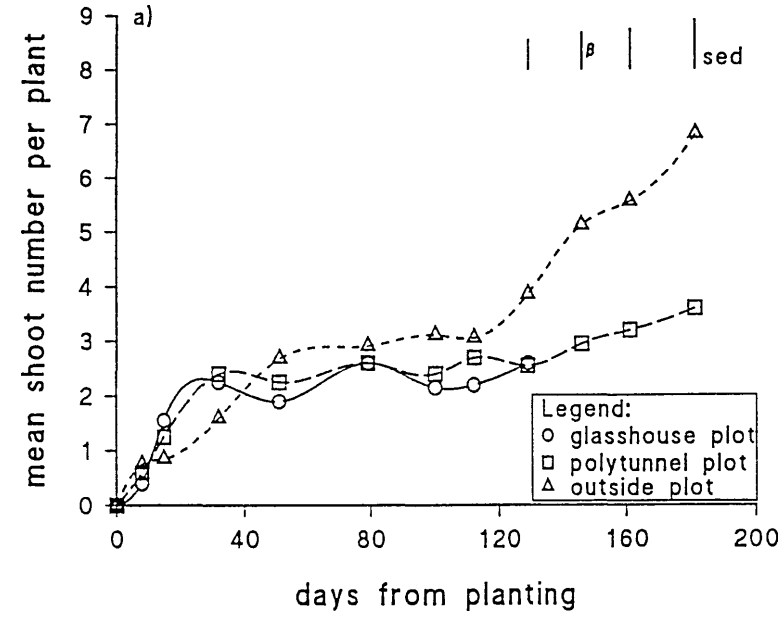


Figure 4.7 Mean shoot height per plant for each environmental treatment



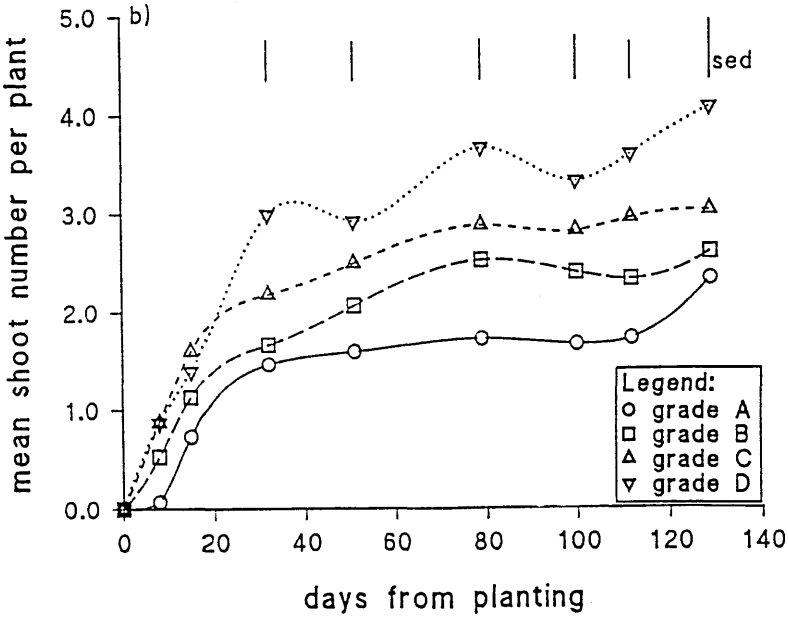


Figure 4.8a - b The relationship between mean shoot number per plant and a) environmental, b) grading treatments (ß - sed to compare two environmental treatments only).

All grades (and environmental treatments) produced a curve, which illustrated bounded population growth (Newby, 1980), reaching an initial maximum of approximately 2 (grade A), 2 - 3 (grade B and C) and 4 (grade D) shoots per plant. This was followed by a second maximum of 4, 5, 6 and 6 (grades A - D, respectively) shoots per plant, although, for this second maximum glasshouse plants had been harvested, so that the number was sampled from polytunnel and outside plants only (not shown in Figure 4.8b, see Appendix 4.1, Table 4.1.9). This "double" logistic curve indicates the establishment of two populations of shoots, from one parent stool. Flowering and fruiting occurred towards the end of the lifetime of the first population, as new shoots were formed at the commencement of fruiting.

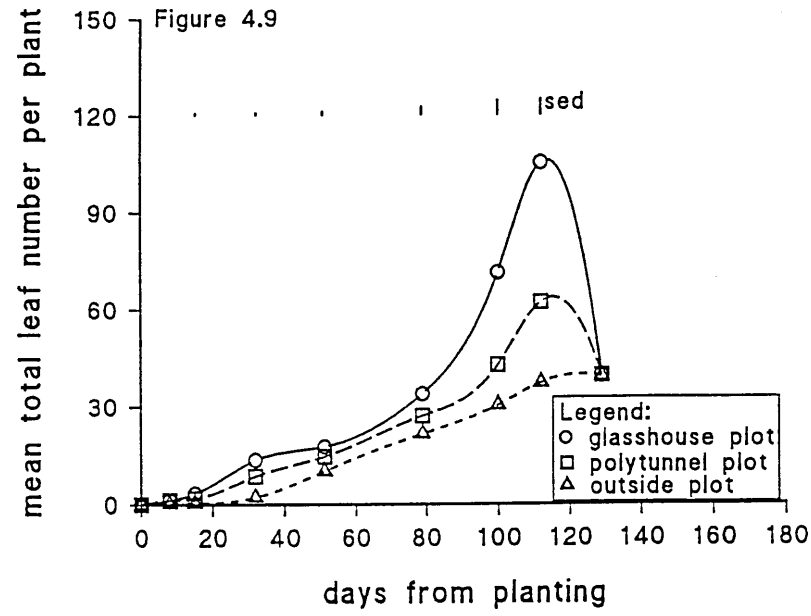
The rate of shoot production was significant between environmental treatments (Figure 4.10)(Appendix 4.1, Table 4.1.12). The initial rate of establishment was rapid and then dropped to a minimum (negative values were indicative of shoot mortalities due to self-thinning), followed by gradual recolonisation with new shoots. All plots exhibited an initial establishment period. However, once the maximum number was established in glasshouse and polytunnel plots, the existing shoots elongated without any further increase in numbers until their maturation and death.

Outdoor plants exhibited shoot production and elongation simultaneously. There appeared to be a specific cohort of shoots in glasshouse and polytunnel plants, which developed and died *en masse*. There were few significant differences between grades (Appendix 4.1, Table 4.1.13).

Correlation coefficients were calculated (Table 4.9) to find out if there was any dependence of the overall yield and shoot number on the original plant characteristics. The regression equation obtained for the relationship between shoot diameter and total fresh weight of the mother plant was used in succeeding experiments to grade plants:

$$W_0 = 48.79 d_0 - 17.19 \qquad (4.1)$$

Where: W_0 = fresh weight of the mother plant (g), d_0 = mean shoot diameter of mother plant canes (taken at 4cm above soil level)(cm).



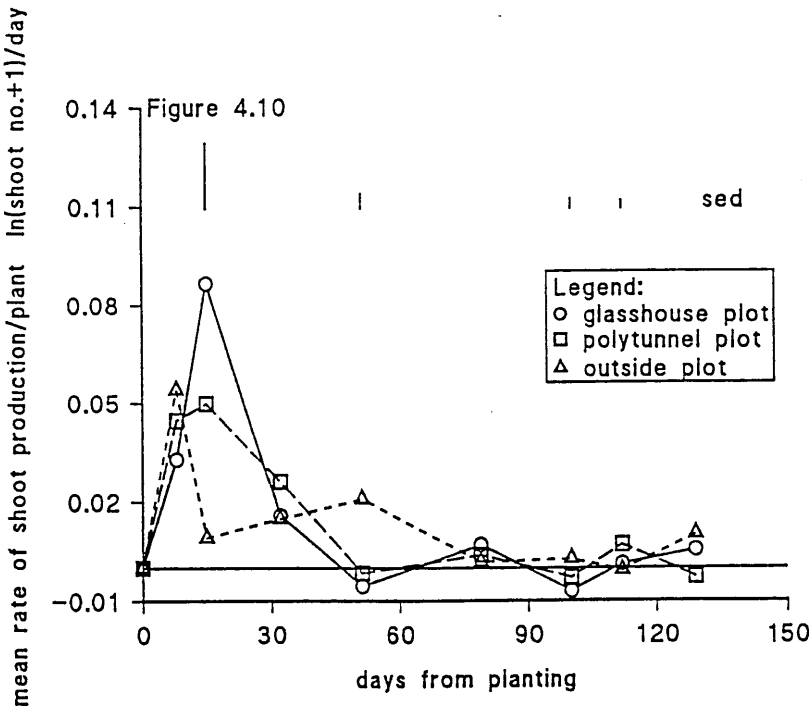


Figure 4.9 The change in mean total leaf number per plant for each environmental treatment.

Figure 4.10 Change in mean rate of shoot production per plant (ln (shoot number +1) per day) for each environmental treatment.

Table 4.9 Correlation coefficients (r) to test the dependence of total yield and shoot number on grading characteristics (mother plant fresh weight, shoot diameter and shoot number)

VARIABLE	fresh weight of mother plant (g)	shoot number of mother plant	shoot diameter of mother plant (cm)	shoot number at harvest	total fruit weight per plant (g)	total fruit number per plant
fresh weight of mother plant (g)	1.00	0.65	0.65	0.24	0.02	0.07
shoot number of mother plant	-	1.00	0.25	0.27	0.11	0.01
shoot diameter of mother plant (cm)	-	-	1.00	0.25	0.03	0.03
shoot number at harvest	-	-	-	1.00	0.25	0.19
total fruit weight per plant (g)	-	-	-	-	1.00	0.46
total fruit number plant per plant	-	-	-	-	-	1.00

NOTE: Where the critical value = 0.222, at P = 0.05 for 56 degrees of freedom

This ensured that different grade plants were spread evenly between treatments.

As shown by the correlation coefficients, there were no clear relationships between mother plant characters and yield or shoot number at harvest.

4.3.5 The effect of treatments on the rate of cropping

Table 4.10 shows the effect of environment on the timing and duration of the cropping period. The start of cropping was also influenced by interaction of grading and environmental treatments. Glasshouse plants cropped earliest and with the shortest season (16.5 days earlier and 12.5 days longer than polytunnel plants, respectively). Outside plants did not crop until 37 days later.

Table 4.10 Environmental treatment effects on the timing and the duration of cropping

components (per plant)	environmental treatment means			significance	
	G[9]	P	O	P	$LSD_{0.05}$
start of cropping (days)	115.1	131.6	152.3	<0.001 (0.004 E x G)	5.35 (10.70)
length of cropping period (days)	43.9	56.4	66.8	<0.001	5.41

4.3.6 The effect of treatments on yield and cropping period

4.3.6.1 Yield

Tables 4.5 and 4.6 show the effects of treatments on some of the components of yield (Hoover *et al.*, 1986). Shoot number at harvest and number of laterals were all significantly higher for outside plants. The weight of fruit produced per plant was significantly lower in glasshouse plants. Polytunnel plants produced the greatest number of berries per lateral. The number of berries and the number of buds set (and percentage bud set) were significantly higher for plants grown in the polytunnel. Berry size, however was significantly higher in outside-grown plants.

[9]Where; G - glasshouse, P - polytunnel and O - outside plot.

There were significant differences in yield components for grading treatments. Lower grade plants (grades A and B) produced greater fruit weights per lateral and fruit bud numbers than the higher grades (Tables 4.5 and 4.6).

4.3.6.2 Patterns of crop development over the cropping period

The percentage of the total yield per plant (weight and number of fruit picked per day) was calculated to show the spread of cropping (Mason and Topham, 1981). Figures 4.11a - c and 4.12a - c respectively show clearly the protracted cropping season of the outside plants compared with glasshouse plants. Typically, berry numbers increased to a maximum and berry weight fluctuated (according to position of ripe fruit on the cane). Peak cropping was difficult to predict in the glasshouse (Figure 4.11a) as there was a mid-season drop in production, possibly due to the delayed development of secondary and tertiary fruit. Polytunnel cropping was more consistent (Figure 4.11b) and longer; cropping in the outside-plot was longer still, but less consistent on a daily basis (Figure 4.11c). Glasshouse berry numbers were initially very low (possibly due to scorching of terminal buds) but later increased markedly. Individual berry size remained very low. Polytunnel plants produced a more consistent berry size with a typical normal distribution. Outside plants showed the same pattern, but the development time for secondary and tertiary fruit was much longer. Generally, outside and polytunnel plants produced a more consistent size as the number and weight of berries followed the same pattern. The time from planting to 50 % harvest was 133 days (glasshouse), 154 days (polytunnel) and 192 days (outside plot).

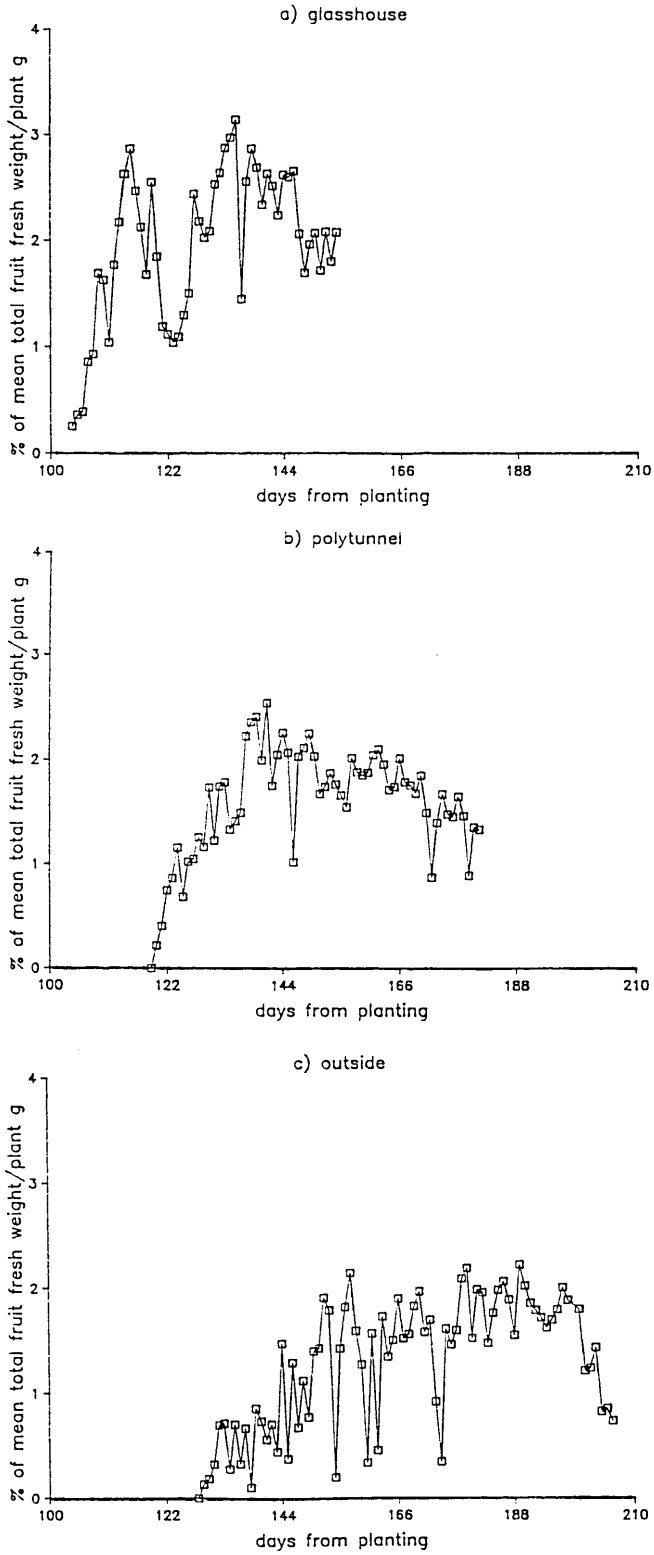


Figure 4.11a - c Change in mean fruit fresh weight (expressed as a percentage of the total yield per plant) over the cropping period. Where: a) glasshouse plot, b) polytunnel plot and c) outside plot

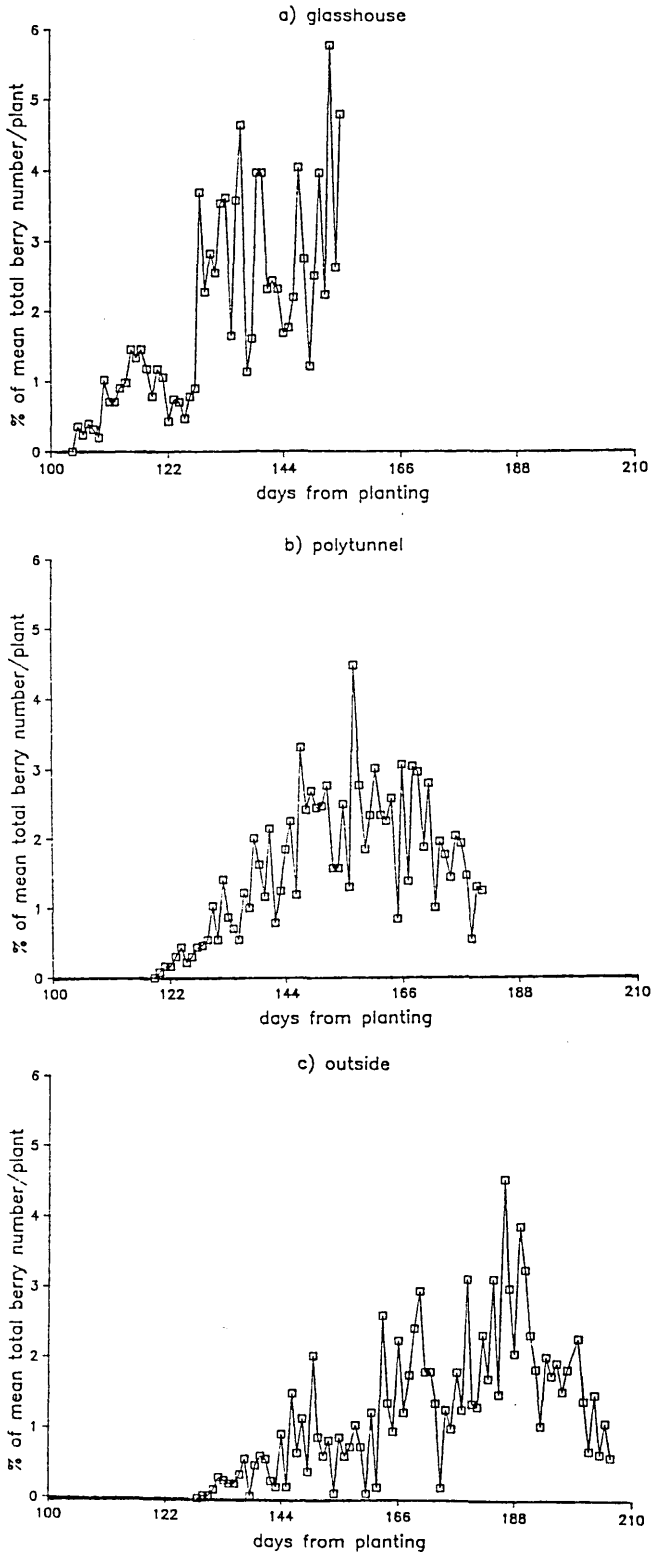


Figure 4.12a - c Change in mean berry number (expressed as a percentage of total number per plant) over the cropping period. Where: a) glasshouse plot, b) polytunnel plot; c) outside plot

4.4 DISCUSSION

4.4.1 The implications of grading for plant growth and development

As can be seen from the results, shoot number was significantly different among grades. Plants were measured and graded in order to find out what aspect of the mother plant or stool could be related to the ensuing shoot population, and whether this could be applied to commercial practice. As replacement shoots are produced from basal buds for each successive year's population of canes, some aspect of the mother plant may be related to the number of basal buds present, thus producing a relationship to determine the number of potential shoots by estimating basal bud number from grading characteristics. As none of these characteristics related directly to final shoot number, it can be assumed that the relationship is more complex and needs further investigation.

The significance of grading was shown in the amount of vegetative growth (greater with respect to grade D plants) during development and at maturity. Of special note was the greater number of laterals produced in higher-grade plants, although this was offset by the high bud number and fruit weight per lateral in lower-grade plants. Even though more shoots were produced by higher-grade plants this did not appear to relate to yield. Overall, the rate of emergence of shoots and the number of shoots were grade dependent.

Rice and Duna (1986) studied the effect of initial plant size on the yield components of two strawberry cultivars. Early yields correlated highly with initial plant fresh weight and crown diameter. However, late yields were unaffected by plant size. This suggests (as is the case with cv. "Autumn Bliss") that the length of time from planting to cropping was too long for original plant characters to have any effect on the final yield.

Commercially, grading is carried out on plants by visual assessment of mother cane quality. MacKerron (1978) carried out grading on spawn cane according to commercial practice and found that this had no bearing on the number or height of shoots produced. He concluded that grading by cane quality was misleading, but grading by root mass was more accurate. The grading system employed here would

therefore prove important in bringing about rapid establishment and vigorous growth of the young shoot population. Grade D plants showed most significant differences over and above the other three grades; mother plants were typically in the range of 22.5 - 114.5g (average shoot number 1 - 12, shoot diameter 0.6 - 1.6mm).

4.4.2 Canopy establishment with respect to shoot population per plant

Leaf number and shoot height contribute to canopy establishment, but both depend on the rate of initiation of the shoot population. Outside plants produced, a large number of shoots, with fewer leaves and greater dry weight of plant parts, at a slower rate, whereas polytunnel and glasshouse-grown plants produced fewer, taller shoots, with more leaves which developed rapidly and simultaneously. This suggests that the plants in these environments tend to grow and develop in an age-class or cohort, flowering and fruiting together before more shoots could establish. This may be due to limitations in the amount of available light and resources in the roots or other factors. Shoots were less effective as sinks during fruiting than during vegetative development. The apex does not act as a sink in the mature cane. Fruits form slight sinks, but a large proportion of assimilate translocation goes to developing replacement shoots (Erasmus and Staden, 1983).

It was difficult to see, by the nature of the data obtained, when shoots emerged and for how long they survived, *ie.* their individual emergence and death rates. This information would give more of an indication of individual shoot age and of when the population age structure changes (whether production balances out senescence in a continual renewal of shoot population). The mother plant (stem base, including basal buds and the root system) is the true plant (genet) and the shoots (ramets) are not the true progeny, but can be likened to a branch system. However, the extent of plasticity of the plant form means that it reacts to stress by the "birth" and death of its organs. Therefore these organs can be treated as individuals as they have an age structure (Harper, 1977; White, 1984). In order to understand and model the plasticity of the plant architecture it is important to consider the timing of individual shoot production.

4.4.3 Environmental effects on growth and development

Very little research has been done to examine the effects of environment on the growth and yield of raspberries (Dale, 1989). Keep (1988) stated that climate (rainfall and temperature), together with daylength and the length of the growing season, all have a marked effect on the season of autumn-fruiting raspberries. However, there is little evidence to back this up.

4.4.3.1 The effect of ambient temperature on the rate of shoot maturity and crop development

The rate of shoot elongation reached a maximum at about the same time as terminal flower primordia appearance. Maximum mean shoot height occurred at the same time as terminal flower anthesis, although the maximum exhibited for total shoot height did not particularly relate to either. The latter was probably as a result of the extension of younger shoots. Similar data for cv. "Heritage" in growth chambers at 25°C, 16°C and 13°C showed the same rapid development and termination of shoot elongation for plants held at 25°C. The two lower-temperature growth cabinets produced plants with taller canes and longer internodes (Ourecky, 1976).

Although node number was not recorded, shorter outdoor grown plants produced significantly greater numbers of laterals, which indicated the production of a larger number of nodes in these shoots. However, nodes are produced at a constant rate on the vegetative shoot, so that variations in the rate at which the shoot elongates lead to differing internode lengths (Jennings and Dale, 1982; Dale, 1989). Greater lateral production may be due to higher light levels or to the extent of release of the lateral buds from correlative inhibition.

Release of basal buds throughout the growth period and the higher light levels in the outside plot were causal in the greater number of shoots produced.

The timing of flowering influences the size and architecture of the mature cane. Cultural practices for raspberry production leading to precocious flowering had

no effect on yield (Crandall and Chamberlain, 1972). This agrees with the results obtained here as similar yields were obtained from polytunnel plants and outside-plot plants indicating that other factors were involved. The time of flower initiation was not examined in detail for this experiment. The interaction of these plant components with temperature needs further investigation and will be discussed in the next chapter.

4.4.3.2 Environmental effects on yield components and cane architecture

The environment affects the sequential development of the fruiting cane architecture (Dale 1986). There is a large body of research on yield components in raspberry and their interactions. Due to the relative complexity of the fruiting cane structure, any number of components can be said to have an effect on the overall yield. The literature on these components will be reviewed and specific components studied in the following chapter. These results verified those produced by Dale (1986). Pot-grown plants of six cultivars (tipped at 25 nodes), grown in a glasshouse, produced longer laterals and a greater number of buds, flowers and fruit per lateral than outdoor-pot -grown plants or field plants.

Significantly larger mean berry weights for outside plot plants were probably due to other environmental factors apart from temperature, such as reduced water stress.

4.4.3.3 Other environmental effects on growth and development

Some basic assumptions were made during the course of the experiment. These were that light, water availability and nutrients were not limiting (daylength assumed to have no effect on the timing or rate of flowering) and that the plants were disease-free. However, due to the low light levels experienced, an infestation of *P. ulmi* Koch. and leaf scorching it is important to look at the effects of other environmental factors on shoot growth.

4.4.3.3.1 Water stress

The water content of the leaves was significantly less in plants treated in the polytunnel than those treated in the glasshouse and outside-plots (54.78% compared with 55.97% and 56.12% respectively; $LSD_{0.05}$ = 0.81). Goulart (1989b) studied the effect of water stress in the cultivars "Heritage" and "Titan" in a glasshouse environment. She showed that stress decreased the node number and postulated that this had a direct effect on reducing the number of inflorescences. In addition to this Ben-Tal (1986) discusses the issue that factors which inhibit growth promote flowering and gives the example of flower promotion in water-stressed *Citrus* trees. Water stress hastens the development of raspberry floral primordia, but reduces yield, as it affects the amount of stored carbohydrate per bud (Crandall and Chamberlain, 1972; Crandall, Allmendinger *et al.*, 1974; MacKerron, 1982).

4.4.3.3.2 The effect of levels of photosynthetically active radiation in each plot

Dry matter accumulation occurs at a rate determined by the amount of intercepted radiation (Porter and Delecolle, 1988). The distribution of flowers and fruit at anthesis and pre-harvest were highly correlated with leaf area. The number of fruit per unit leaf area and per lateral node increased with increasing light exposure in canes of cv. "Willamette" (Braun *et al.*, 1989). These observations may explain the greater number of laterals and greater dry-matter content of canopy plant parts and total leaf area exhibited in shoots of plants grown outside.

4.4.3.3.3 Wind exposure

Wind exposure is thought to be a factor causing bud suppression (Jennings *et al.*, 1986) and is known to reduce growth and yield (Waister, 1970). The cultivar "Malling Jewel" produced taller, higher yielding canes in sheltered plots (wind screened) compared with exposed plots (Waister, 1970). Jennings (1964a) found that exposed canes tended to be shorter, with shorter internodes.

Outside plants may have been affected by wind damage, although the plot was sheltered. This may have been the cause of the low mean cane heights and low percentage fruit set and fruit number, due to lateral damage, in these plants.

4.4.3.3.4 Stress as a result of pot-bound roots

Root parameters were not measured in this experiment, however at harvesting roots were entirely pot-bound. Cultivation of avocado (*Persea americana* Mill.) and *Citrus* sp. trees in pots of different volumes showed that, where roots were confined to small pots, vegetative growth was reduced and flowering was earlier and more profuse (Ben-Tal, 1986). This was not displayed in the graded plants of this experiment as plants with larger root systems produced a greater number of shoots, and hence more vegetative growth than this evidence indicates.

4.4.3.3.5 Frost damage

Outside plot plants were exposed to freezing temperatures on two occasions over the experimental period. The first was in April 1988 (with a minimum of -2°C) and the second in November (minimum of -4°C). Raspberries held for 45 minutes in special frost chambers at -2°C had reduced yields (Ruxton and Modlibowska, 1954). Here the critical time was in April during shoot emergence and development, so that this temperature probably caused a certain amount of frost damage.

4.4.3.3.6 Pests and disease

Spider mite infestations (*P. ulmi* Koch.) on glasshouse (and to a lesser extent polytunnel) plants were particularly heavy and caused loss of leaf material. This probably contributed to the contracted cropping period of the glasshouse plants. Severe mite defoliation reduces starch and sugar reserves (Doughty *et al.*, 1972).

4.4.4 The effect of a protected environment on cropping

It is difficult to compare yields with a commercial holding as the plants were pot-grown. Although this controlled the amount of growth, it enabled a study of individual plants to be made in isolation. Goulart (1989a) discusses the use of plant growth regulators to control vegetative vigour in cv. "Heritage". This did not appear to be a problem in cv. "Autumn Bliss", nor should it be necessary to employ growth regulators to advance flowering, unless this was required for a specialised market, as the annual habit of cv. "Autumn Bliss" is not obligate with respect to vernalization treatments.

The difference in total weight of fruit produced per plant was not significant between polytunnel and outside-grown plants. Total berry number and percentage fruit set were higher for the polytunnel plot, although the mean berry weight (berry size) was greater in outside grown plants.

Mason and Topham (1981) modelled daily crop production in order to produce a crop profile, which would predict cropping in order to obtain a suitable economic interval for mechanical harvesting. They found large daily variations in ripe fruit production; fruit ripened in flushes due to frost damage or temperature fluctuations. They required a sufficiently high daily rate of production. The cropping profiles of the three plots varied in length of cropping season significantly and also in the consistency of berry size and number. Although glasshouse plants fruited much earlier there was a large variation in fruit size and number compared to polytunnel plants.

Smaller yields in the glasshouse, as well as the cost of heating, makes it less economically viable than the polytunnel for the commercial cultivation of cv. "Autumn Bliss". The prevalence of spider mite infestations in the polytunnel and glasshouse indicates that these two environments are more favourable to Spider mite than the outside plot.

Overall the results lie in the favour of the use of plastic tunnels to protect the crop from unfavourable environmental conditions, increase the fruit set and promote the fruiting season. These results agree with Dutch and United Kingdom growers

with respect to trials on the use of plastic tunnels to extend the cropping period. Verwijs (1983) and Dijkstra and Van Oosten (1984) covered the crop from early spring onwards. Fruit size was improved by removing the tunnel sides during cropping to slow down ripening. Yields were improved by 12% and were 15 days earlier (cropping was brought forward by approximately 25 days) than field-grown equivalents. Verwijs (1983) concluded that although providing protection was quite labour intensive, there was a high turnover and it provided the crop with frost protection. He suggested the need to provide bees as pollinators, but the high fruit set in this experiment contradicts this. Partis (1987) found that 50% harvest dates and fruit size were similar for crops from plots only protected during bad weather and unprotected plots. Burgess (1986), also studying the effect of protection during cropping only, found that protection saved wastage (80-90% marketable fruit) and extended the cropping period (when it would otherwise have rotted on the canes). Nonnecke and Taber (1989) studied the effect of polyethylene covers on the rate and extent of growth in raspberry. Covers were employed for a month (April to May), but they had no effect on the subsequent cane height or node number.

Clearly protection for part of the developmental cycle has little effect apart from improving the existing fruit quality. As discussed above the effect of grading (due to the plasticity of raspberry morphology and architecture) appears to have no bearing on the final yield. To encourage rapid shoot elongation Hoover *et al.* (1989) suggested the use of maximum temperature differentials in polytunnels, in order to subject plants to more heat units to produce an early crop.

All of this serves as evidence for the employment of longer term protection, as demonstrated here and in Holland, if there is a need for intensive cultivation. Goulart (1989a) suggests such a need in the United States due to a high demand, which has increased the market value of raspberries. From the evidence presented in the last chapter, cv. "Autumn Bliss", unlike the other American autumn-fruiters, does not require chilling to induce flowering. It is a suitable candidate, therefore, for all-year-round protected cropping.

4.5 CONCLUSIONS

Individual plants are composed of a population of shoots, which can be considered as individuals. Two populations were produced over the growth cycle; the first was rapid (invasive) and the second slower, as it competed with the senescing existing population. There is a need for further investigation of the population dynamics of the plant.

Shoot development was simultaneous as a cohort in glasshouse and polytunnel plants, however less uniform development was shown in outdoor plants. Grading had a significant effect on the amount of vegetative growth, on the establishment rate and the overall size of the shoot population per plant.

Knight (1986) and Jennings (1988) called for improvement of autumn-fruiting cultivars by advancing and condensing the cropping season. This was shown in glasshouse plants.

Other environmental effects such as water stress, wind and frost damage had some effect on crop growth, but light levels at each plot probably had the most direct effect. Overall, environmental factors probably have an indirect effect on flower bud initiation, through effects on the physiology of the plant as a whole (Jennings, 1988). Yields from the polytunnel plot agree with the commercial research cited. The polytunnel is a suitable option for commercial protected cultivation of cv. "Autumn Bliss".

CHAPTER 5

THE EFFECT OF DIFFERENT CONSTANT DAY/NIGHT TEMPERATURE TREATMENTS ON THE RATE OF FLOWER INITIATION AND YIELD COMPONENTS OF FIRST COHORT SHOOTS IN PLANTS OF CV. "AUTUMN BLISS" EXPOSED FROM PLANTING TO TERMINAL FLOWER BUD APPEARANCE

5.1 INTRODUCTION

The last chapter showed significant differences in the timing and length of cropping, as a result of plants being exposed to different environmental regimes. The rate of shoot elongation was higher, with higher mean temperature of environment.

Keep (1961) and Ourecky (1976) found that the autumn-fruiting character was additive. That is, genes controlling this character interact, but show no dominance (Ayala and Kiger, 1980). Keep (1961) initially stated that variation in the character was due to the interaction between meristem flowering and cane elongation with the environment. She later (Keep, 1988) qualified environmental effects as climate (temperature and rainfall), daylength and length of growing season. Flowering is determinate and therefore associated with the cessation of shoot elongation. Williams (1960) and Hudson and Williams (1961) proposed a dual control mechanism for meristem flowering, concerning in some way the physiological age of an individual shoot and temperature. Goulart (1989a) hypothesised that this could be related to the size of the shoot or leaf number. Research on growth regulators (and water stress treatments) designed to suppress vegetative growth (Redalen, 1980; Braun and Garth, 1984a; Braun and Garth, 1986) shortened the length of the vegetative phase (Crandall and Chamberlain, 1972; Crandall, Allmendinger *et al.*, 1974) promoting flower initiation (Crandall and Chamberlain, 1972; Braun and Garth, 1986). This supports the findings above, which suggests that temperature affects the rate of shoot development and this in turn affects flower induction and initiation.

This chapter aims, in part, to investigate the effect of temperature on the rate

of flowering with respect to shoot age by looking at individual shoot development in first cohort shoots.

Dale (1989) proposed more research on the effect of environment on yield in *Rubus*. He suggested modelling the growth of the first year shoots and testing this against growth in different environments. He noted that this would be particularly applicable to autumn - fruiting cultivars. Models have been developed for other crops of determinate growth, for example maize and corn (Tollenaar *et al.*, 1979; Warrington and Kanemasu, 1983a; Russell and Stuber, 1984; Grant, 1989). For example, Kirby (1985) described and modelled the phenology of wheat (*Triticum aestivum* L.) based on the rate of production and duration of spikelets from emergence to flowering. The determinate nature of shoot development in this cultivar is important in modelling the timing of the release of lateral buds, subsequent from flower initiation.

The range of papers written on the yield components of *Rubus* is wide. There is considerable variation with respect to definitions, relative importance and the relationship of components to each other. It is important to define these components, to gain a clearer understanding of their relationship to yield and in deciding which are suitable for use in the model.

5.1.1 Definition of yield and yield components

Variation in yield can be looked at from three different angles: biological yield (t/ha of dry matter), fruit yield (translating dry matter into harvestable yield) and economic yield (higher crop value with lower production costs) (Dale, 1989). Marketable yield has been modelled as a function of cane number, lateral length, node number, reproductive node number, fruit bud number, fruit number, fruit set, berry size and weight of marketable fruit. It was found that only cane number, lateral length and an index of fruit size were necessary to accurately estimate yield (Freeman *et al.*, 1989).

Conventionally, breeding is carried out in order to obtain a "good bearing surface". In the case of autumn-fruiters, this means a moderate number of strong

early emerging shoots, with well developed laterals which crop well down the length of the cane (Jennings, 1988; Knight *et al.*, 1989; Jennings and McGregor, 1989).

The principal yield components derived from such studies were found to be:-

i) Cane height (Darrow and Waldo, 1933; Wood *et al.*, 1961; Oydvin, 1969; Fejer and Spangelo, 1974; Orkney and Martin, 1980; Dale, 1986).

ii) Cane diameter (Darrow and Waldo, 1933; Lawson and Waister, 1972; Crandall, Allmendinger *et al.*, 1974; Crandall, Chamberlain and Biderbost, 1974; Dale and Daubeny, 1985; Dale, 1986).

iii) Node number (Jennings and Dale, 1982; Hoover *et al.*, 1988; Freeman *et al.*, 1989).

iv) Shoot number (Darrow and Waldo, 1933; Wood *et al.*, 1961; Ljones and Sakshaug, 1967; Oydvin, 1969; Lawson and Waister, 1972; Crandall, Allmendinger *et al.*, 1974; Crandall, Chamberlain and Biderbost, 1974; Waister, *et al.* 1977; Hoover *et al.*, 1986; Hoover *et al.*, 1988; Nehrbas and Pritts, 1988; Freeman *et al.*, 1989).

v) Cane vigour (Darrow and Waldo, 1933; Crandall, Chamberlain and Biderbost, 1974).

vi) Number of fruiting laterals (Wood *et al.*, 1961; Fejer and Spangelo, 1974; Crandall, Chamberlain and Biderbost, 1974; Orkney and Martin, 1980; Jennings and Dale, 1982; Hoover *et al.*, 1986; Redalen, 1986; Dale, 1988; Hoover *et al.*, 1988; Nehrbas and Pritts, 1988; Jennings and McGregor, 1989; Knight *et al.*, 1989).

vii) Lateral productivity (Wood *et al.*, 1961; Crandall, Chamberlain and Biderbost, 1974; Ourecky, 1975; Ourecky, 1976; Orkney and Martin, 1980; Hoover *et al.*, 1986; Dale, 1988; Hoover *et al.*, 1988).

viii) Lateral type/vigour (Wood *et al.*, 1961; Dale, 1979; Dale, 1988).

ix) Berry number (Ljones and Sakshaug, 1967; Waister and Barritt, 1980; Dale, 1988; Hoover *et al.*, 1988).

x) Berry size/weight (Ljones and Sakshaug, 1967; Oydvin, 1969; Crandall, Chamberlain and Biderbost, 1974; Hoover *et al.*, 1986; Redalen, 1986; Hoover *et al.*, 1988; Jennings and McGregor, 1989; Knight *et al.*, 1989).

5.1.1.1 Cane height

Cane height is positively correlated to yield (Crandall, Chamberlain and Biderbost, 1974; Orkney and Martin, 1980). Taller canes tend to elongate faster, having fewer nodes and fewer laterals (Crandall, Chamberlain and Biderbost, 1974; Jennings and McGregor, 1989). Height is negatively correlated to node number, but positively correlated to cane diameter (Jennings and Dale, 1982). Average shoot height in a stool bed is affected by intraplant competition. As more shoots are produced, individual shoot height decreases (Waister, *et al.* 1977; Wright and Waister, 1982a; Wright and Waister, 1982b).

As shoot-elongation rate and final height are very sensitive to environmental conditions (Chapter 4),(Jennings, 1964a; Ourecky, 1976; Jennings and Dale, 1982; Dale, 1989; Jennings and McGregor, 1989) and shoot height is not a constant character (Jennings and Dale, 1982) they are less suitable as determinants of yield.

5.1.1.2 Cane diameter

Increased cane diameter is related to increased fruitfulness (Lawson and Waister, 1972; Crandall, Allmendinger *et al.,* 1974) with respect to berry number and fruit set. Larger diameter canes have fewer laterals. Berry number is related more directly to diameter than height (Crandall, Chamberlain and Biderbost, 1974). Not surprisingly, therefore, cane diameter is positively correlated to cane height and negatively correlated to node number (Jennings and Dale, 1982; Jennings and McGregor, 1989).

Cane diameter is affected by environment; both thick and thin canes can yield poorly if held in favourable or unfavourable conditions respectively. It relates to the timing of flower initiation. Small diameter shoots initiate flowers more rapidly (Crandall and Chamberlain, 1972; Crandall, Chamberlain and Biderbost, 1974). Early bud growth was exhibited in larger diameter canes and was thought to be related to carbohydrate supply (Crandall, Allmendinger *et al.,* 1974; Waister and Barritt, 1980).

Although cane diameter was found to be unstable for selection purposes (Oydvin, 1969) it is of importance as a measure of assimilate availability to developing buds (Crandall, Allmendinger *et al.,* 1974).

In conclusion, Dale (1989) stated that there "appears to be an optimum diameter for widespread adaptation". This justifies further research into the effect of cane diameter on yield.

5.1.1.3 Node number

Treatments which reduce node number reduce yield (Hoover *et al.,* 1988). Reduction in internode length (*ie.* increase in node number per cane) gave a greater yield in biennial and part-biennial cropping systems (Waister, *et al.* 1977; Wright and Waister, 1982a; Wright and Waister, 1982b). Node number is important as it relates to the number of fruiting laterals (Jennings and Dale, 1982; Jennings and McGregor, 1989) and inflorescence number (Goulart, 1989b). Axillary bud size varies with node position, due to the effects of correlative inhibition (Jennings, 1987; Jennings and McGregor, 1989), thus the development of each bud and subsequently the lateral is influenced by its position on the cane (Dale, 1979).

Nodes were shown to be produced at a constant rate irrespective of environment (Jennings and Dale, 1982; Jennings and McGregor, 1989). This stability of character and the fact that each node relates to the position and vigour of potential laterals highlights node number as an important yield component.

5.1.1.4 Shoot number

Shoot number is an important yield component (Hoover *et al.,* 1986; Nehrbas and Pritts, 1988; Hoover *et al.,* 1988). However, many papers give evidence for a negative correlation between shoot number and yield (Crandall, Allmendinger *et al.,* 1974; Waister, *et al.* 1977; Crandall *et al.,* 1980; Orkney and Martin, 1980; Buszard, 1986; Hoover *et al.,* 1988; Dale, 1989; Freeman *et al.,* 1989). Canes grown in a biennial or part-biennial cropping system (where shoots were allowed to mature

without competition from younger vegetative shoots) produced higher yields due to increased shoot numbers compared with the annual cropping system (Wright and Waister, 1982a; Wright and Waister, 1982b). Plants in experiments, where shoot number was reduced showed considerable ability to compensate by an increase in individual cane productivity (Lawson and Waister, 1972; Crandall, Allmendinger *et al.*, 1974; Waister, *et al.* 1977; Dale, 1989; Freeman *et al.*, 1989). There appears to be an optimum where shoot number is proportional to yield (Sullivan and Dale, 1989), such that shoot numbers above or below this value can lead to reductions in yield.

5.1.1.5 Cane vigour

Cane vigour encompasses the above yield components as it can be defined as a product of the number of canes per row (Sullivan and Dale, 1989; Darrow and Waldo, 1933) and cane size (Crandall, Chamberlain and Biderbost, 1974; Ourecky, 1976). It also includes cane diameter, height and bud number per length of cane and per lateral (Darrow and Waldo, 1933) and relates to fruit number (Darrow and Waldo, 1933; Crandall, Chamberlain and Biderbost, 1974). Cane vigour was shown to be negatively correlated to node number (Jennings and Dale, 1982).

5.1.1.6 Lateral number

Lateral number relates to cane productivity (Orkney and Martin, 1980). It depends on node number (Dale and Topham, 1980; Jennings and Dale, 1982; Jennings and McGregor, 1989) in the cropping zone and the proportion of nodes which develop into laterals (Wood *et al.*, 1961; Hoover *et al.*, 1988; Jennings, 1988). This is influenced by the environment - on average 2/3 of the total nodes per cane develop into laterals (Jennings, 1988). Most important is the productivity of individual laterals. The number of fruit per cane is a measure of individual lateral productivity and the number of laterals (Dale, 1988). Like shoot number, individual lateral productivity increases with a decrease in the number of laterals per cane

(Ourecky, 1976; Dale and Topham, 1980; Dale, 1988).

The laterals, together with the cane population, form the support and framework for the raspberry crop. Some distinction is made in the literature between fruiting and vegetative laterals. All axillary buds are potentially lateral and flower buds (Wood and Robertson, 1957; Waldo, 1934), therefore it is logical to assume that all laterals are fruiting, certainly among autumn-fruiting cultivars.

5.1.1.7 Lateral productivity

Lateral productivity relates to the number and size of berries per lateral. Taller canes tend to have fewer laterals, but individual lateral productivity is increased, correspondingly the same occurs with large diameter canes (Crandall, Chamberlain and Biderbost, 1974). Removal of vegetative shoots around the fruiting cane increases lateral productivity, but not lateral number (Lawson and Waister, 1972; Waister and Barritt, 1980; Crandall, Chamberlain and Garth, 1980; Dalman, 1989). This is more marked on lower laterals (Crandall *et al.*, 1980).

5.1.1.8 Berry number and berry weight

Berry number and berry weight are the components of harvestable yield (Dale, 1989). Fruit number is negatively correlated to the number of fruiting laterals per cane (Dale, 1989). Its relationship between lateral number and lateral productivity is well established (Redalen, 1986; Dale, 1988; Jennings and McGregor, 1989). It is the result of the combination of node number per cane, the ability of the cane to produce laterals and the ability of the node to produce more than one lateral (Dale, 1989).

Berry weight or fruit size relates to ovule number, druplet set and druplet size (Dale, 1989). Berry size increases in response to treatments which reduce berry number (Brierley, 1931; Lawson and Waister, 1972). A high positive correlation was shown to exist between fruit size and leaf area/leaf weight (Khanmai and Brown, 1940).

5.1.1.9 Lateral type/lateral vigour

Lateral vigour (lateral length and node number) increases towards the centre (Brierley, 1931) and base of the cane (Dale, 1979). Lower laterals were shown to yield a 70% greater weight of fruit than upper laterals (Khanmai and Brown, 1940). This vigour also varied with the total number of laterals. The higher the node number per cane the more variation in vigour (Dale and Topham, 1980; Jennings and Dale, 1982). It was concluded that the position of the lateral was important in determining yield components. Vegetative characters for lateral vigour showed more variability than reproductive ones (Dale, 1979).

As the components of lateral characteristics are interrelated, independent variables were isolated to describe the variation in lateral morphology, vigour and productivity (Dale and Topham, 1980). Dale (1979), Dale and Topham (1980) and Dale (1988) described principal components analysis, which resolved three vectors for lateral characteristics. The first vector was denoted General Lateral Vigour which relates to plant shape, *ie.* the number of lateral bearing nodes per cane. This vector was found to be associated with later fruiting laterals, which are located on the lower half of the cane. The second vector was denoted Reproductive Vigour. These laterals were vigorous with a high proportion of fruiting nodes. Reproductive vigour tended to be low in lower laterals. The third vector described Unachieved Reproductive Potential, that is the number of flower buds and the percentage of reproductive nodes per lateral (Dale and Topham, 1980).

Overall, the development of the axillary bud and lateral is influenced by its position on the cane at all stages of development. Therefore there is a need to take into account lateral position in yield component studies (Dale, 1979).

In summary (Figure 5.1) the research carried out on yield component analysis is varied and very often not backed up by statistical evidence for direct relationships between components. The most notable work, which provides clear statistical evidence, is the above on lateral vigour and path analyses carried out by Nehrbas and

Pritts (1988) and Hoover *et al.*, (1988). The latter path analyses outlined the yield components which contributed most to yield (the sum of the yield components). Multiple regression equations were based on path diagrams. These showed the dependence of individual components. For summer-fruiting varieties they were cane number and the number of fruiting laterals per cane. For autumn-fruiting varieties fruit number per node, cane number, total node number, the percentage of fruiting nodes and fruit weight were deduced as important.

5.1.2 Reasons behind the variations in relationships between yield components

5.1.2.1 Phenotypic plasticity

The stability of yield components is indicated by their heritability (proportion of phenotypic variance attributable to genetic effects) and additivity. Fejer and Spangelo (1974) found very low heritability for yield, berry weight and timing of flowering. They found high heritability for early vigour and plant height. Fejer (1977) determined from 4 x 4 diallel crosses that this inheritance was additive for fruit yield, weight, autumn-fruiting habit and day of flowering, but non-additive for lateral number.

The relationships between yield components can be modified by many environmental factors including humidity, planting distance, soil moisture, day length and temperature (Darrow and Waldo, 1933). As the environment affects the sequential development of these components (Dale, 1986) this affects overall genotypic expression and is expressed as phenotypic plasticity (Bradshaw, 1965). Dale (1979) states that too much should not be read into genotypic relationships as they are modified by changing environmental pressures.

Phenotypic plasticity is important regarding adaptation of plants to fluctuations in the environment - which allows buffering against rare conditions (Ford, 1975; Jefferies, 1984). Theoretically, the phenotype is the set of all measurable characteristics of an individual during its lifetime, excluding measurements which can only be made by breeding experiments (MacArthur and Connell, 1966).

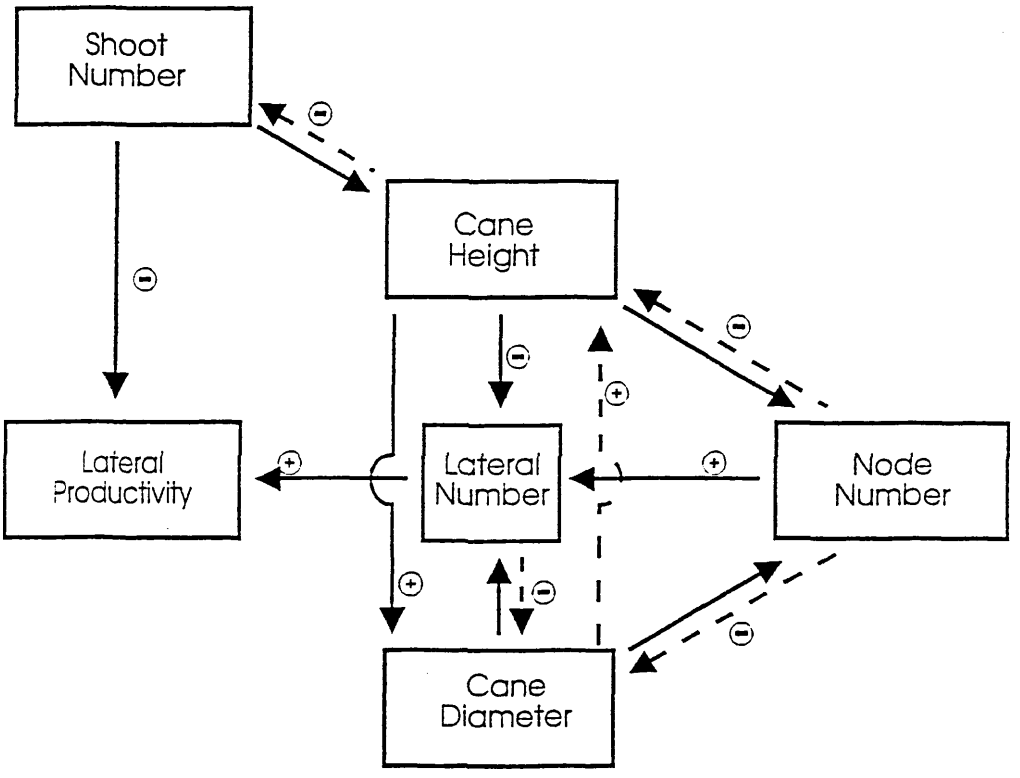


Figure 5.1 Schematic diagram to show the relationship between principal yield components from previous research on *Rubus* (symbols indicate the nature of the relationship).

The amount of change in a character from a chosen reference point is a measure of its plasticity. Logically, characters formed as a result of long periods of meristematic activity, are more subject to environmental influence and are therefore more likely to be more plastic than those formed rapidly during ontogenesis (White, 1984).

There is much evidence for variation and compensation among plant parts (Wood *et al.,* 1961; Waister and Barritt, 1980) for example, the development of secondary and tertiary laterals as a result of death or damage to primary laterals (Wood and Robertson, 1957; Jennings, 1979a).

The control mechanisms governing these plastic responses involve the transport of metabolites, thus the plant must be considered as a whole (Jefferies, 1984), when discussing the development of phenotypes.

There are indications that yield compensation and plasticity in the raspberry is limited by correlative inhibition and assimilate supply. Evidence for both was provided by work done by Braun and Garth (1984b) where removal of upper buds increased the number of fruit, but not the lateral number. Further to this, removal of lower buds induced no yield compensation in the upper laterals.

5.1.2.2 Correlative inhibition

Fruit bud number is affected by apical dominance - release of dominance increases bud number (Zraly, 1978; Jennings, 1987). Timing of flowering in the lateral apices determines the variation in expression of lateral characteristics (Jennings, 1964a; Dale, 1979; Dale and Daubeny, 1987).

5.1.2.3 Carbohydrate economy and intraplant competition

Whitney (1982) and Erasmus and Staden (1983) carried out detailed studies on carbohydrate economy and assimilate translocation in *Rubus* species. Overall assimilate translocation is determined by the mobilising strength of the apical region and root system as sink regions (Erasmus and Staden, 1983). Sinks can be described as tissues or organs which utilise or store assimilates (Braun and Garth, 1984b).

During active extension growth of the vegetative shoot the apical region was shown to form the major sink (by measuring the pattern of translocation of *in situ* ^{14}C Sucrose)(Erasmus and Staden, 1983). Low levels were encountered in the stem and root tissue during leaf expansion (Whitney, 1982). Some assimilate translocation from fruiting canes to newly developed replacement shoots was observed. The apex was not a sink in the fruiting cane. The developing fruit formed a minor sink, but after the completion of fruiting the replacement shoots became dominant as sinks. In late summer, transport was basipetal, the roots then becoming the major sink (Whitney, 1982; Erasmus and Staden, 1983). During development the upper laterals act as a sink: this is reflected in a reduction in dry weight (Waister and Wright, 1989).

The competitive advantage of plant organs depends on their development stage; buds only become strong sinks after anthesis (Braun and Garth, 1984b). The latter is reflected in the nutrient composition of the leaf, which varies with its position on the cane (Cline, 1964). There is a clear relationship between leaf production on the fruiting cane and fruit production (Khanmai and Brown, 1940; Waister and Barritt, 1980; Whitney, 1982). A reduction in leaf area at the critical point of fruit development was shown to reduce lateral yield (Wright and Waister, 1982b).

The removal of vegetative shoots appeared to deplete the vigour of the existing canes as it reduced the carbohydrate replenished to the roots from the developing vegetative canes (Dalman, 1989). This intercane dependence is reflected during leaf loss in fruiting canes, which are dependent on reserves in the adjacent vegetative shoots (Waister and Wright, 1989). Further to this the fruiting canes appeared to act as a source as removal of fruiting canes weakened the growth of adjacent vegetative shoots (Dalman, 1989).

Within the fruiting cane the evidence for the relationship between cane diameter and yield can be explained in terms of the mobilisation of assimilates. In the spring, at the time of bud expansion in second year canes, diameter becomes unimportant as assimilates are translocated from the roots (Crandall, Allmendinger *et al.*, 1974).

5.1.3 Summary

This study is concerned with the plasticity of cane architecture and its rate of development with respect to temperature. However, it must be emphasised that much attention should be paid to the consequences of light on yield components and plant form (Wright and Waister, 1984, 1986). As yield has been shown to be a function of light interception and leaf area (Khanmai and Brown, 1940; Palmer, Jackson and Ferree, 1987; Nehrbas and Pritts, 1988).

5.2 METHODS

Fifty graded one year old mother plants were randomly selected and potted up in March 1989. Ten plants were placed at random in five temperature control cabinets, held at the constant day/night temperatures of 10, 15, 20, 25 and 30°C.

Although plants were fed weekly with standard NPK liquid feed from terminal flower bud appearance onwards, it may have been appropriate to apply this at an earlier stage. Plants showed symptoms of probable magnesium deficiency at about the same time as anthesis and terminal bud set. This was alleviated to some extent by the application of a magnesium sulphate foliar spray (2% w/v, 20g/l) at weekly intervals for a period of 2 - 3 weeks.

Levels of photosynthetically active radiation were measured in the cabinets at 14.00hr on a bright summer day, with sensors held at 1.5m above the pans. Readings ranged from 346 - 457 μmol $m^{-2}s^{-1}$. The effect of canopy development was assessed using a hand held Watt Meter.

Plants were randomised within each cabinet at weekly intervals. As individual shoots elongated, the pans holding the plants were lowered to accommodate the expanding canopy at 48 and 68 days after planting. Plants were thinned from 10 plants per cabinet to 8, at 38 days and then from 8 to 6 plants at 48 days. This allowed more light interception per individual plant canopy. Once 50% of the canes per plant exhibited terminal flower bud appearance, they were removed to a glasshouse held at 15°C (± 2.64°C). Plants held at 25°C were removed at 68 days,

those at 20°C at 84 days and those at 10 and 15°C at 94 days. Plants in the 30°C cabinet died shortly after emergence.

Measurements were taken at five day intervals for the first four shoots to emerge up to terminal flower bud appearance and then at approximately two week intervals. This allowed a cohort of similar aged shoots to be monitored throughout the experiment. Cane diameter (from 15 nodes), node number, shoot height and shoot number were measured per plant. Primary leaf area was estimated for every fifth node of each measured shoot using a general linear regression model to calculate the actual area from non-destructive length and breadth measurements of the leaves (Appendix 5.1).

Stages of shoot development were denoted:

E - emergence,

TPC - appearance of the terminal floral primordia complex (≡ Stage I, Mathers, 1952).

TF - the point at which i) the terminal flower bud is distinct and hence ii) the number of nodes in the TPC is definitive (≡ "green bud" stage, Mathers, 1952).

BR - first ripe berry (≡ TB).

Dates of lateral expansion at every fifth node were recorded for comparison between treatments. Evidence from Chapter 4 (section 4.3.2.1) supported the assumption that laterals at equivalent node positions were of the same morphological type, irrespective of environmental treatment. Lateral data was then collected for these same nodes for lateral node number, lateral length, leaf number, secondary leaf area (estimates were calculated according to leaflet number to improve the accuracy of such small areas; see Appendix 5.1), flower bud number, fruit number and fruit weight.

Fruit was picked when ripe and recorded for each cane measured and as a total per plant. Once fruiting was complete plants were harvested and leaf areas and dry weights of total above ground plant matter recorded.

5.3 RESULTS AND DISCUSSION

5.3.1 Weighted replication

As the number of shoots sampled varied (some shoots produced fewer than the maximum of four shoots sampled) treatment means were weighted (Steel and Torrie, 1980) according to this number (Payne *et al.*, 1988). Individual shoot data were not independent, as each shoot was connected to a common stool and root system. Therefore, shoot data were meaned per plant, producing six independent replicates per treatment. Analysis of variance, involved the calculation of treatment means for a weighted number of replicates of approximately 18, based on 6 replicates per treatment.

The standard error for the comparison of treatment means (sed), where marked with an asterisk, was for the comparison of means with the maximum and minimum number of weighted replicates only. Standard errors were only quoted where means were significantly different (for details see Appendix 5.2).

5.3.2 Rate of shoot development

Rates of development were obtained for four phenological stages of shoot development. Plants exhibited a linear increase in emergence rate with temperature (Figure 5.2a). However, although rates of TPC were significant, there was no clear trend with treatment (Figure 5.2b). There was no significance in the rates of TF (Figure 5.2c). A linear trend with increasing temperature was also exhibited for rates of BR (Figure 5.2d). Although, a linear trend (as shown from a significant linear sum of squares) does not signify a straight line relationship (Dawkins, 1981) between the rates of E and BR, it does show that these rates are significantly higher for the 25°C treatment than for the 10°C treatment.

The high rate of TPC at 15°C was as a result of high residuals for plants in this treatment (Appendix 5.2, Table 5.2.2), although this was not apparent from the coefficient of variation obtained (Appendix 5.2, Table 5.2.1). Three plants reached TPC after 38 days at 15°C, compared with 54 days for plants treated at 25°C.

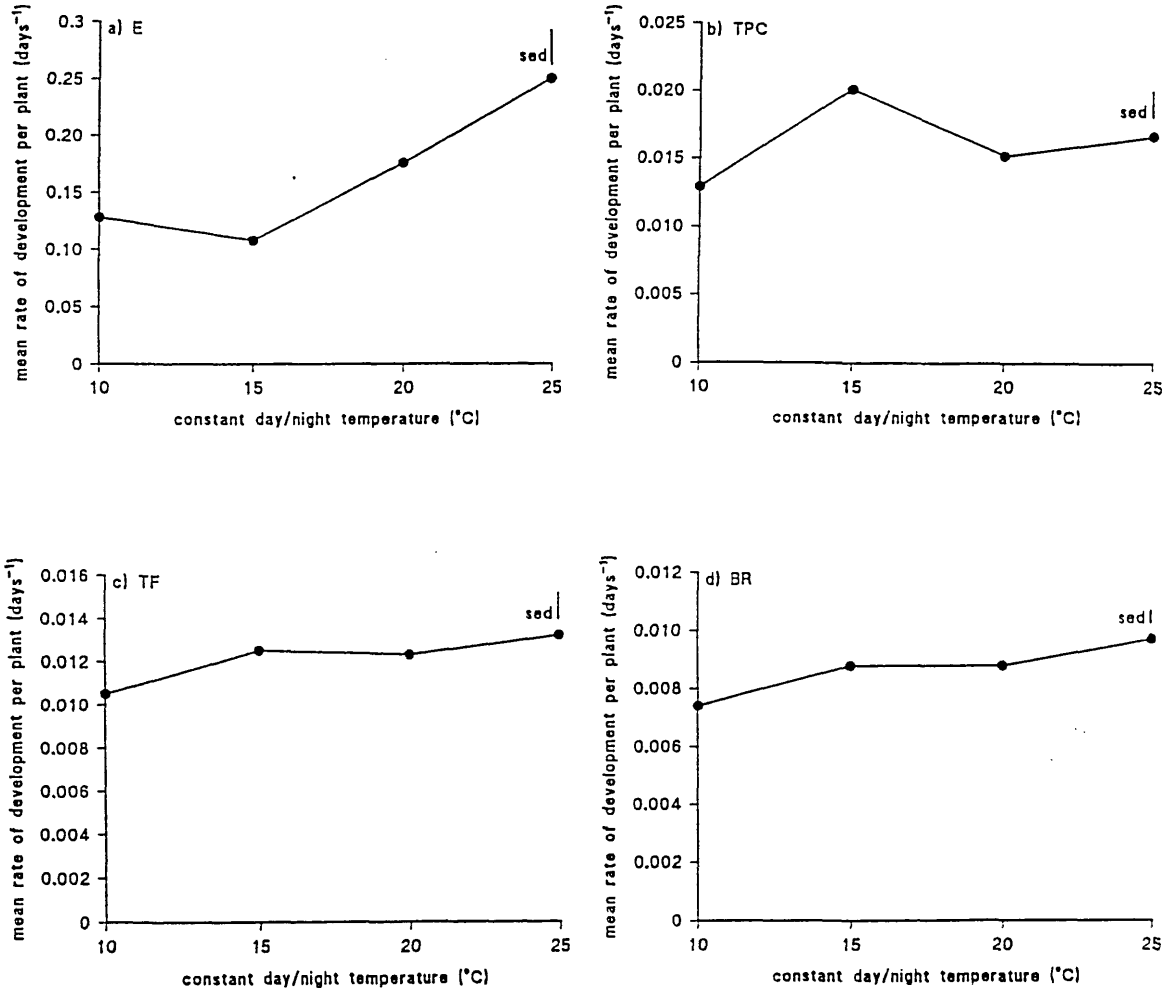


Figure 5.2 a - d The relationship between rate of development and temperature, for four phenological stages (of the first shoot per plant to develop to that stage). Where: E - emergence, TPC - appearance of the terminal floral primordia complex, TF - "green bud" stage and BR - berry ripening.

5.3.3 Node number

Mean node number of samples of first cohort shoots per plant increased rapidly to a maximum of 30 - 33 nodes (Figure 5.3). Linear sums of squares were significant for this period, indicating that node number increased more rapidly in the higher temperature treatments (Appendix 5.2, Table 5.2.3). After reaching this maximum, a decrease in node number was recorded as a result of fruit production and death of the lateral formed at the node. Residuals were high for two plants in the 25°C temperature treatment (Appendix 5.2, Table 5.2.4).

5.3.3.1 Node number in relation to stage of shoot development

Node number was counted from soil level. Results did not take into account the number of nodes below soil level.

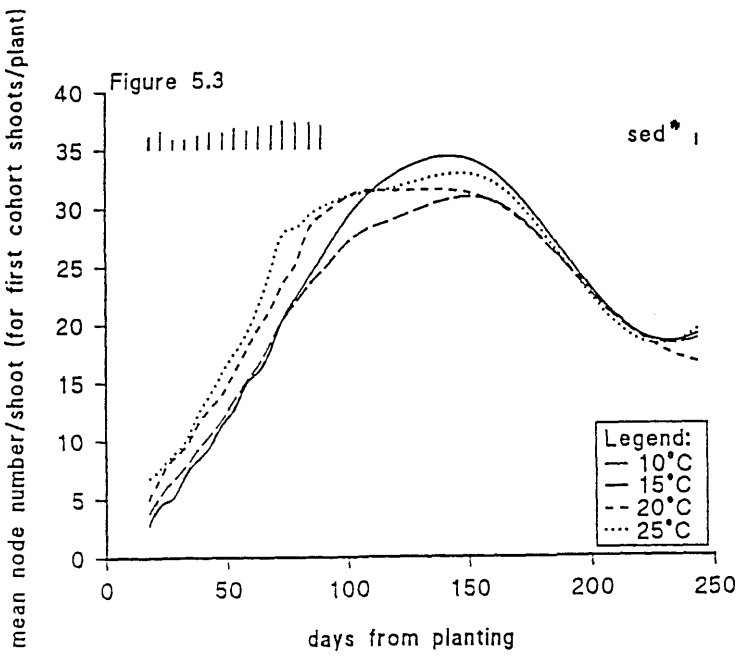
Two assumptions were made:

i) Node number at emergence was zero. This assumption was made for ease of sampling, but is incorrect as shown by evidence presented in Chapter 1.

ii) As the time at which the original basal or root bud was formed was unknown it was assumed that formation occurred at planting.

Therefore figures where the dependent variable is time are plotted from the time of planting.

Mean node number at TPC produced a significant quadratic sum of squares (Tables 5.1 and 5.2). Plants in the 10°C treatment appeared to produce more nodes prior to TPC (Figure 5.4). Residuals were low in this treatment, eliminating the possibility of variation among individual plants. Mean node number at TF was not significant between treatments (Tables 5.1 and 5.2). Figures 5.5a - d show the relationship between the timing of E, TPC, TF and BR ($\mathbf{T_1}$ - $\mathbf{T_4}$ respectively) and the node number at which TPC and TF occurred.



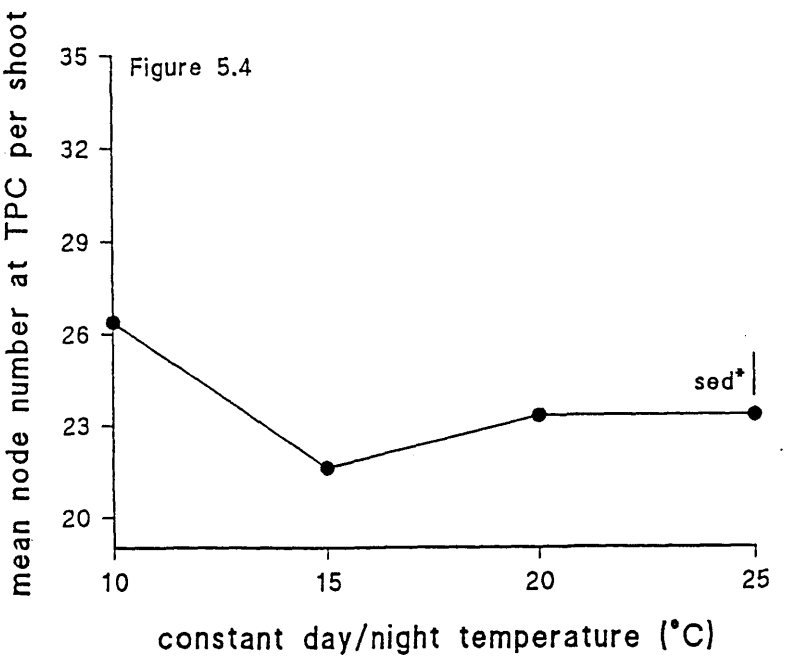


Figure 5.3 Node production in samples of first cohort shoots from emergence to completion of cropping.

Figure 5.4 Mean node number at TPC (for samples of first cohort shoots per plant).

Table 5.1 Mean node number at a given stage of shoot development (for the first shoot per plant to develop to that stage).

stage[10]	mean node number per temperature treatment					variation		
	10°C	15°C	20°C	25°C	mean	significance of partitioned sum of squares	sed	%cv
TPC	27.17	22.17	23.00	24.17	24.12	0.05[11]	2.09	15.0
TF	37.17	31.33	32.67	32.33	33.37	ns	2.58	13.4

Table 5.2 Mean node number per shoot (of samples of first cohort shoots per plant) at a given stage of shoot development

stage[10]	weighted mean node number per temperature treatment (number of weighted replicates in brackets)					variation	
	10°C	15°C	20°C	25°C	mean	significance of partitioned sum of squares	sed*[12]
TPC	26.39 (18)	21.60 (19)	23.32 (19)	23.31 (16)	23.63	0.02[11]	1.36
TF	33.83 (18)	30.05 (19)	31.42 (19)	31.56 (16)	31.69	ns	1.50

[10]Where: TPC - appearance of the terminal floral primordia complex
TF - "green bud" stage

[11]significant quadratic sum of squares

[12]see text (section 5.3.1)

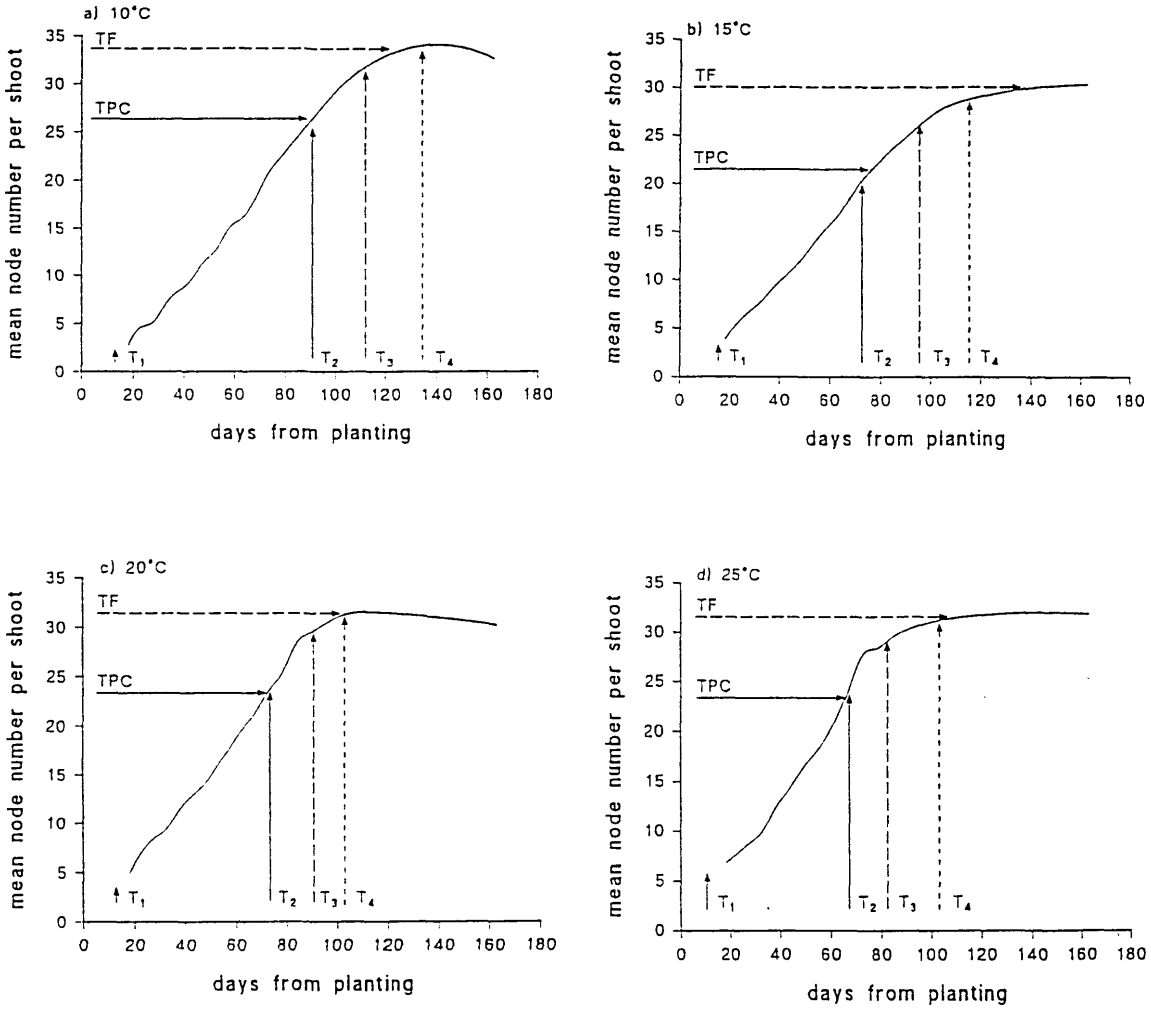


Figure 5.5a - d The relationship between the timing of E, TPC, TF and BR (T_1, T_2,T_3 and T_4 respectively) and the mean node number (of samples of first cohort shoots per plant) at which TPC and TF occurred.

Overall, node number was a simple indicator of the stages of cane development. Initial rapid elongation reduced after TPC. The relationship between increase in cane height and time is logistic in nature (Williams, 1959a; Ourecky, 1976; Jennings and Dale, 1982; Wright and Waister, 1982a; Dale, 1989). The latter phase of reduced rate of cane elongation is closely associated with terminal flower initiation (Keep, 1961; Ourecky, 1976; Keep, 1988). Although it is clear from the above results that temperature affected the rate of node production, it had no effect on the final number of nodes produced per cane. Therefore the linear section of the curve varied according to temperature treatment, but the "plateau" or asymptote remained the same.

5.3.3.2 Rate of node production

The nature of the relationship between node number and time (Figure 5.3) suggests that a logistic function, such as Richards, could be suitably fitted to the data to elucidate the significance between the rates of shoot development at different temperature treatments.

5.3.3.2.1 The Richards function

The Richards function can be expressed as:

$$N = \frac{A}{(1+e^{b-kt})^{1/n}} \qquad (5.1)$$

Where:

N - node number of shoot, (nodes).

A - maximum number of nodes produced per shoot, (nodes).

n - defines the shape of the curve.

b - a constant (nodes).

k - rate constant for node production, (nodes per day).

t - time, (days).

Richards function is defined by $-1 \leq \mathbf{n} \leq \infty$, but $\mathbf{n} \neq 0$.

(Causton *et al.*, 1978).

The advantages of this function are as follows:

i) As the function is asymptotic, this allows a maximum (**A**) to be fitted, which is independent of the shape of the curve (**n**). This is shown when the function is derived (Appendix 5.3).

ii) The function can be derived to determine a point of inflexion (Thornley and Johnson, 1990) and turning points, where the rate of node production and the rate of change of node production are at a maximum respectively (Appendix 5.3).

iii) As the function does not pass through the origin, the number of nodes on the pre-emergent shoot can be estimated.

iv) Causton *et al.* (1978) showed the biological significance of the derivatives, which employ the shape of the curve **n** and the rate constant **k**. These give estimations of the weighted mean relative growth rate:

$$\frac{k}{n+1} \qquad (5.2)$$

and mean absolute growth rate:

$$\frac{Ak}{2(n+2)} \qquad (5.3)$$

5.3.3.2.2 Determination of n

Unweighted values of **A** were used to make initial estimates of **b** and **k** for values of **n**, ranging from -1 to 10 in 0.25 steps. These estimates were fitted to the weighted treatment means, taken from the date of the first measurement to 163 days from planting. At 163 days from planting, all canes sampled had reached their maximum node number.

A SAS[13] curve-fitting program was used to run these sets of estimates to obtain fitted values with the lowest number of iterative steps and the highest nonlinear regression sum of squares (Appendix 5.4). The fitted values of **A** and **n** are shown in Table 5.3a and Figures 5.6a - b. The values of **n** increased with increase in temperature treatment. This was indicative of a higher rate of node production in the linear portion of this curve.

Table 5.3a - b Summary of derived parameters obtained from a curve fit of the Richards function to weighted mean node number (of samples of first cohort shoots) per plant for each temperature treatment
Table 5.3a

Parameter		temperature treatments			
		10°C	15°C	20°C	25°C
Maximum	**A**	33.49	30.67	31.25	31.52
Shape of curve	**n**	1.4051	1.1938	3.9490	4.1713
Wtd. mean relative growth rate (nodes day^{-1})	$\frac{k}{(n+1)}$	0.0224	0.0217	0.0207	0.0225
Mean absolute growth rate ($nodes^2 day^{-1}$)	$\frac{Ak}{2(n+2)}$	0.2654	0.2290	0.2697	0.2970
Intercept $\mathbf{n_0}$ (nodes)	$A(1 \pm e^{b})^{-1/n}$	1.99	2.33	4.03	4.12
$\mathbf{n_1}$ (node number at $\mathbf{t_2}$)	$A(n \pm 1)^{-1/n}$	17.93	15.88	20.84	21.25

[13]SAS Institute Inc., Box 8000 Cary, North Carolina, USA.

Table 5.3b

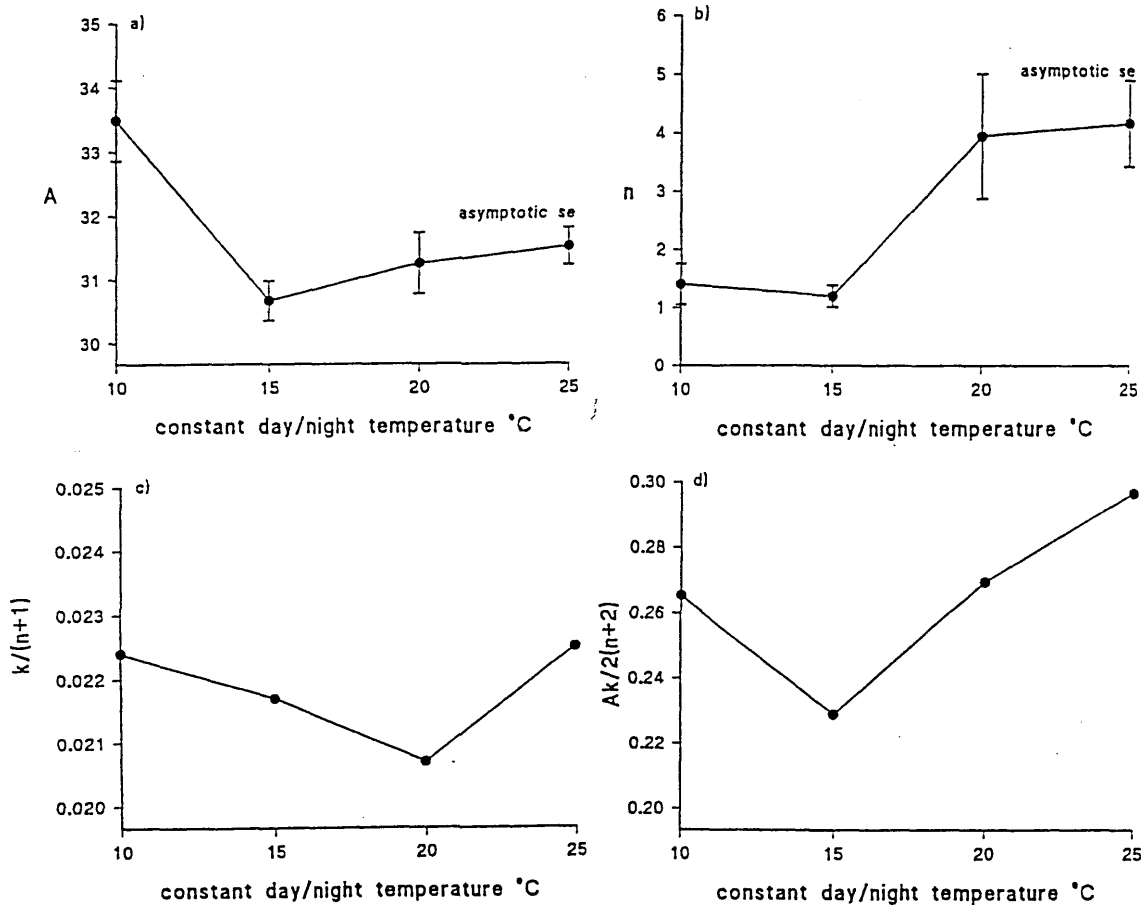
Turning points of the Richards function (days)		treatments			
		10°C	15°C	20°C	25°C
t_1	$\frac{b-x}{k}$	40.24	31.05	46.75	43.88
t_3	$\frac{b+x}{k}$	92.89	88.54	84.09	77.42
t_2	$\frac{b-\log_e n}{k}$	66.57	59.80	65.42	60.65

5.3.3.2.3 Growth rates

The weighted mean relative growth rates were relatively similar between treatments (Table 5.3a)(Figure 5.6c). Mean absolute growth rate (Figure 5.6d) decreased (as expected) as temperature treatment decreased. However, plants held at 10°C appeared to have a similar absolute growth rate to those held at 20°C.

5.3.3.2.4 Location of and relationship between turning points t_1 - t_3

The locations of, and equations for, the point of inflexion t_2 and the two turning points t_1 and t_3 are shown in Figure 5.7a and Table 5.3b respectively.



Figures 5.6a - d Derivatives of the Richards function, fitted to node data (of first cohort shoots per plant) from each temperature treatment. a) maximum node number, A; b) shape of curve, n; c) weighted mean relative growth rate and d) mean absolute growth rate.

The relationship between the observed time to stages E, TPC, TF and BR (T_1 - T_4) and the derived parameters t_1 - t_3 is shown in Figure 5.7b.

The significance of each turning point can be postulated as:

i) t_1 occurs prior to TPC. This suggests that it may be connected with the point of floral induction.

ii) As t_2 occurs between t_1 and TPC it may mark the actual point of floral initiation. TPC is merely the stage at which initiation is apparent to the naked eye. Derivation of the actual point of initiation is therefore more accurate and very useful.

iii) t_3 may be associated with the expansion of the terminal floral primordia complex.

Time intervals between stages of shoot development were longer for shoots at lower temperatures (Figure 5.7b).

5.3.3.2.5 Summary of findings for node data

In conclusion, the total number of nodes produced per cane was unaffected by temperature treatment. The rate of node production and mean absolute growth rates increased with increasing temperature treatment. However, the latter was markedly higher for plants held at 10°C. Verification of such a relationship is difficult based on four points. This clearly needs further investigation over a wider temperature range.

As plants died rapidly at 30°C, this indicates their approximate upper threshold temperature. In reality, temperatures experienced by plants in this cabinet averaged 33°C (maximum temperature) and peaked at 37°C for 4 days. This data will be examined in more detail in the next chapter to define an upper and lower threshold temperature for incorporation into the model.

Variation was high in plant material with respect to the timing of TPC. This was not so for node number at TPC. Overall, there is substantial evidence that shoot maturity can be related to node number.

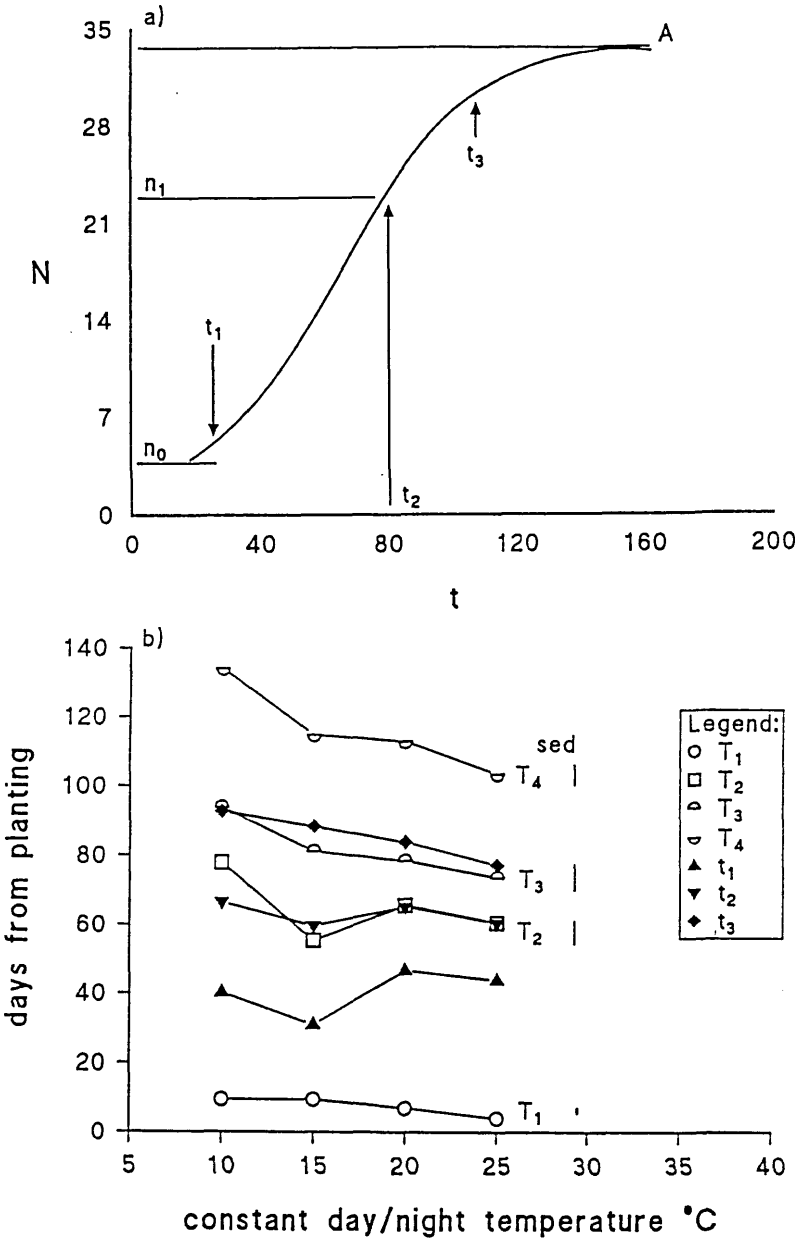


Figure 5.7 The relationship between the rate of node production and shoot development

a) The relationship between fitted node number (N), time (t) and derivatives from the Richards function

b) The relationship between the time to a given stage (for fitted and observed values) and temperature treatment.

Where; t_1 - t_3 are fitted values (equivalent to turning points), T_1 - T_4 observed values equivalent to stages E, TPC, TF and BR, n_0 fitted node number at E and n_1 fitted node number at t_2.

There appears to be a demarcation between the rate of node production at the two lower temperatures and the two higher temperatures. The shape of the curve (**n**) is similar for node production at 10 and 15°C and different to that at 20 and 25°C.

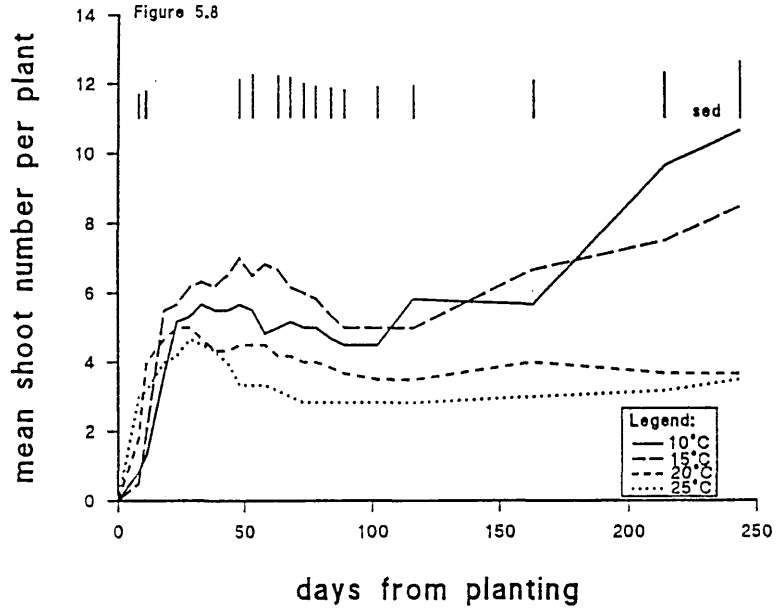
The rate of node production can also be related to stages of development through calculation of turning points.

The number of nodes expanding between TPC and TF was constant regardless of treatment (mean of 8 nodes). This agreed with Mathers research (1952)(Chapter 1).

5.3.4 Shoot number

Mean total shoot number increased rapidly to a maximum over the first 18 days after planting (Figure 5.8). This initial establishment period was followed by a period of much slower increase in shoot number, as a stable population was established per plant. The initial rapid increase in number showed significant differences between treatments. The two higher temperature treatments produced more canes per plant. However, as the plant matured and fruited the numbers of shoots produced by plants at the two lower temperatures continued to increase significantly, whereas cane numbers at the two higher temperatures remained approximately the same. Coefficients of variation (Appendix 5.2, Table 5.2.6) showed that there was considerable variation (up to 84% initially), but this was as a result of high residuals in the same few plants throughout the experiment.

In conclusion, these results showed a more rapid rate of cane population establishment at higher temperatures, followed by a short period when mean shoot population per plant did not differ between treatments. At about the same time as TPC, shoot number appeared to decrease slightly across treatments, presumably equivalent to self-thinning phase. Numbers rose at lower temperatures during fruiting, showing a linear trend.



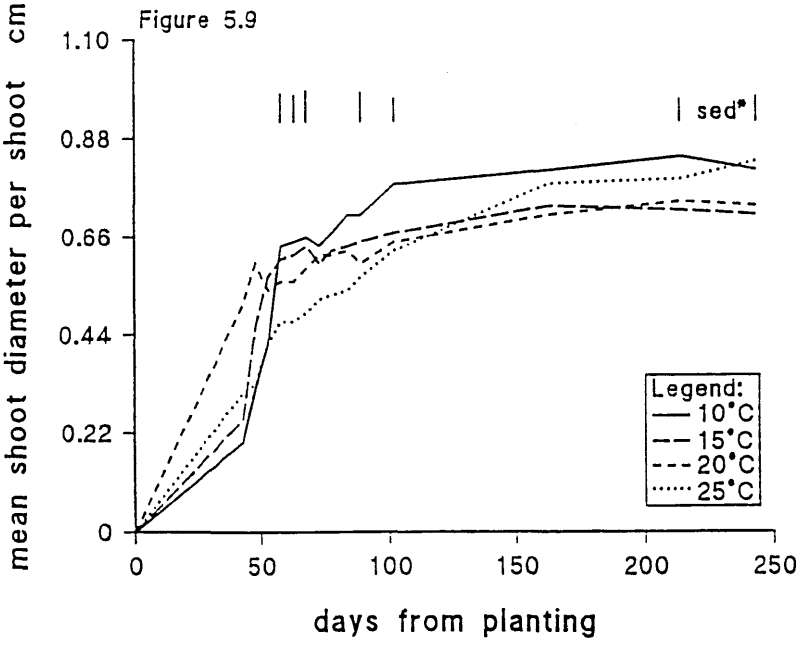


Figure 5.8 The change in total shoot population per plant from planting to completion of cropping.

Figure 5.9 The change in mean shoot diameter per shoot (of samples of first cohort shoots per plant) from planting to cropping

5.3.5 Shoot diameter

The mean shoot diameter of first cohort shoots was significantly higher for lower temperature treatments at approximately TPC (Figure 5.9). However, at harvest the relationship had changed so that shoot diameters at 15 and 20°C were significantly lower.

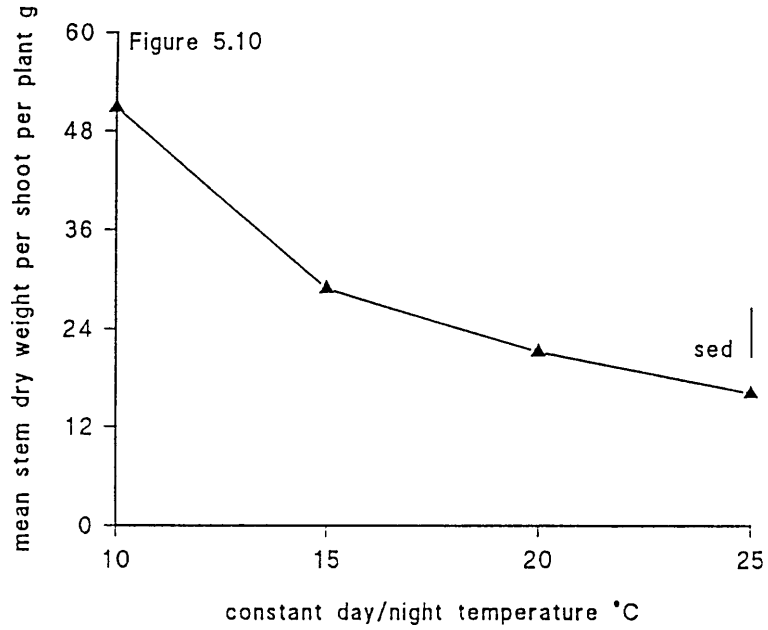
5.3.6 Fruiting cane architecture

5.3.6.1 Plant dry weight

As shoot diameter can be regarded as a measure of assimilate supply to the developing shoot (sections 5.1.1.2 and 5.1.2.3) it is logical to assume this is a reflection of stem dry weight. Although dry matter accumulation could not be measured throughout the experiment (due to lack of sufficient replicates), plant dry weight and stem dry weight were measured at harvest. The mean total above ground dry weight per plant and per sample of first cohort shoots was not significant between treatments. However, the mean stem dry weight in both cases gave a highly significant linear sum of squares (Appendix 5.2, Table 5.2.9) (Figure 5.10).

5.3.6.2 Lateral number

Lateral expansion began at approximately TPC($\mathbf{T_2}$), that is at 78, 58, 63 and 63 days from planting for temperature treatments 10, 15, 20 and 25°C respectively. It was greater initially for canes treated at 10°C and 25°C (Figure 5.11). There are no comparisons between treatments where the lateral number was zero (Appendix 5.2, Table 5.2.10).



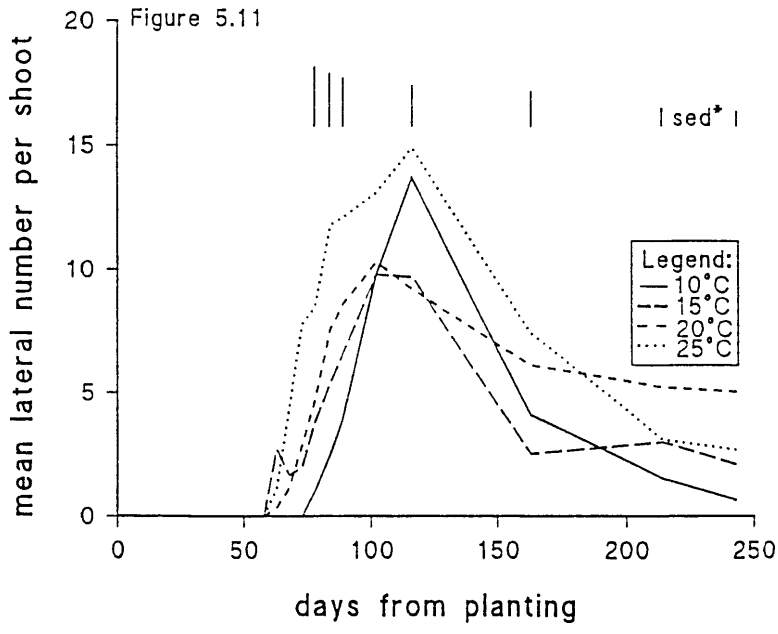


Figure 5.10 The relationship between mean stem dry weight per shoot per plant and temperature at harvest

Figure 5.11 The change in mean lateral number per shoot (of samples of first cohort shoots per plant) over the cropping period

5.3.6.3 Fruit bud number

First cohort shoots treated at 25°C showed the highest rate of fruit bud production (Figure 5.12). However, the maximum number of fruit buds produced per cane was not significantly different between treatments (Appendix 5.2, Table 5.2.11).

5.3.6.4 Percentage of fruiting nodes

The trends in this data were similar to those presented in Figure 5.11, except that as nodes (and laterals) died, the remaining laterals tended to reflect a proportionate increase in the percentage of viable fruiting nodes (Figure 5.13). A maximum of 43% of nodes per cane in first cohort shoots (treated at 25°C) produced laterals. This was surprisingly low (Appendix 5.2, Table 5.2.12).

The main effects on the fruiting cane architecture were:

i) Higher numbers of laterals produced on canes from the 10°C and 25°C treatments.

ii) Rates of lateral expansion and fruit bud production increased with increasing temperature.

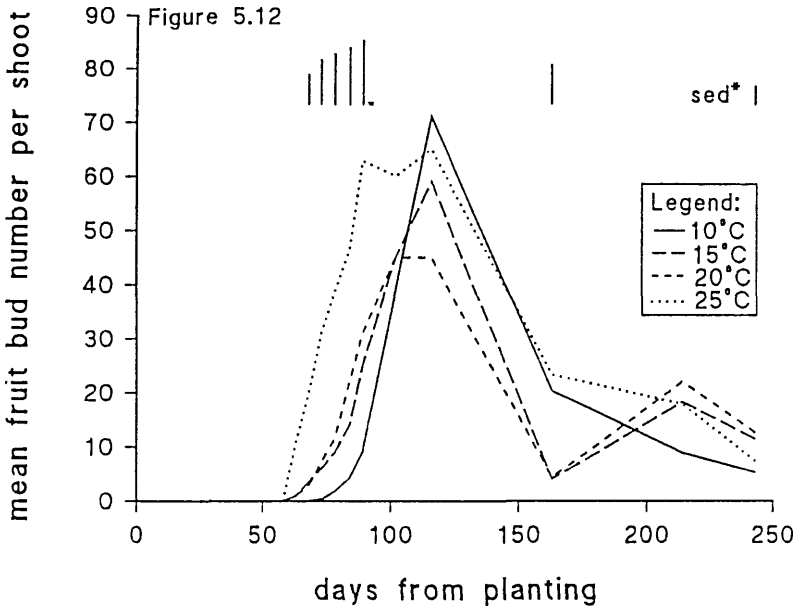
iii) Lateral expansion occurred shortly after t_2 or floral initiation at the apex.

iv) Total above ground plant dry weight or maximum fruit bud number did not differ between environments. This is some indication of the developmental flexibility of this cultivar (Jefferies, 1984).

5.3.7 Yield

The mean total fruit fresh weight per plant and per cane of first cohort shoots displayed a significant quadratic sum of squares (Figure 5.14a) (Appendix 5.2, Table 5.2.13). This was reflected in berry numbers (Figure 5.14b). Clearly, there is no evidence for a linear relationship between yield and temperature treatment.

Fruit size and percentage fruit set were unaffected by initial temperature treatment.



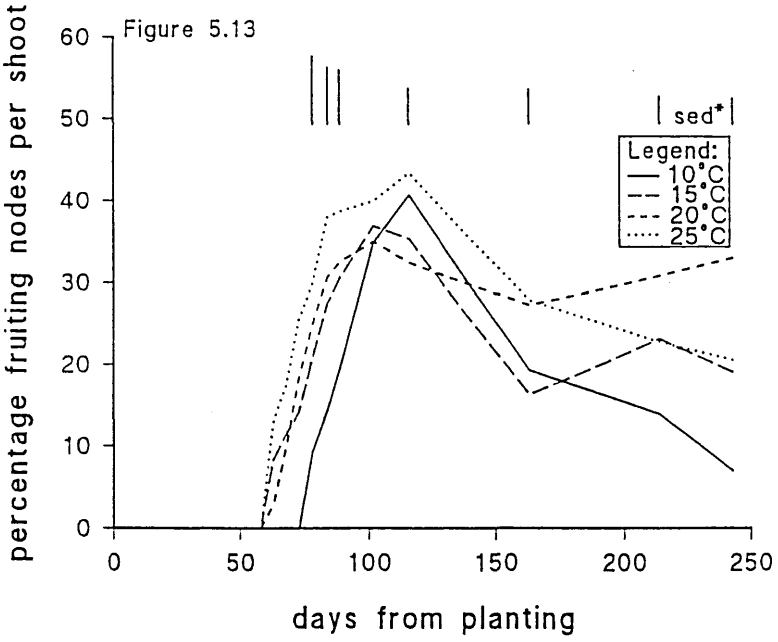
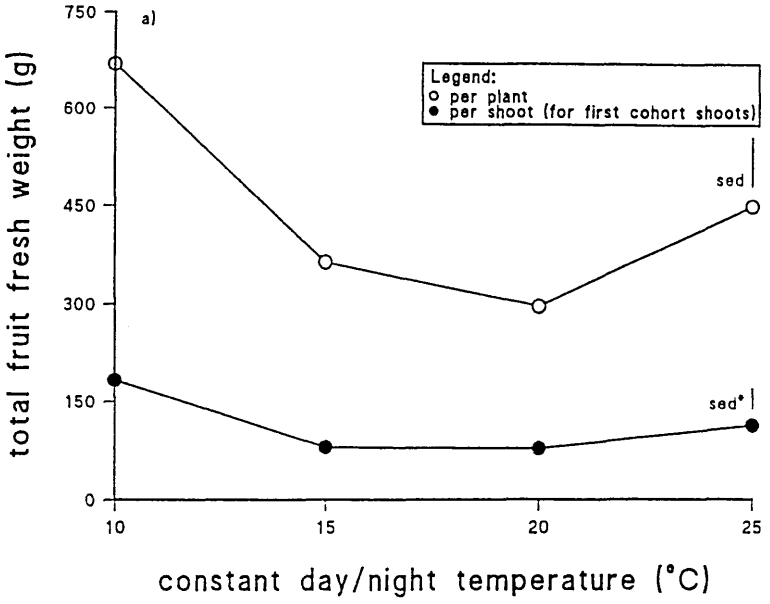


Figure 5.12 The change in the mean fruit bud number per shoot (of samples of first cohort shoots per plant) over the cropping period

Figure 5.13 The change in the mean percentage of fruiting nodes per shoot (of samples of first cohort shoots per plant) over the cropping period



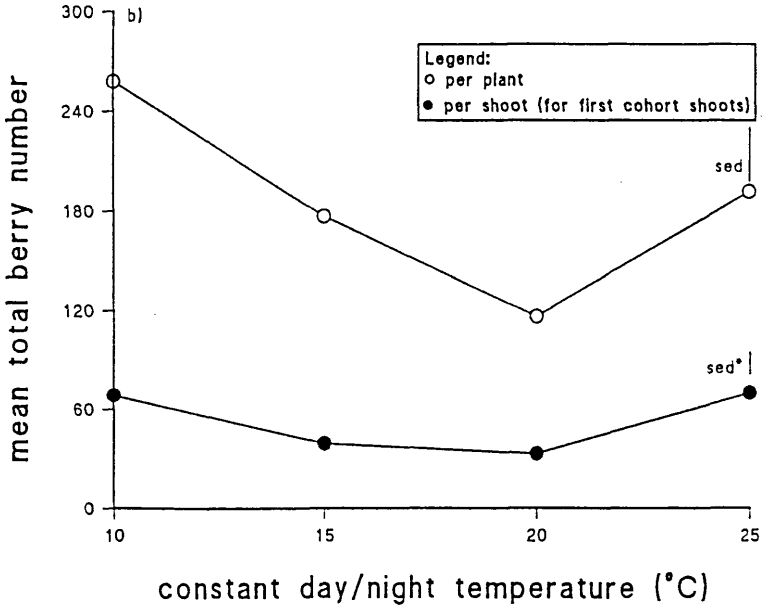


Figure 5.14 The relationship between yield and temperature treatments per plant and per cane (of samples of first cohort canes): a) mean fruit fresh weight, b) mean berry number

5.3.8 Fruit season

The accuracy of the length of cropping period is doubtful, as all plants were harvested at 243 days from planting. At this stage most first cohort shoots had completed cropping. It is arguable whether canes, particularly those treated at 10°C, would have continued to crop sparsely for a long time after this date (Figure 5.15).

5.3.9 Fraction of incident radiation absorbed by the crop canopy

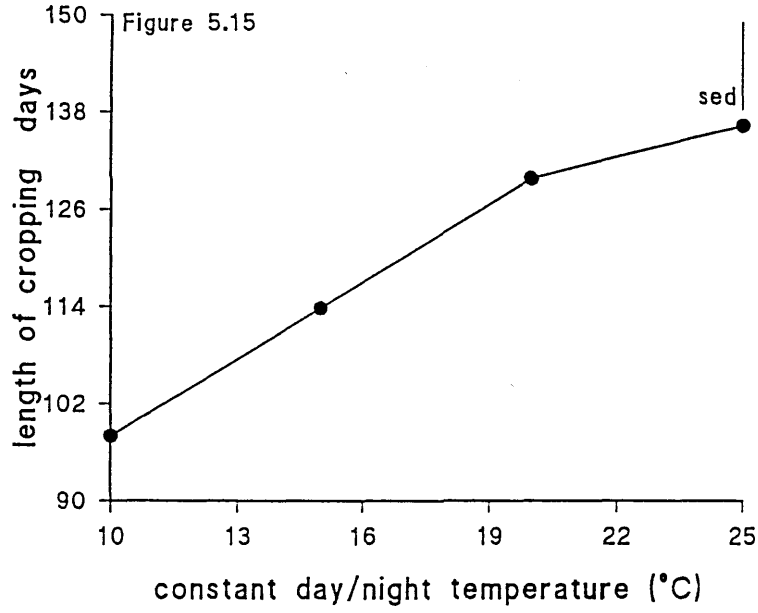
This was measured firstly in the cabinets using a hand-held meter and probe, and later a Ceptometer. Figure 5.16 combined the two sets of data, using f - the fraction of incident radiation absorbed by the canopy (see Appendix 5.2, Tables 5.2.14 and 5.2.15).

The fraction of incident radiation absorbed decreased at approximately the same time as flower initiation (t_3) and continued to decrease until lateral expansion had reached a maximum. This follows the pattern of primary leaf death, which began at approximately the same time as terminal flower bud appearance, and lateral leaf formation (Figure 5.18a - d).

Plants treated at 10°C maintained a high level of absorbance throughout the growth cycle, whereas plants treated at 25°C achieved very erratic and poor levels of absorbance (the comparatively low coefficients of variation verify the data - Appendix 5.2, Table 5.2.14).

5.3.10 Comparison of individual laterals

The aim of studying individual laterals was to monitor primary and secondary leaf production with respect to growth and yield of the lateral, and also to find out whether differences in yield were due to an increase in individual lateral production or to an increase in lateral number.



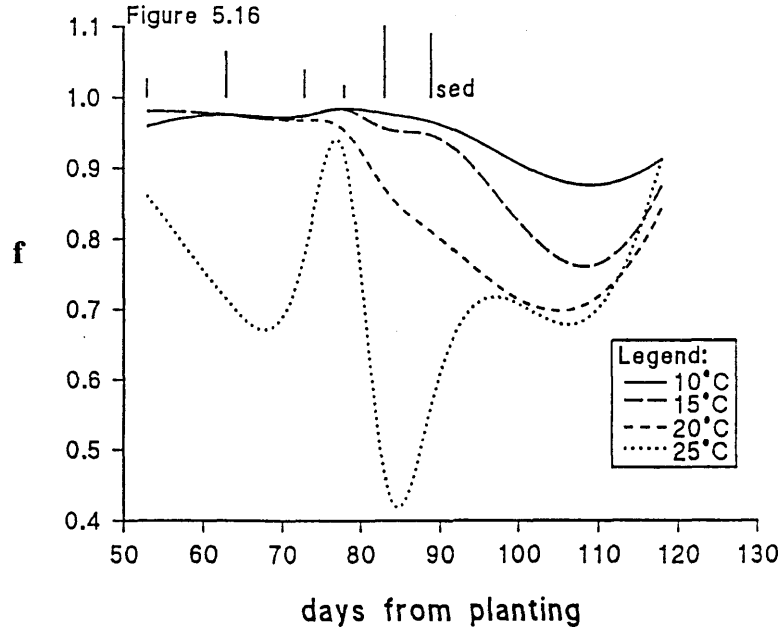


Figure 5.15 The relationship between length of cropping season and temperature treatment.

Figure 5.16 The relationship between mean fraction of incident radiation (f) absorbed by the crop canopy per plant, and temperature treatment.

Relative lateral position was not used to identify individual laterals (Wright and Waister, 1984). Actual node number was considered adequate, as the final node number was not significantly different between treatments.

5.3.10.1 Primary leaf area

Primary leaf area was not measured at harvest as most leaves had died by this stage.

5.3.10.2 Secondary leaf area

There were no significant differences between temperature treatments in mean lateral leaf areas for similar lateral positions on first cohort canes (Figure 5.17a).

5.3.10.3 Comparison of primary and secondary leaf development at various node positions along the cane axis

Figures 5.18a - d show leaf development at each lateral measured. There is a clear overlap of the life of the primary leaf and the secondary leaves for laterals 25, 30 and 35. At the lower nodes, the primary leaf died some time before the lateral and secondary leaves developed.

The rate of secondary leaf production was slower for the lower temperature treatments. This was reflected in the lack of leaf development on lower laterals.The total lateral leaf area produced by laterals 10 and 15 was greater than the primary leaf areas at those nodes.

Clearly, lateral nodes 10, 15 and 20 produce primary leaves with large leaf areas and large numbers of lateral leaves. This relates to their level of juvenility as seen in the lateral morphology described in Chapter 4.

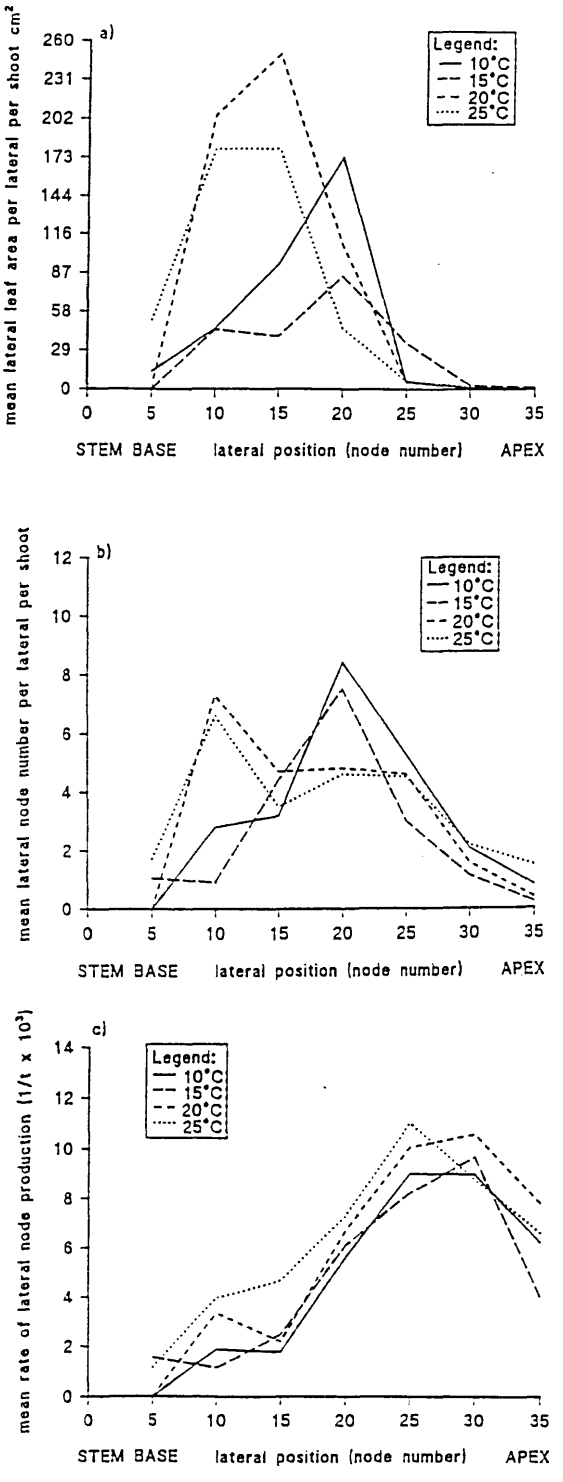


Figure 5.17a - c The effect of temperature treatments on the growth and development of individual laterals (measured at five node intervals along the cane axis of samples of first cohort shoots). a) mean secondary leaf area per lateral: b) mean lateral node number, c) mean rate of lateral node production, (t - time in days).

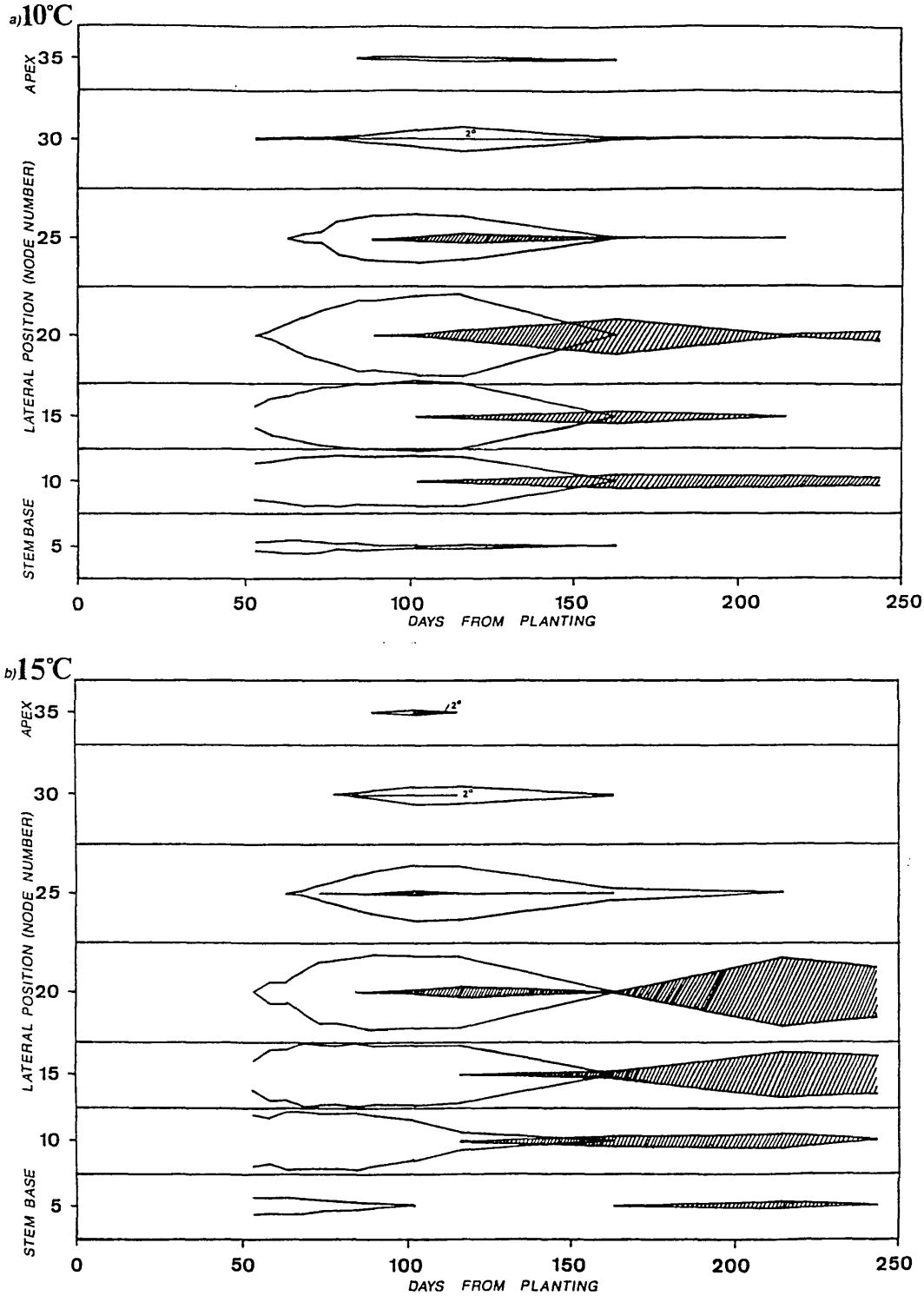
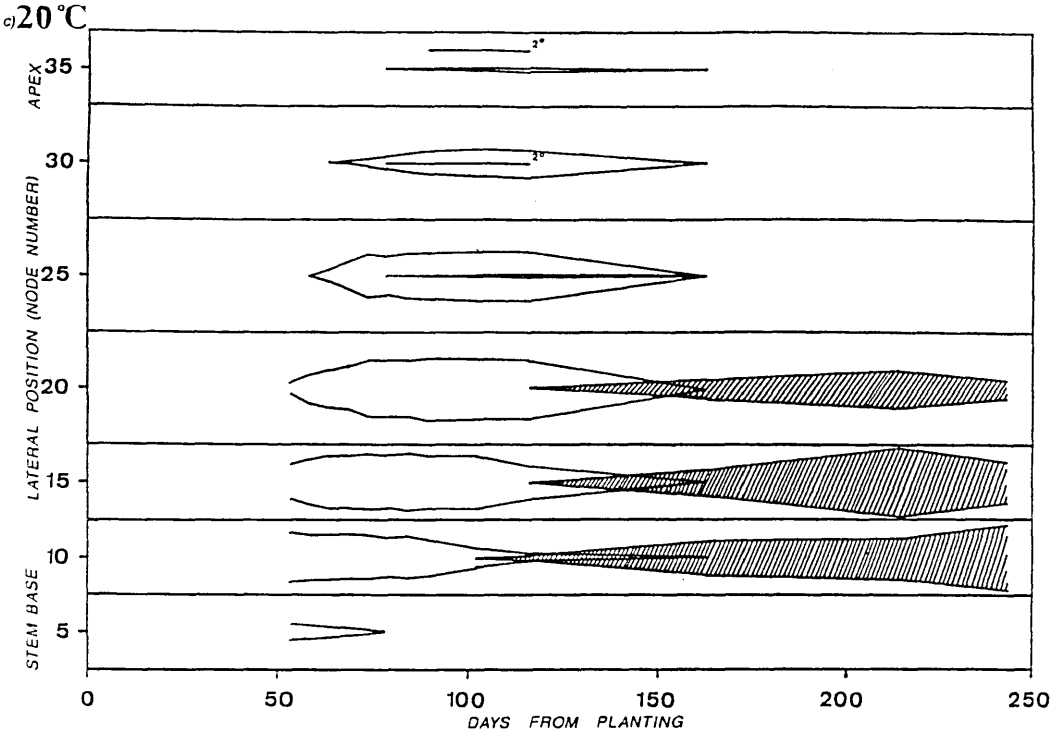
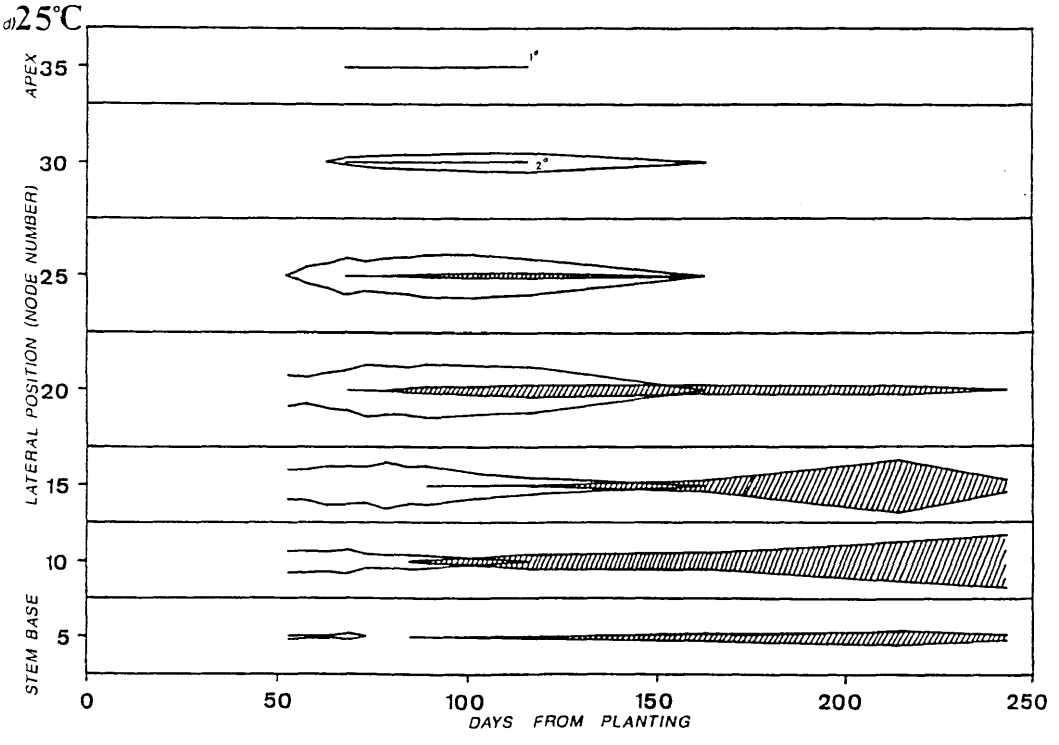


Figure 5.18a - d The effect of temperature treatments on the development of the shoot canopy (of first cohort shoots). Kite diagrams represent leaf areas (0.5mm on vertical axis ≡ 20cm^2) at lateral positions sampled: unshaded = primary leaf area(1°), shaded = secondary leaf area (2°).

c) 20 °C


APEX
35
30
25
20
15
10
5
STEM BASE
LATERAL POSITION (NODE NUMBER)
0
50
100
150
200
250
DAYS FROM PLANTING

d) 25°C


APEX
35
30
25
20
15
10
5
STEM BASE
LATERAL POSITION (NODE NUMBER)
0
50
100
150
200
250
DAYS FROM PLANTING

5.3.10.4 Lateral node number and rate of lateral node production

There were no significant differences between treatments for individual lateral node number or rate of node production at each node position measured (Figures 5.17b - c, respectively).

5.3.10.5 Yield per lateral

Mean fruit fresh weight and fruit number per lateral were not significantly different between treatments, except for the fruit weight at lateral 25 for plants held at 10°C (Figure 5.19a - b, respectively). Generally, yield was greater for laterals 20 and 25.

Fruit bud number and fruit size were not significant. Correlations between individual lateral yield components were not significant. There appeared to be no specific relationship between lateral leaf area and lateral yield.

In conclusion, the increase in yield between treatments must be due to differences in lateral number or shoot number as there were no apparent differences between individual lateral yields.

5.3.10.6 Levels of incident radiation absorbed at each lateral

Levels of radiation absorbed (f) at the tip of each lateral were calculated (Table 5.4). At 107 days from planting the amount of radiation "absorbed" was negative for laterals at and below 15 nodes. At 118 days from planting the radiation absorbed had increased down the plant for plants treated at 25°C. However, plants treated at 10 and 15°C exhibited low levels of absorbance. This indicates that the canopy was more open for higher temperature treatments, allowing more light availability to the lower laterals.

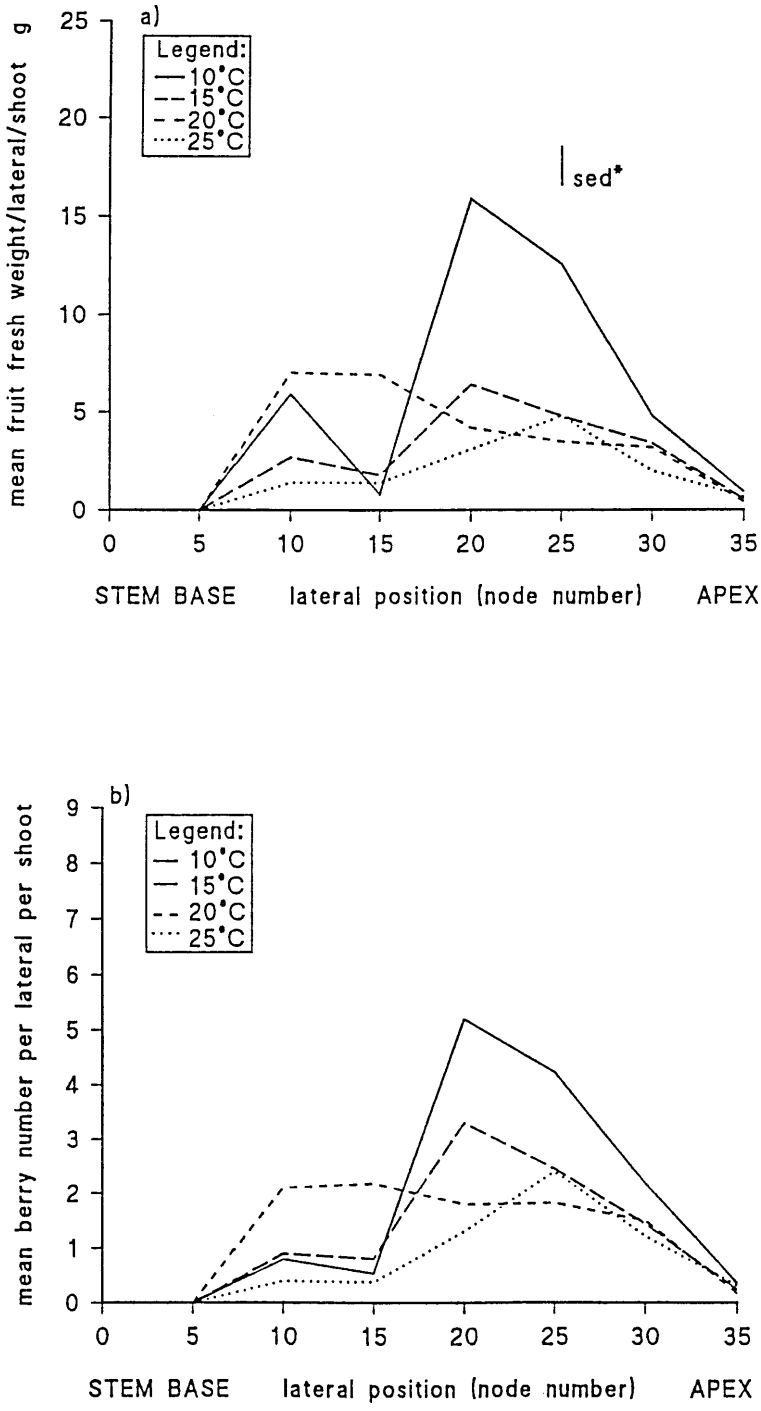


Figure 5.19a - b The effect of temperature treatments on the yield of individual laterals (measured at five node intervals along the cane axis of samples of first cohort shoots). a) mean fresh weight of fruit per lateral, b) mean berry number per lateral.

Table 5.4 Profile of Incident Radiation absorbed by the crop canopy (f)[14], measured at the tip of every fifth node

node no.[15]	levels of f, for each temperature treatment							
	sample means (107 days from planting)				sample means (118 days from planting)			
	10°C	15°C	20°C	25°C	10°C	15°C	20°C	25°C
apex	0.883	0.620	0.714	0.997	0.918	0.940	0.956	0.984
35	-	-	-	-	0.888	-	-	-
20	0.807	-	0.678	0.698	0.828	0.921	0.937	0.980
25	0.597	0.645	0.351	0.573	0.678	0.850	0.965	0.973
20	-	0.556	0.456	0.385	0.829	0.823	0.875	0.970
15	-	0.574	0.195	-	0.635	0.400	0.873	0.889
10	-	-	-	-	-	0.271	0.840	0.869
5	-	-	0.113	0.158	-	0.535	0.846	0.899

5.4 CONCLUSIONS

Yield components which showed significant differences between temperature treatments were shoot number, node number, stem dry weight, lateral number and overall yield in terms of fruit weight and fruit number per cane and per plant.

The rate of shoot production briefly appeared to increase linearly with temperature treatment. The population of shoots "stabilised" at approximately 6 shoots per plant for plants from each treatment. Re-establishment of shoot population occurred after fruiting in plants treated at 10 and 15°C. No such increase

[14]Where: f=1-t, t is the fraction of photosynthetically active radiation (PAR) absorbed by the canopy and is calculated by dividing the amount of PAR at the soil surface (T) by the amount of PAR immediately above the crop canopy (S) (Anon., 1988; after Monteith, 1965).

[15]Node number (counted from the base of the stem upwards)at which the lateral is located

in shoot numbers was observed in plants treated at 20 and 25°C. This was thought to be due to exhaustion of metabolites from the root system as a result of the rapid rate of growth and development exhibited by these plants. Consequently, this deprived basal buds of a sufficient carbohydrate supply for expansion and development.

Node number was determinate - the total node number produced per cane was unaffected by temperature. The rate of node production increased with increasing temperature. This resulted in a reduction in the time intervals between emergence, flowering and fruiting.

When the Richards function was fitted to the data for node production, three turning points were identified for maximum node production and maximum rate of change of node production. The first two, occurring between E and TPC, were identified as the possible points of induction and initiation of terminal flowering. The third was associated with expansion of the terminal floral primordia. The relationship between node number, the rate of node production and temperature provided indices for shoot development, rendering it a suitable key variable for modelling the phenological development of individual shoots.

Stem dry weight was significantly greater in plants treated at 10°C. Rapid growth and poor canopy development led to low levels of storage metabolites for plants treated at 25°C. Poor canopy development relates to yield. In cereals, which are determinate, the duration of the canopy directly affects yield (Ong and Baker, 1985). Temperature is the most important factor in governing developmental rates (Porter and Delecolle, 1988). Annual plants respond in a negative way to high temperatures, as the increase in rate of development reduces the duration of photosynthesis before crop maturity (Grace, 1988). Here, the early death of primary leaves was alleviated by the production of secondary leaves. The raspberry is extremely plastic in this respect, as each cane is supported by a "pool" of reserve metabolites from photosynthates produced in that cane or in neighbouring canes attached to the same stool (section 5.1.2.3). The differential allocation of these resources depends on the strength of the sinks induced by the developing shoot population. Temperature increases sink metabolism, by speeding up the rate of

transport of metabolites into it (through rates of individual reactions, diffusion or active transport) (Farrar, 1988). This resulted in a non-linear relationship between yield and temperature treatment. Yields in plants treated at 10°C were similar to those in plants treated at 25°C.

Individual lateral yield components did not differ significantly between treatments, nor was there any correlation between individual leaf area and lateral yield. This showed that higher yields resulted from higher numbers of laterals in canes treated at 10 and 25°C. To a lesser extent this could be attributed to higher shoot numbers in plants treated at 10°C.

This enhances the importance of node number, rate of node production, lateral number and rate of lateral expansion as yield components. In conclusion, temperature treatments on shoots up to terminal flower bud appearance affected the sequential development of shoots, resulting in differences in yield.

CHAPTER 6

THE PRODUCTION OF A MECHANISTIC MODEL FOR SHOOT DEVELOPMENT

6.1 INTRODUCTION

Node number provides an index for shoot maturity in cv. "Autumn Bliss" from evidence presented in Chapter 5. Absolute node number was constant, which seems to indicate that it is genetically inherited and expressed phenotypically independently of temperature. Node number (and leaf number: Ong and Baker, 1985) to the first flower is homogeneous in other species (Collins and Wilson, 1974; Hackett, 1985). As node production is a function of the apical region, it has been associated with the transition to shoot maturity (Hackett, 1985).

Plant size appears to be more important than age, as conditions promoting growth reduce the duration of the juvenile period (Hackett, 1980; Wareing, 1982; Thomas and Vince-Prue, 1984; Hackett, 1985). Two general theories have been proposed regarding the aspect of plant size involved in the phase change from juvenility to maturity (Thomas and Vince-Prue, 1984):

i) Involvement of the apex, possibly autonomously, evidence from grafting experiments in a number of species has shown that no phase change occurs when a juvenile apex is grafted onto a mature stock. Apex size in terms of its ontogenetic age was shown to be important. Possibly a critical number of cell divisions in the apical meristem has to occur before flowering can take place. The vegetative phase of cv. "Heritage" was prolonged by removal of the apical meristem prior to floral induction (Dana, In: Braun and Garth, 1984a).

ii) Critical distance of the apex from the roots, with respect to hormone transport, possibly involving gibberellins. For example, juvenility in *Hedera helix* L. was shown to be related to gibberellin content of adventitious roots.

In summary, the maturation process involves the whole plant, quite probably the leaves (Hackett, 1985), roots and apex (Thomas and Vince-Prue, 1984).

Having modelled node production and shoot development for different temperature treatments in the previous chapter, the aim of this chapter is to modify these to produce a model suitable for field estimation of shoot development using day degree accumulation.

Evidence to support the theory that the first shoot to emerge exerts dominance over subsequent shoot production (Hudson, 1954; Robinson, 1975; Cormack *et al.*, 1976; Waister *et al.*, 1977; Vasilakakis and Dana, 1978; Wright and Waister, 1982a) led to the inclusion of node data for the first shoot to emerge only. This removed the need to use weighted means.

6.2 Determination of a lower threshold or base temperature for shoot development

The Temperature-sum method, or day degree accumulation, can be used to predict development in plants grown outside a controlled environment (Roberts and Summerfield, 1987). It is a means of accurately predicting the developmental events of a plant species (Thornley, 1987). More precisely, it enables a scalar variable **h** to be associated with each phase of plant development. The value of **h** is of interest as it marks the plant's progression through a particular phase of interest (Thornley and Johnson, 1990).

Two assumptions are made when employing the Temperature-sum method:

i) There is a linear relationship between the rate of growth and temperature (Baskerville and Emin, 1969; Baker and Gallagher, 1983; Johnson and Thornley, 1985; Roberts and Summerfield, 1987).

ii) Temperatures at which the rate of development is zero do not contribute to the temperature-sum (France and Thornley, 1984; Johnson and Thornley, 1985; Thornley and Johnson, 1990). Temperatures below this value are detrimental to the plant.

The temperature-sum, **h**, for a particular phase was calculated in day degrees (day°C) according to the following:

$$h=\sum_{i=1}^{j} k(\overline{T}_i-T_0) \quad (6.1)$$

where:

k = 1, $T_0 \leq T \leq T_2$

k = 0, for values of T outside the range defined above.

and: k is a constant.

T_0 is a base temperature and

T_2 is an upper threshold temperature.

Temperatures below the base and above the upper threshold temperature inhibit development.

(after Thornley and Johnson, 1990).

Base temperatures of 5 or 6°C have been previously chosen for studies on *Rubus* species (Jennings, 1979a; Dale and Jarvis, 1983; Hoover *et al.*, 1989). Dale and Jarvis (1983) used a base temperature of 6°C to accumulate temperature-sums from anthesis to fruit ripening in raspberry. Jennings (1979a) used the same base temperature to study flowering dates in a number of blackberry cultivars. He found a large year-to-year variation for temperature-sums accumulated for the phase to flowering within individual cultivars. However, there was no significant variation for the phase between flowering and ripening. He concluded that temperature summation was operative for this stage and not the former. Hoover *et al.* (1989) employed a base temperature of 5°C and claimed there was a correlation between day °C and shoot height in cv. "Heritage". There was no evidence to support this claim. Large fluctuations in the temperature-sum data and the lack of experimental evidence for the employment of these base temperatures shows a need for more research in this area.

Field data were collected and a small pilot experiment set up to accurately determine a base temperature for this cultivar.

6.2.1 Field assessment of node production to obtain a base temperature for the rate of node production

Field data were used to calculate a base temperature for node production for the phase: planting to TPC (emergence rates were not recorded in this experiment).

6.2.1.1 Methods

A field plot was set up in March 1989, consisting of two double rows (1m apart) of canes planted at 0.4m apart. The inter-row width was 2.5m. The plot was open and bordered to the North by a windbreak of *Betula* species. The soil type was good, brown earth (grade 1 land). Plants were irrigated when necessary.

Five plants were harvested at 7 - 10 day intervals, from the end of April onwards. The number of nodes for each cane per plant were recorded and the mean per plant taken. The timing of TPC was noted at each harvest. Mean daily temperatures were obtained from daily maximum and minimum screen temperatures (2m above the ground). It was assumed that the air temperature at the screen, rather than the grass minimum was the same as that experienced by plants (Waister and Gill, 1979) in the field plot.

Base temperature was calculated by determining the y intercept, *ie.* the mean temperature at which the rate of development was zero (Arnold, 1959; Baker and Gallagher, 1983; Warrington and Kanemasu, 1983a; Johnson and Thornley, 1985; Roberts and Summerfield, 1987; Thornley and Johnson, 1990). Other methods for the assessment of base temperature were proposed by Arnold (1959) and Cross and Zuber (1972); some of these employed least variability methods for a range of proposed temperatures. These methods were not used as they gave no clear indication of the true base temperature.

6.2.1.2 Results

Rates of node production for individual plants at each harvest were calculated by dividing the mean number of nodes per shoot for each plant by the number of days from planting. These rates were plotted against the mean air temperature from planting to each harvest - calculated from mean daily air temperatures (Figure 6.1). Data were used from successive harvests up to and including the first harvest, where terminal flower buds were apparent. This follows a method employed by Baker and Gallagher (1983) to determine the base temperature for primordium initiation rate for winter wheat (*T. aestivum* L. cv. "Maris Huntsman"). This assumes that field temperatures are within the linear response range of temperatures bounded by the probable base and the optimum temperature for the rate of primordium initiation (also Arnold, 1959). Here (Figure 6.1) the mean temperature was from 6.92 - 8.32°C. Although it is a narrow range it probably lies within the boundaries specified.

Variation in rate of node production between plants and harvests was fairly consistent as shown by the standard error and confidence limits (Appendix 6.1, Table 6.1.1). Regression analysis yielded a fairly good linear relationship, although with a large error variance (70.4%). The base temperature obtained was 4.79°C.

6.2.1.3 Discussion

The base temperature derived was realistic, in terms of physiological viability. However, due to the lack of emergence data, the variation in the data and the narrow temperature range over which the base temperature was assessed, further data were needed to supplement this result.

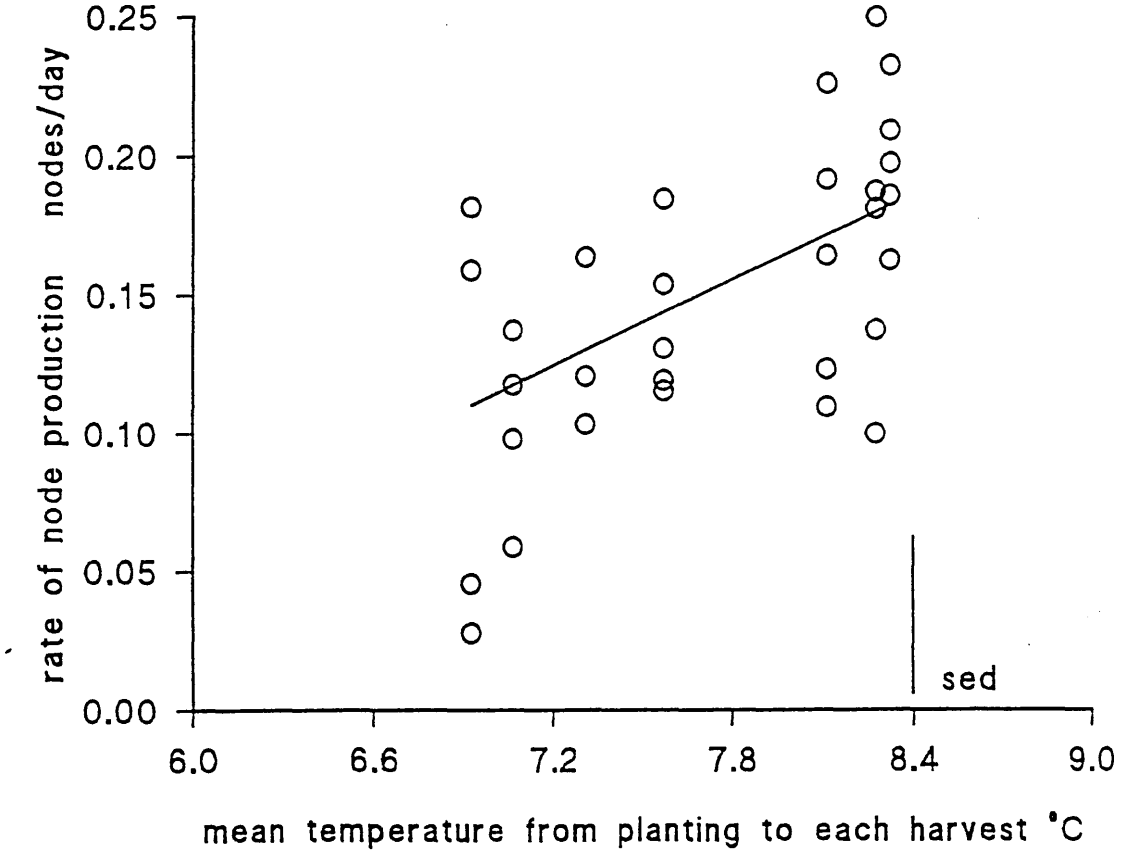


Figure 6.1 The relationship between the rate of node production and mean air temperature for sequentially harvested field-grown plants. r=0.563 (P < 0.001), Adjusted R^2 statistic = 29.6%, regression equation y=0.0518x - 0.2480, base temperature = 4.79°C

6.2.2 Determination of a base temperature for the phases: P → E and E → TPC, from growth cabinet data.

6.2.2.1 Methods

Plants were randomly selected from 3 - 4 year old plants used in previous glasshouse experiments and assumed to be of relatively uniform root and stool mass. Grading was not carried out as it was impossible to assess accurately total plant fresh weight, either directly or indirectly via shoot diameter measurements (section 4.3.4.2). The latter was inappropriate as each plant contained a large number of stem bases or stools. Seven plants were again randomly selected, repotted and placed in each of six temperature control cabinets in late July 1990. Plants were re-randomised at weekly intervals. Cabinets were set at the following mean air temperatures: 10°C, 13°C, 16°C, 19°C, 25°C and 31°C.

Mean air temperature was assessed by taking the daily maximum and minimum temperature from a max/min thermometer located at pot height within each cabinet. Adjustments were made to the temperature where necessary, in order to maintain as constant an environment as possible. Due to an electrical fault in the cooling system of the 10°C cabinet in the middle of the experiment, this was shut down and the results abandoned.

The emergence rate of the first shoot to emerge was recorded per plant. Subsequently, this shoot alone was allowed to develop. Additional emergent shoots were removed. Node number was measured. The base temperature was calculated in the same way. After a period of 68 days, when all the canes within each treatment were still vegetative, the experiment was ended. This was as a result of very low light levels as days shortened in the autumn and the completion of my three year research contract.

6.2.2.2 Results

The mean daily temperature was calculated from daily maximum and minimum temperature readings. An average temperature was obtained for the whole

experimental period for each cabinet (Table 6.1). Confidence intervals for the mean daily temperature were low, but overall maximum and minimum temperatures recorded showed very large deviations from these means. This can be seen more clearly in Figures 6.2a - 6.2e. However, large variations were exhibited in rates of emergence for plants treated at "13°C" and "31°C", as seen from the 95% confidence limits (Appendix 6.1, Table 6.1.2). The rate of emergence was plotted against mean temperature from planting to emergence (Figure 6.3).

Table 6.1 Confidence Limits for the mean air temperatures experienced by plants in temperature control cabinets in the 1990 experiment

Temperature treatment	Average temperature (calculated from mean daily max/min)	95% Confidence Limits (for daily mean temperature	Overall maximum and minimum temperatures recorded
13°C	13.56°C	13.56±0.6176	29/5.75°C
16°C	13.60°C	13.60±0.1349	19.5/10.5°C
19°C	17.50°C	17.50±0.2454	25/13°C
25°C	24.83°C	24.83±0.3376	35.5/20.5°C
31°C	28.34°C	28.34±0.2788	34/19°C

The rate of node production ΔN was calculated according to the following:

$$\Delta N = \frac{N_{68} - N_e}{t_{68} - t_e} \quad (6.2)$$

Where;

N = node number per cane

N_e = node number at emergence, assumed = 0

N_{68} = node number at the end of the experiment

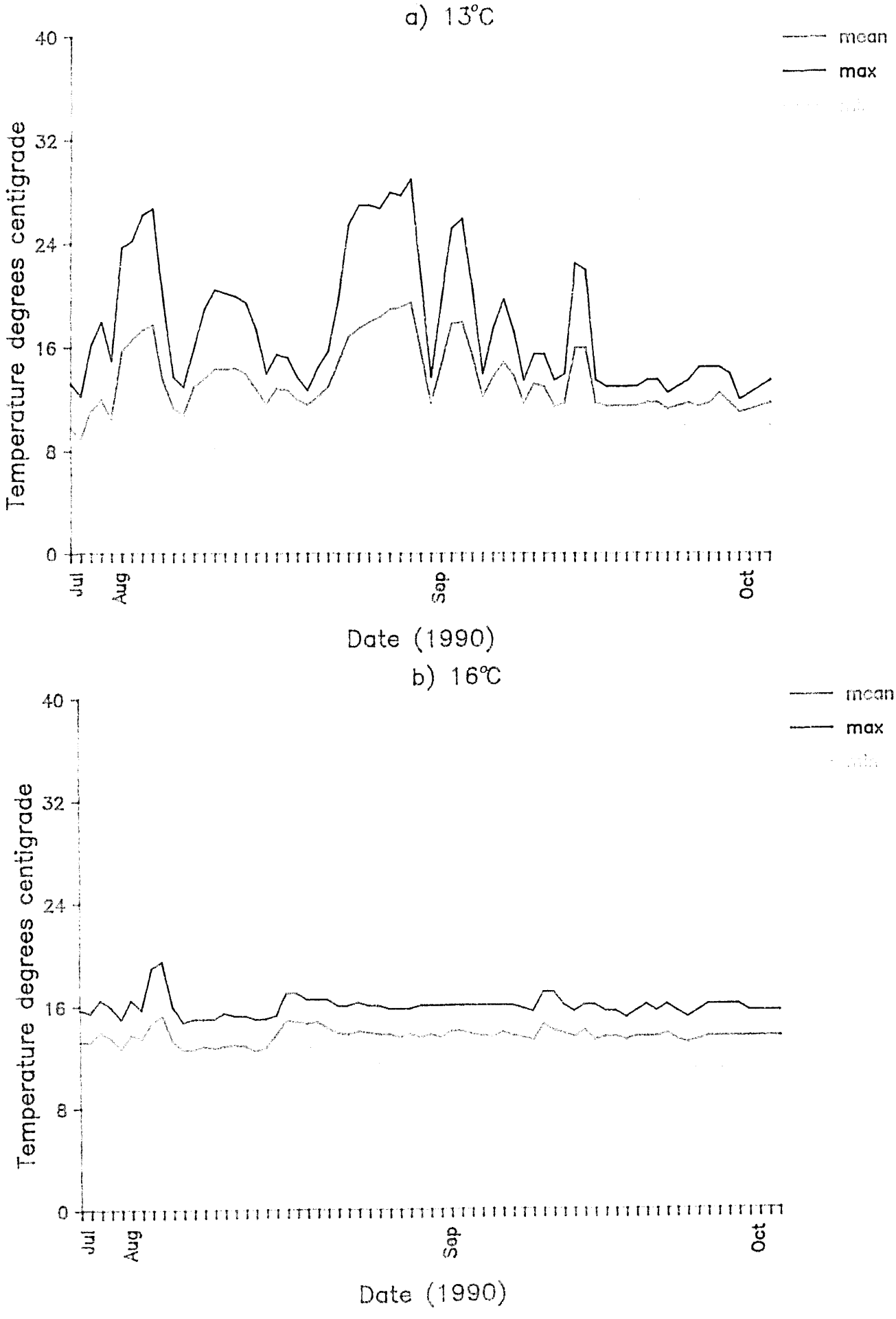
t_e = mean time to emergence = 14.16 days

t_{68} = time at the end of the experiment = 68 days

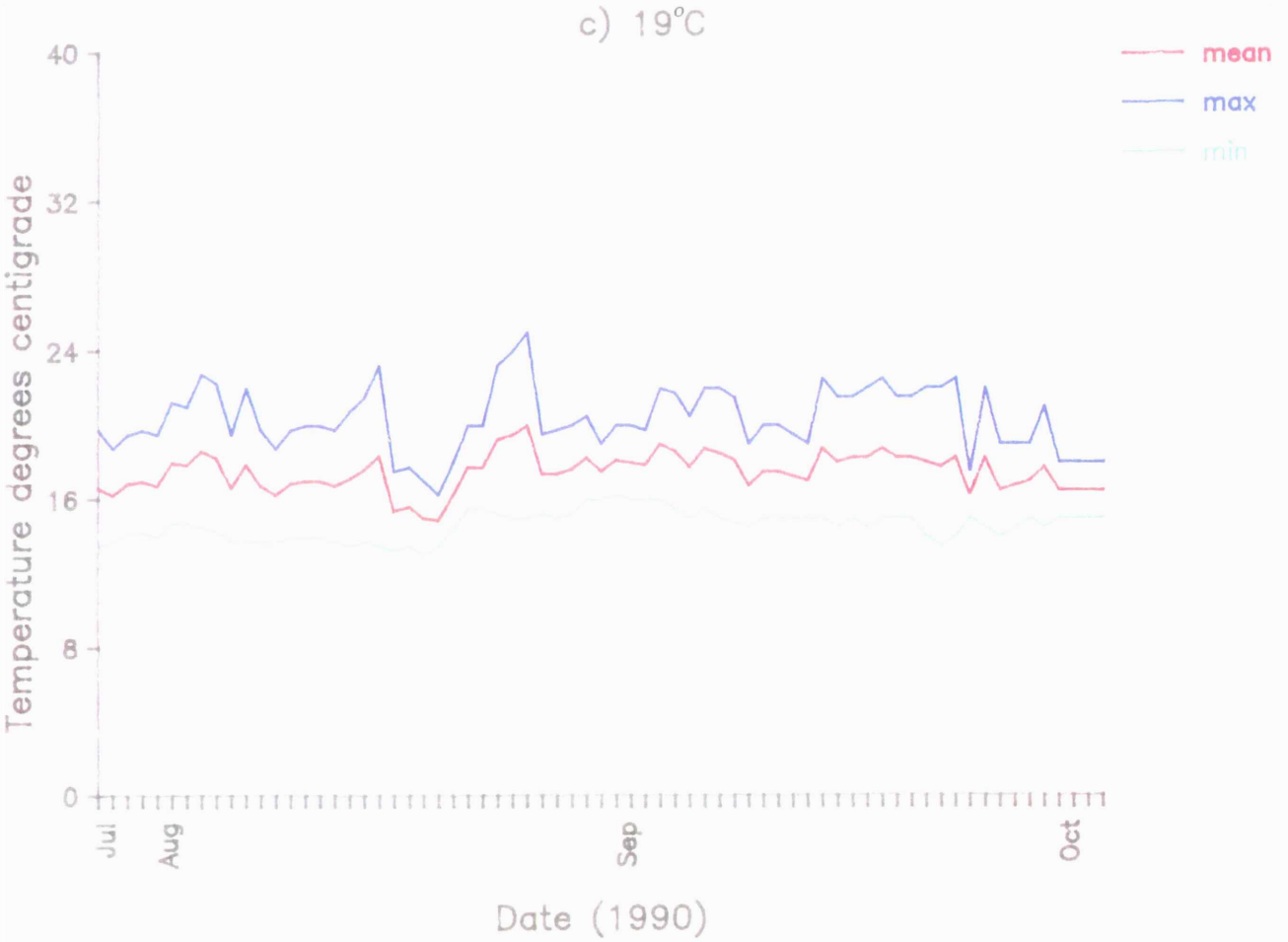
The rate of node production was plotted against mean temperature (Figure 6.4). Analysis of variance revealed a much lower variation between plants. The rate of node production was highly significant between treatments (Appendix 6.1, Table 6.1.2). Regression analysis produced a very good linear relationship with a base temperature of 5.84°C.

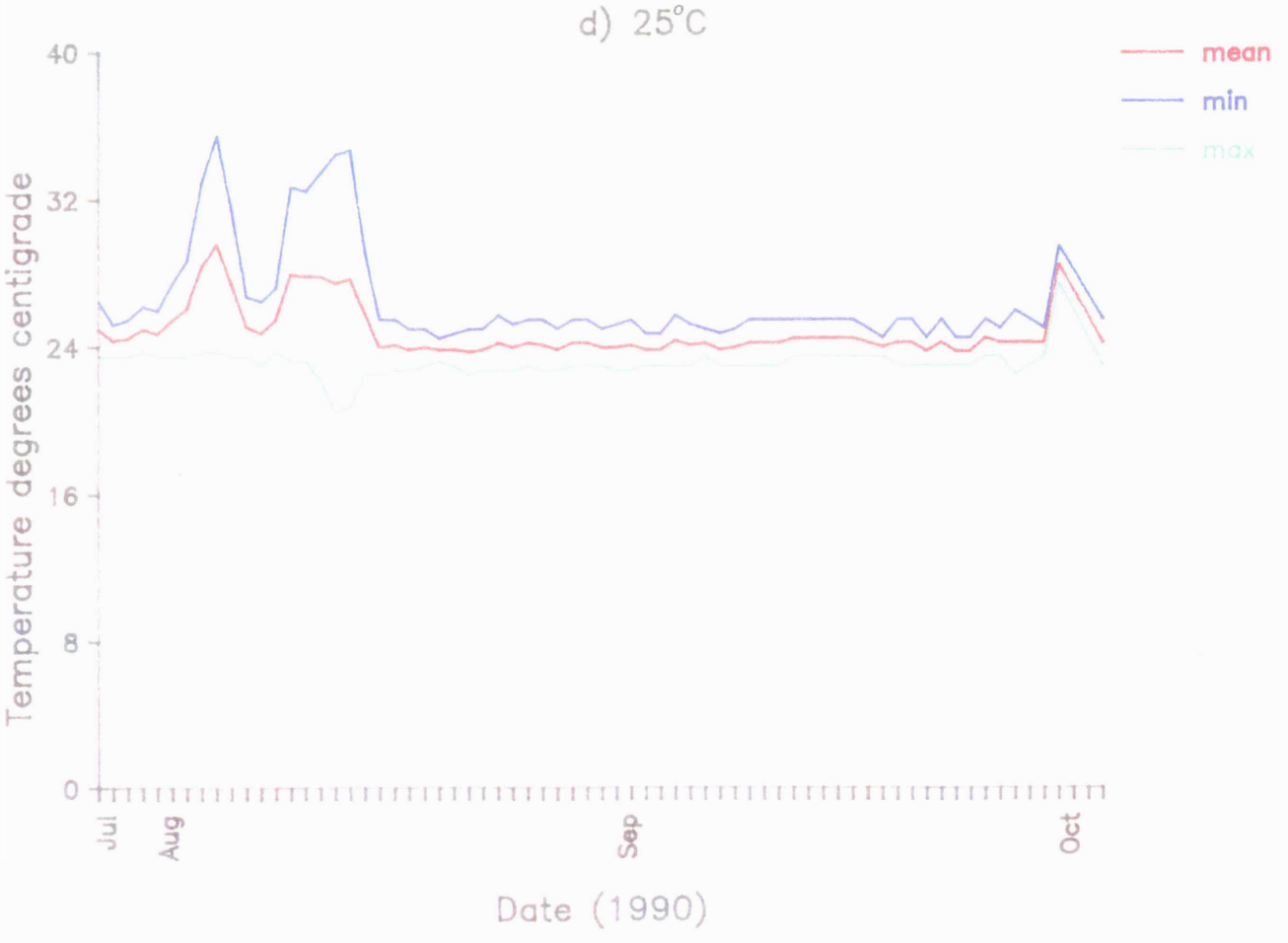
6.2.2.3 Discussion

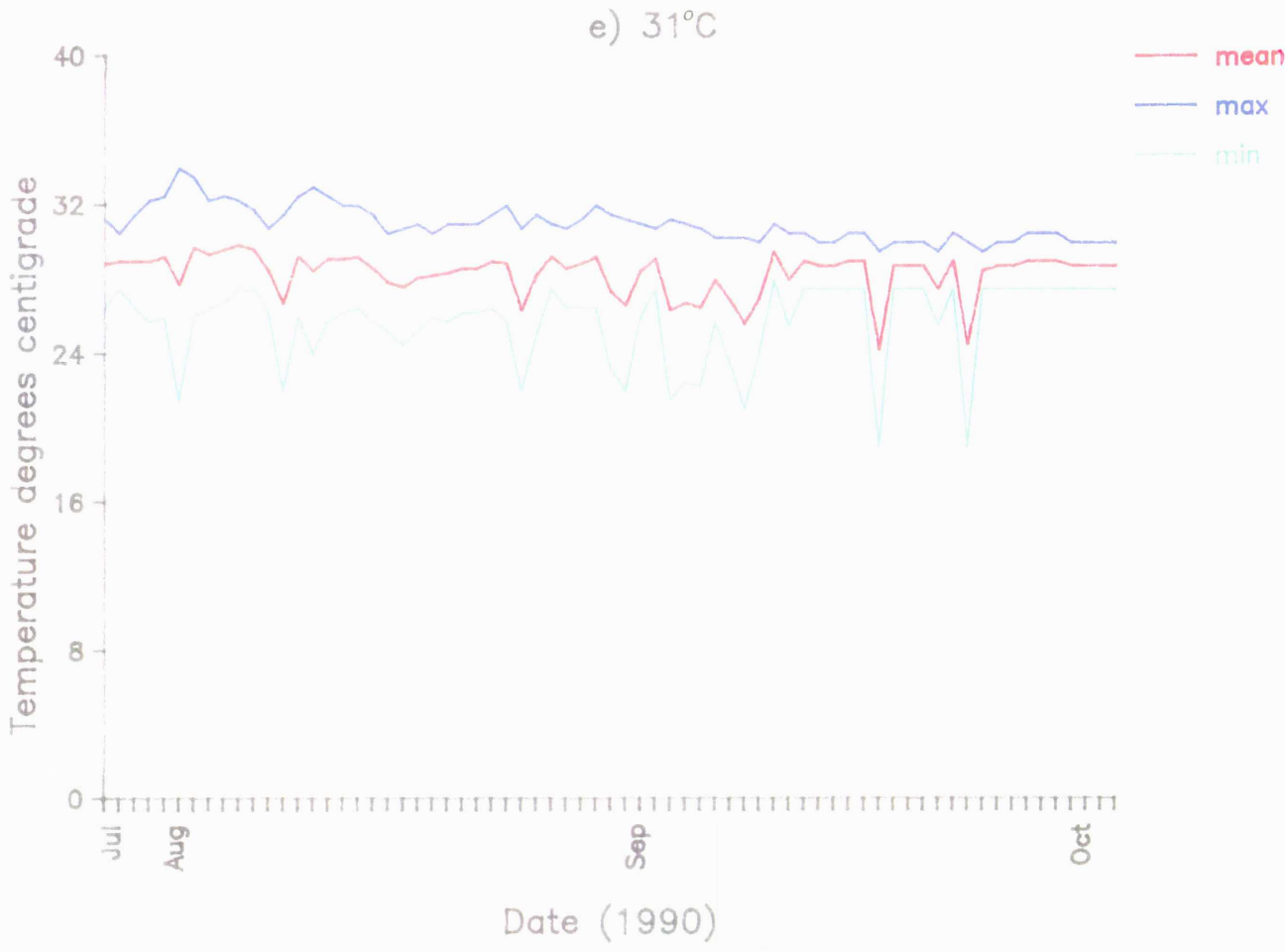
There appeared to be no clear relationship between the rate of emergence and mean air temperature. Plants treated at "13°C" exhibited the lowest mean rate of emergence, the error was probably due to the very low temperatures actually experienced by these plants compared with those treated at "16°C". Absolute maximum and minimum temperatures recorded for the "13°C" cabinet were 26.75°C and 5.75°C, compared with 19.50°C and 10.50°C for the "16°C" cabinet. This implies that, although maximum temperatures were higher in the "13°C" cabinet, they were experienced for shorter periods of time. Thus, the temperature recorded on the max/min thermometer was as a result of short bursts of high temperature, giving unrealistically high mean daily temperatures. Evidence that these temperatures were relatively short-lived was supplied by the cabinet engineering design. The ambient temperature was excessively high during the course of the experiment (July-August 1990).

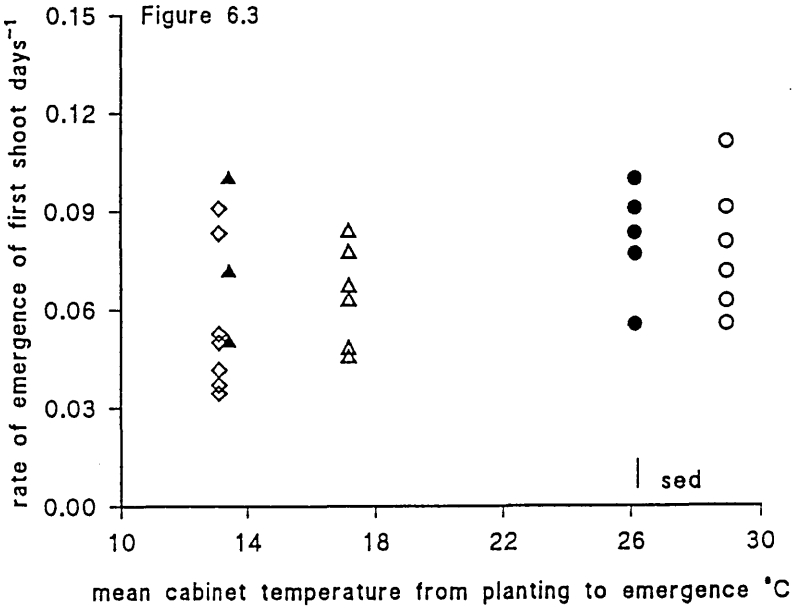


Figures 6.2a - e Daily maximum, minimum and mean temperatures taken from max/min thermometer readings in each of five temperature control cabinets. The treatment temperature is indicated for each graph.


c) 19°C
mean
max
min
Temperature degrees centigrade
40
32
24
16
8
0
Jul
Aug
Sep
Oct
Date (1990)


d) 25°C
mean
min
max
Temperature degrees centigrade
40
32
24
16
8
0
Jul
Aug
Sep
Oct
Date (1990)


e) 31°C
mean
max
min
Temperature degrees centigrade
40
32
24
16
8
0
Jul
Aug
Sep
Oct
Date (1990)



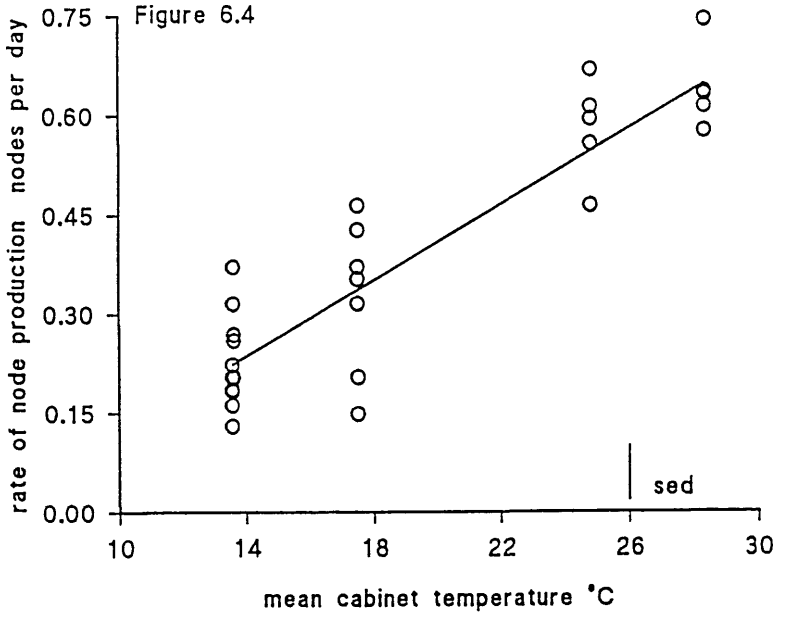


Figure 6.3 The relationship between the rate of emergence and mean air temperature from planting to emergence. No significant difference between treatments.

Figure 6.4 The relationship between the rate of node production and mean air temperature. r=0.909 (P < 0.001), Adjusted R^2 statistic = 82%, regression equation y = 0.0289x - 0.1687, base temperature = 5.84°C

This led to cooling in the "13°C" cabinet. Demonstrations of airflow in the cabinets have shown that air does not readily circulate upwards from the fans over the pan holding the plants. Over-cooling occurred in the cabinet as a whole, as the system tried to lower the temperature, registered by the thermocouple located above the pan. In reality, this resulted in extreme over-cooling of the lower cabinet, so that it caused freezing of the cooling system. This in turn raised the temperature abnormally in the upper cabinet. In conclusion, more accurate measurement of the temperature using a thermograph or a Datalogger (connected to thermocouples) would have revealed these fluctuations.

The large error between plants was probably partly due to non uniformity of plant material. This may have been displayed through the existence of pre-emergent shoots, which subsequently emerged rapidly at the beginning of the experiment. Care was taken to remove these shoots, but as the root mass was so compact some inevitably were missed. Their rate of emergence would therefore be independent of the temperature treatment employed.

"Rosetting" was exhibited in emergent shoots of plants in the "13°C" cabinet. From the base temperature obtained for node production it is clear that these plants were unable to develop rapidly. Williams and Hudson (1956) and Williams (1959b) showed that plants of cv. "Malling Promise" formed rosettes at low temperatures and short daylengths. Although, rosettes formed at 10°C irrespective of daylength. Rosetting can be indicative of long day photoperiod sensitive plants. There is no evidence for this in cv. "Autumn Bliss".

The base temperature obtained was higher than that derived from field data. The former base temperature was calculated for plants from planting to TPC. This would have resulted in a lower gradient and interception point for these data. Correspondingly, the latter data set may be inaccurate as only vegetative shoots were measured.

Overall, as the fit of the regression line was better and the temperature range was physiologically broader, this base temperature was used in further analysis in preference to that obtained from the field data.

6.2.3 Determination of a base temperature for the development phase from P → E taken from growth cabinet data collected in 1989

Data from the previous chapter were used to determine a base temperature for shoot development from planting to emergence.

As linearity between rate of development and temperature is assumed, only two environments in theory are required to define and quantify the relationship (Roberts and Summerfield, 1987). However, statistically, at least five environments are recommended. This gives higher value for the degrees of freedom and more confidence in the fit of the regression line (here there are only four environments, therefore only two degrees of freedom). As with the former regression analyses, all data points were used to obtain a more realistic fit to the regression, by increasing the degrees of freedom. At the same time this showed the true variation between experimental units (plants).

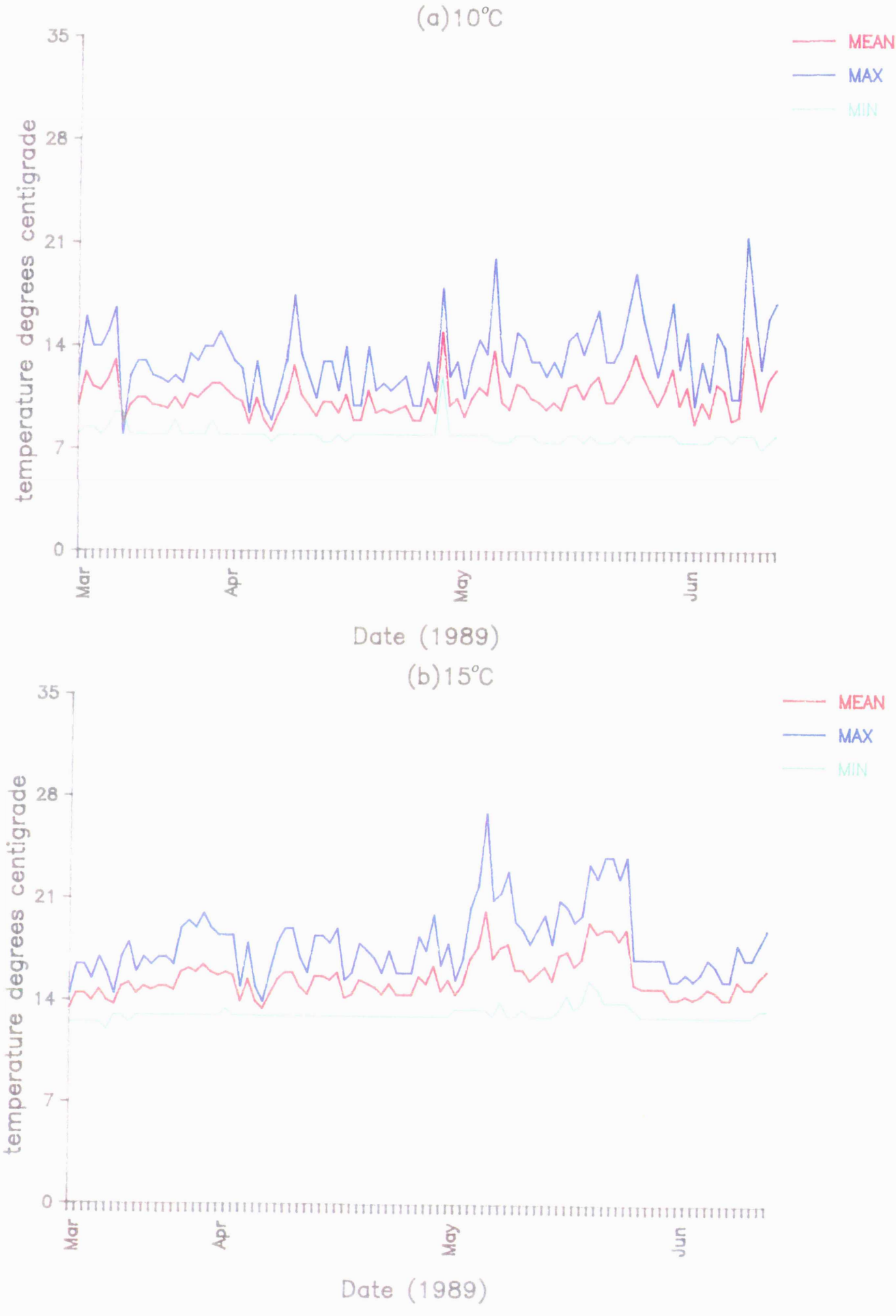
6.2.3.1 Methods

Please refer to section 5.2 for details.

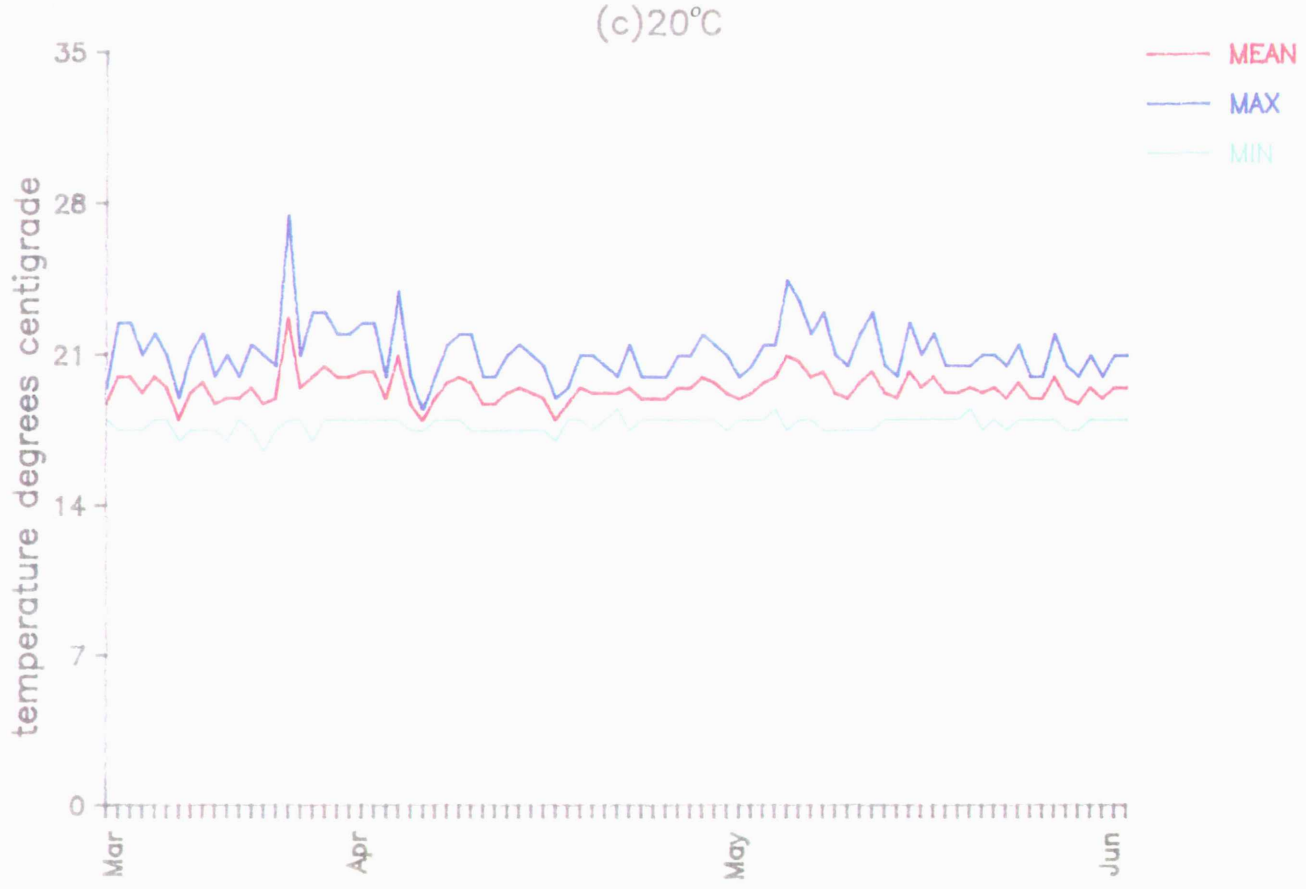
6.2.3.2 Results

Daily mean temperatures were calculated from maximum and minimum temperatures. As can be seen from Figures 6.5a - 6.5d, variation in mean temperature was higher for the "10°C" cabinet (Table 6.2). This reflects the difficulty in keeping these cabinets at mean temperatures in the range of 10°C.

The overall mean temperature from planting to emergence was plotted against the inverse of the time taken for the first cane to emerge (Figure 6.6). This was highly significant between treatments (Appendix 6.1, Table 6.1.3). Variation between treatment means and between plants was of the same order. Regression analysis yielded a fairly good linear relationship. The base temperature obtained was 0.86°C.



Figures 6.5a - d Daily maximum, minimum and mean temperatures taken from max/min thermometer readings in each of four temperature control cabinets. The treatment temperature is indicated for each graph.


(c)20°C
MEAN
MAX
MIN
35
28
21
14
7
0
temperature degrees centigrade
Mar
Apr
May
Jun
Date (1989)

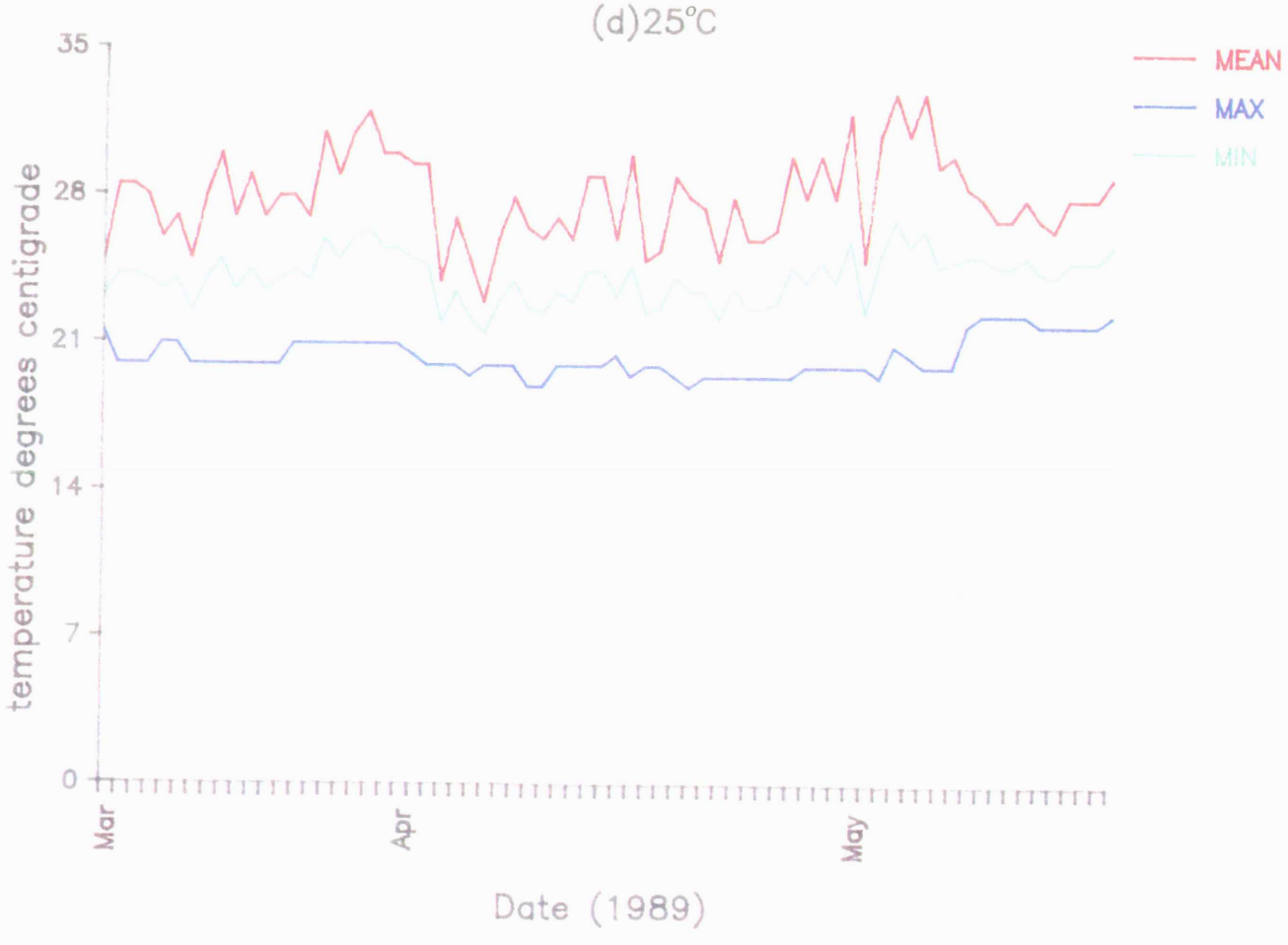

(d)25°C
MEAN
MAX
MIN
35
28
21
14
7
0
temperature degrees centigrade
Mar
Apr
May
Date (1989)

Table 6.2 Confidence Limits for the mean air temperatures experienced by plants in temperature control cabinets in the 1989 experiment

Temperature treatment	Average temperature (calculated from mean daily max/min)	95% Confidence limits (for daily mean temperatures)	Overall maximum and minimum temperatures recorded
10°C	10.91°C	10.91±0.8421	16.6/8°C
15°C	14.38°C	14.38±0.3772	18/12°C
20°C	19.34°C	19.34±0.5523	22.5/17°C
25°C	23.85°C	23.85±0.5042	28.5/20°C

6.2.3.3 Discussion

Hudson (1956) found that buds of cultivars "Lloyd George" and "Malling Promise" remained dormant at temperatures below 7°C. Further to this, larger buds elongated at lower temperatures than smaller ones. In contrast, here and elsewhere (Chapter 3) there is evidence that buds, of cv. "Autumn Bliss", elongate at lower temperatures. This verifies the low base temperature obtained here.

6.3 Observational data for shoot phenology

6.3.1 Node number

Node number at TPC and TF from field data collected in 1989 (TPC = 22.75 (±2.76) and TF = 31.57 (±4.33)) compared well with data obtained from the 1989 growth cabinet experiment (refer to section 5.3.3.1), supporting evidence that absolute node number is independent of the effect of air temperature. Figures of shoot development to show the timing and extent of lateral development in terms of node and lateral node production are shown in Appendix 6.2, Figures 6.2.1a - u.

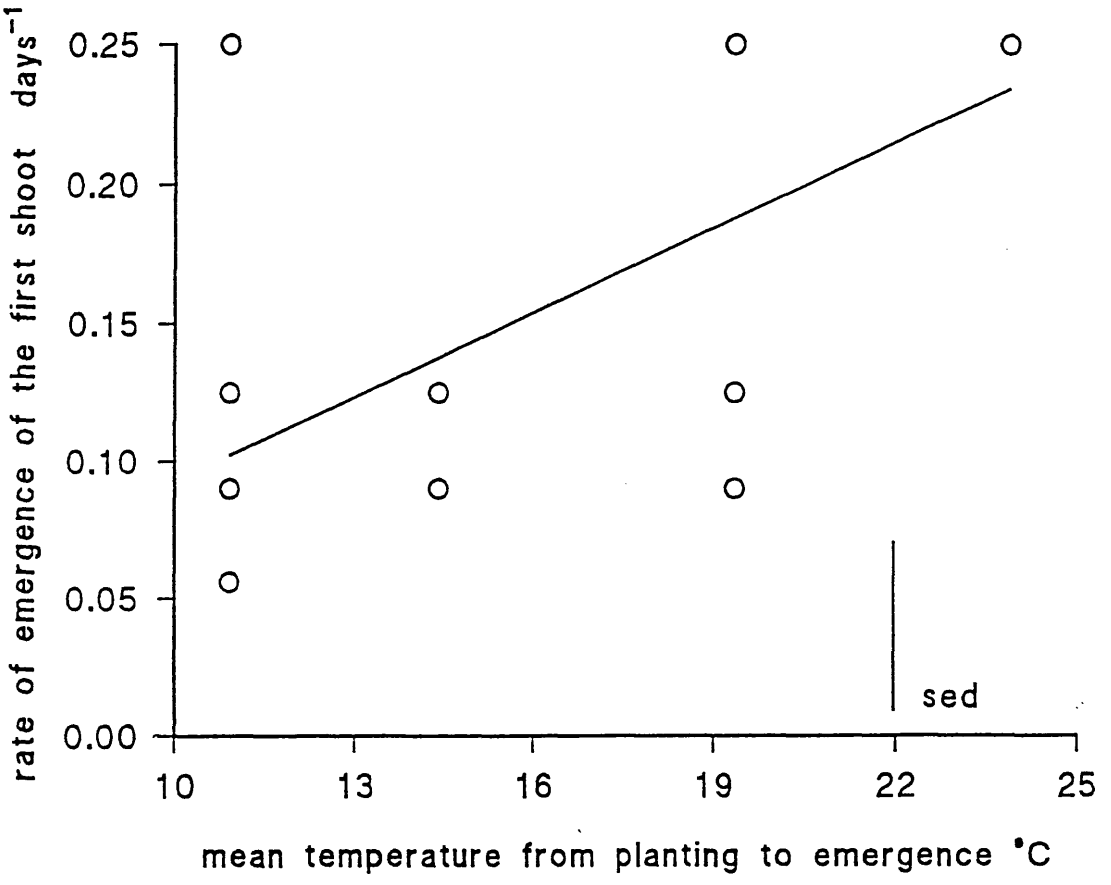


Figure 6.6 The relationship between the rate of the first shoot to emerge and the mean air temperature between planting and emergence. r = 0.681 (P < 0.001), Adjusted R^2 statistic = 44%, regression equation y = 0.0102x - 0.008, base temperature = 0.86°C

6.3.2 Temperature-sums for phases of shoot development

Temperature-sums were calculated for the following phases of development:

H_1 P → E

H_2 E → TPC

H_3 TPC → TF

H_4 TF → BR

(P - planting).

H_1 T_0 = 0.86°C, T_2 = 30°C

For the phase;

H_2 - H_4 T_0 = 5.84°C, T_2 = 30°C

These were tabulated for 1989 growth cabinet experiment data (Table 6.3a) and field data (Table 6.3b). Errors (in days) were calculated by dividing the standard deviation by the mean temperature for each cabinet (Arnold, 1959). There was little difference between temperature-sums for H_1 and to a lesser extent H_4 (the temperature-sum for plants treated at "10°C" was higher). More variation was shown for H_2 (up to 70 days error) and H_3. Temperature-sums were higher for higher mean air temperature treatments at H_2. Arnold (1959) found that this was indicative of too high a base temperature. The high temperature-sum (H_4) calculated for plants treated at "10°C", reflected the pronounced delay in ripening rate for these plants. As all plants were grown under the same temperature regime from TF → BR, this indicated an intrinsic cause for this delay. Damage to terminal flowers at anthesis due to scorching in some plants in this treatment resulted in poor fruit set. As fruit at these nodes ripen first, the actual figure for ripening rate was based on fruit located at laterals lower down the cane.

Tables 6.3a - b Temperature thresholds (H) for phases of cane development (day°C)
Table 6.3a 1989 growth cabinet experiment

phase	temperature thresholds (day°C) for each temperature treatment				mean (se)
	10°C	15°C	20°C	25°C	
H_1 P → E	104.61 (2.16)[16]	144.31 (1.43)	142.89 (1.13)	109.97 (0.90)	125.45 (21.08)
H_2 E → TPC	316.28 (70.10)	440.86 (34.22)	807.44 (24.48)	1042.62 (18.17)	651.80 (333.68)
H_3 TPC → TF	81.56 (17.36)	274.00 (8.48)	176.08 (6.06)	228.58 (4.50)	190.06 (82.65)
H_4 TF → BR	636.33 (20.08)	429.87 (9.80)	490.87 (7.01)	438.23 (5.20)	498.83 (95.56)

Table 6.3b 1989 field data

phase	temperature threshold (day°C)
P → TPC	439.10
P → TF	660.31
P → BR	1109.26

6.4 A mechanistic model for first shoot development per plant

The model aims to:

i) relate phenological events to field temperatures, by demonstrating a relationship between day degree accumulation and the rate of node production.

ii) suggest a relationship between the development of the first shoot and succeeding shoots.

Large errors were obtained for the parameters **b** and **n**, when these modified data were used to fit equation 5.1; substituting **t** for **h**. The Richards function has

[16]Errors in days in brackets for details see text.

greater flexibility (four parameter model) than the three parameter logistic function. However, it is noted for its instability of parameter estimation (Ratkowsky, 1983), particularly with respect to **n** (Thornley and Johnson, 1990). The Richards function was replaced by a modified version of the logistic function. Landsberg (1974) employed the function in a model of apple fruit bud development:

$$G=\frac{A}{1+be^{-k(I).P}} \quad (6.3)$$

This incorporated a chilling/dormancy index, **I** and temperature-sum, **P** for bud development once dormancy was broken.
Here the equation is in the form:

$$N=\frac{A}{1+be^{-kh}} \quad (6.4)$$

Where:
N = node number (nodes)
A = maximum number of nodes produced (≡ **TF**) (nodes)
b - a constant (nodes), **k** - a rate constant (nodes day°C^{-1})
h = temperature-sum from planting (day°C)

6.4.1 Application of the model

Estimates of **b** and **k** were calculated and a curve fitted to each data set by non-linear least squares iteration, using a SAS program. Fitted and observed values were plotted (Figure 6.7a - d) and parameter estimates summarised in Table 6.4. Note that temperature thresholds (H) for Figure 6.7a - d were calculated from planting to a given stage (Appendix 6.1, Table 6.1.4) whereas figures quoted in Table 6.3a were calculated for a single phase.

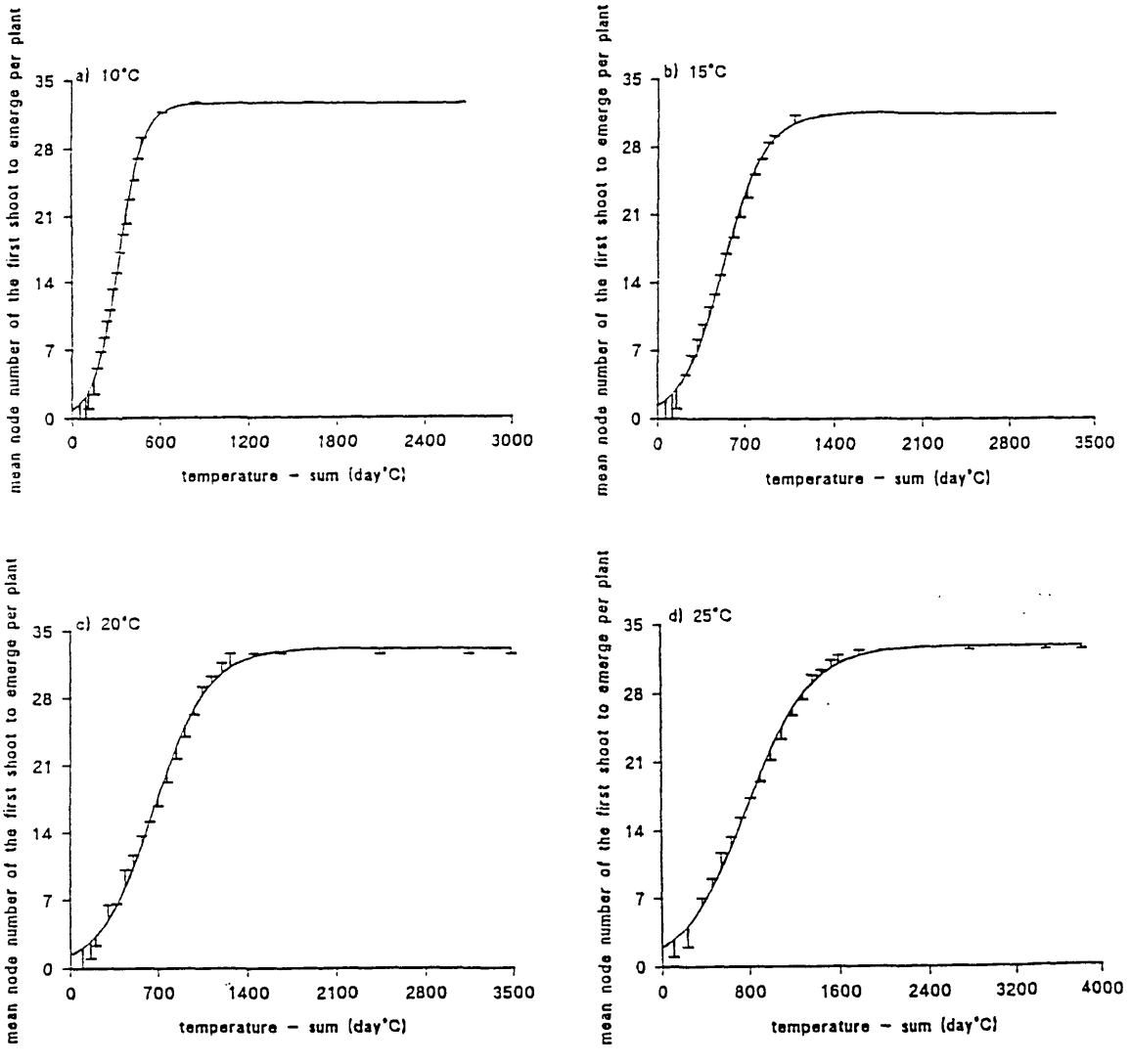


Figure 6.7a - d Fitted curves and residuals for each of the four temperature treatments. The non-linear mean square ratios are as follows: a) 10°C, 2918 ($P < 0.001$), b) 15°C, 2849 ($P < 0.001$), c) 20°C, 2877 ($P < 0.001$), d) 25°C, 3456 ($P < 0.001$) (corrected total degrees of freedom = 22).

Table 6.4 Parameter estimates for curve fits of node data from each temperature treatment

PARAMETER	temperature treatment (°C)	estimate	asymptotic standard error	asymptotic 95% confidence interval	asymptotic correlation between b and k
A (nodes)	10	32.70	0.4757	31.71-33.69	
	15	31.53	0.4964	30.50-32.56	
	20	33.25	0.5224	32.16-34.34	
	25	32.67	0.4839	31.66-33.68	
b (nodes day^{-1})	10	37.54	6.1394	24.77-50.31	
	15	23.13	3.4821	15.89-30.37	
	20	22.73	3.6683	15.10-30.36	
	25	15.84	2.2733	11.10-20.58	
k (nodes day^{-1})	10	0.0116	0.0005	0.0104-0.0127	0.9484
	15	0.0059	0.0003	0.0053-0.0065	0.9195
	20	0.0046	0.0002	0.0041-0.0051	0.9216
	25	0.0035	0.0001	0.0031-0.0039	0.9099

Errors for parameter estimates were low, although there was some variation in the values of **b** and **k** obtained.

Correlation between **b** and **k** was good. However, when curves from each data set were compared (Figure 6.8) plants treated at "10°C" appeared to exhibit a more rapid rate of node production. This was shown in the values of **b** and **k** obtained (Table 6.4) and was further shown by linear regression of the linear portion of each curve. This showed a markedly higher rate of node production per day°C for plants from this treatment (Table 6.5).

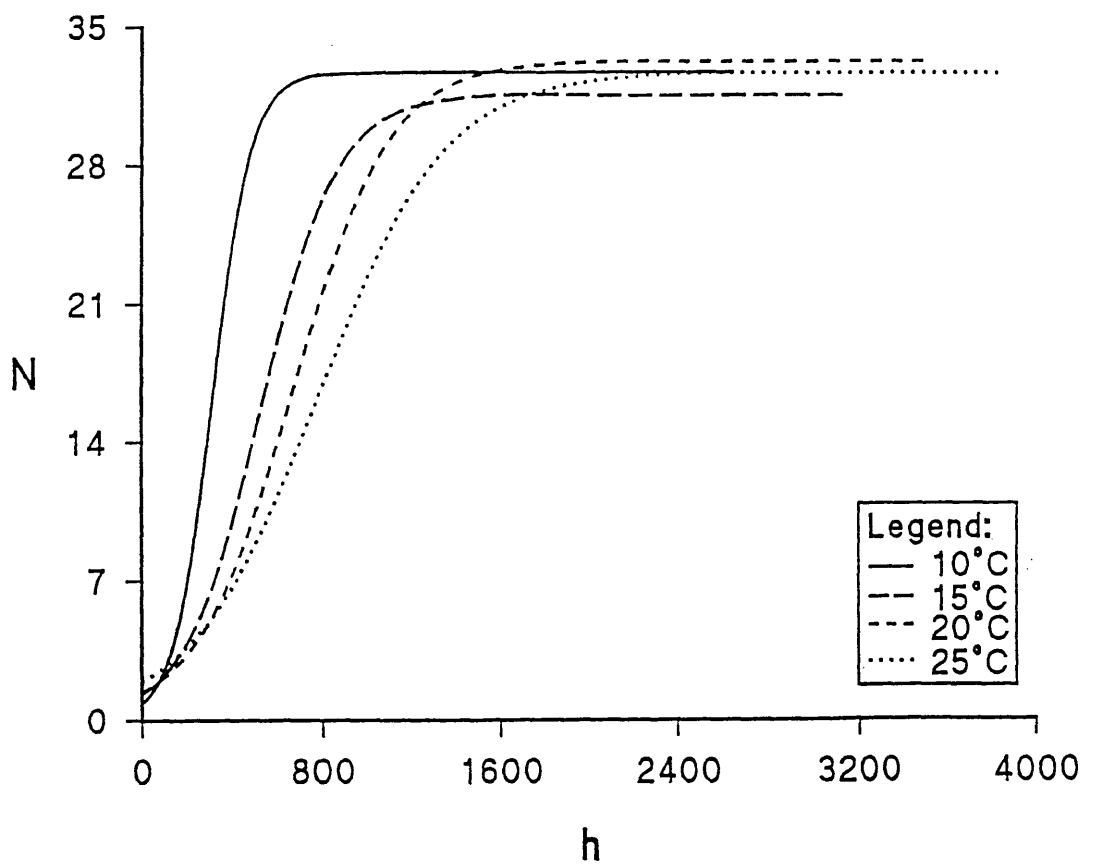


Figure 6.8 Comparison of fitted curves for the four temperature treatments; Where N - fitted node number per shoot and h - temperature-sum.

Table 6.5 Linear estimates of the rate of node production for fitted data from each treatment (taken from the linear portion of each curve)

temperature treatment (°C)	equation of line	gradient (rate of node production, nodes day°C^{-1})	degrees of freedom	R^2 statistic
10	N=0.0772h-7.59	0.0772	14	99.0
15	N=0.0378h-4.22	0.0378	13	99.1
20	N=0.0320h-4.68	0.0320	11	100
25	N=0.0243h-2.70	0.0243	10	100

Table 6.6 Derived parameters for curve fits of node data from each temperature treatment

DERIVED PARAMETERS		temperature treatment			
equation	parameter	10°C	15°C	20°C	25°C
$\frac{\log_e b - 1.317}{k}$	$\mathbf{h}_1$ (day°C)	199.00	309.22	392.75	413.01
$\frac{\log_e b + 1.317}{k}$	$\mathbf{h}_3$ (day°C)	426.07	755.66	965.36	1165.58
$\frac{\log_e b}{k}$	$\mathbf{h}_2$ (day°C)	312.53	532.44	679.06	789.29
$\frac{A}{1+b}$	Intercept($\mathbf{n}_0$) (nodes)	0.84	1.30	1.40	1.94

A point of inflexion and turning points were again derived from the function (Appendix 6.3). $\mathbf{h}_1$,$\mathbf{h}_3$ (points of maximum rate of change of node production) and

$\mathbf{h_2}$ (point of maximum rate of node production) were calculated in day°C (Table 6.6) as well as an estimation of the node number at planting ($\mathbf{n_0}$).

Node number was assumed to be zero prior to emergence for ease of measurement. However, day degrees were accumulated from planting to include node production and elongation of pre-emergent shoots from bud expansion to appearance at the soil surface.

The latter model enabled extrapolation of node number at planting and emergence. This led to under-estimation of total node number and over-estimation of the rate of node production. As the model is asymptotic at $N = 0$ ($h \rightarrow \infty$), then $N \neq 0$ at planting. This is merely a property of the function, although in concept it allows for the presence of a small but an unknown number of nodes in the pre-emergent shoot.

6.4.1.1 Significance of derived parameters h_1 - h_3

Values for observed and derived temperature-sums were shown (Figure 6.9a - d) in relation to node production from planting to maturity. Although there is variation between observed and derived parameters for each phase, the variation is less marked for E → TPC ($\mathbf{H_2/h_3}$), whereas values for $\mathbf{h_1}$ were higher and values for $\mathbf{h_2}$ were lower than observed values. The same argument can be used for this model as for the previous Richards model, whereby $\mathbf{h_2}$ pinpoints the actual event of floral initiation in terms of the maximum rate of node production.

Lyndon (1990) described the order of events occurring in the apex at the cellular level. Characteristic is a temporary increase in the growth rate of the apex as it transfers from the production of leaves to floral organs. This may be associated with $\mathbf{h_2}$. Following this increase in growth rate, the apex enlarges (at TPC). Finally, the rate of initiation of primordia increases, along with cellular changes such as RNA synthesis and an increase in cellular respiration. These latter events are probably marked by $\mathbf{h_3}$. Correspondingly, it can be assumed that $\mathbf{h_1}$ relates to the increase in leaf primordia initiation at the apex after shoot emergence. Comparative changes have been observed in wheat (*T. aestivum* L.) at the transition from leaf to spikelet

initiation and at the end of ear initiation (Kirby, 1985).

$\mathbf{H_4}$ does not have an equivalent derivative, however BR occurs at **A** - the second asymptote. The use of node number as a predictor for berry ripening is difficult as $\mathbf{N \rightarrow A}$, $\mathbf{h \rightarrow \infty}$. However, the temperature-sum from TF → BR is important commercially (Waister and Wright, 1989) as this marks "berry filling".

This is equivalent to grain filling in cereals, when there is major allocation of photosynthetic assimilates to the developing grain (Gifford and Evans, 1981). The build-up of sucrose, fructose and other assimilates occurs over a period of approximately 500 - 700 day°C.

6.4.1.2 Significance of the model with respect to shoot production

Shoot number per plant increased after the first shoot to emerge had initiated terminal flowers (at TF). Prior to this the shoot population was more or less constant (Figure 6.10). Day degrees were expressed as developmental units (Roy and Gallagher, 1985), *ie.* as a percentage of the temperature-sum per treatment taken from:

a) P → TPC, b) P → TF and c) P → BR. (Figures 6.11a - c)

The initial population or first cohort reached a peak prior to TPC. This decreased from TPC to TF. Following TF, shoot population increased again - particularly at the two lower temperature treatments - to form a second cohort.

In terms of modelling plant cane population dynamics, $\mathbf{h_1}$ marks the beginning of establishment of the first cohort. From $\mathbf{h_2}$ - $\mathbf{h_3}$, a self-thinning phase occurs and from $\mathbf{h_3}$ onwards the second cohort is established.

Field measurements taken at sequential harvests of cane populations per plant reflected this shift in population, in relation to the timing of TF (Figure 6.12a - b). Roy and Gallagher (1985) found linear relationships in tiller production and dry matter content at stem extension, and between stem extension and anthesis in wheat.

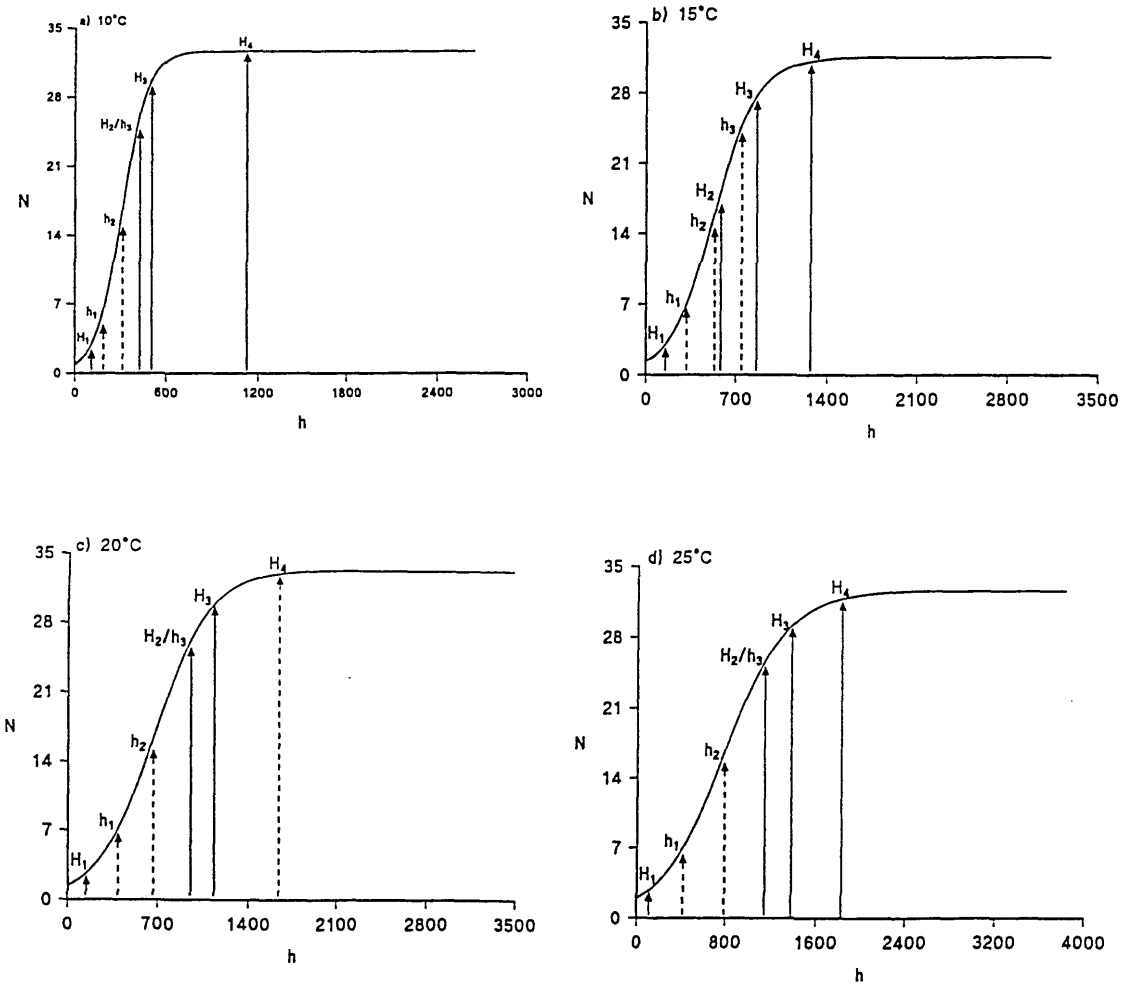


Figure 6.9a - d The comparison of the timing of observed and derived temperature-sums for phases of shoot development in relation to node production for each temperature treatment. Where: N - node number per shoot; h - derived temperature-sum; H_1-H_4 - observed temperature-sums for the stages E, TPC, TF, BR respectively; h_1-h_3 - turning points on the graph (see text).

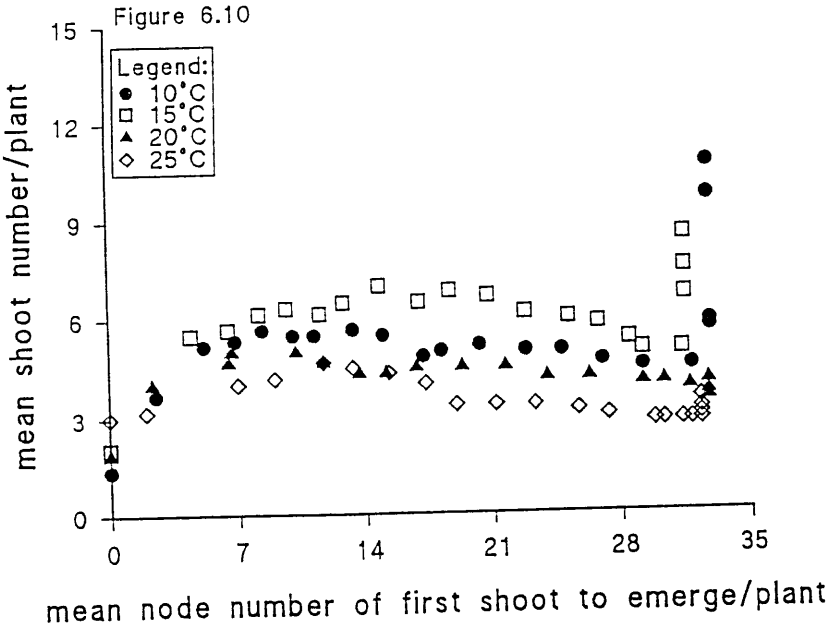


Figure 6.10 The change in mean shoot number per plant in relation to node production of the first shoot to emerge

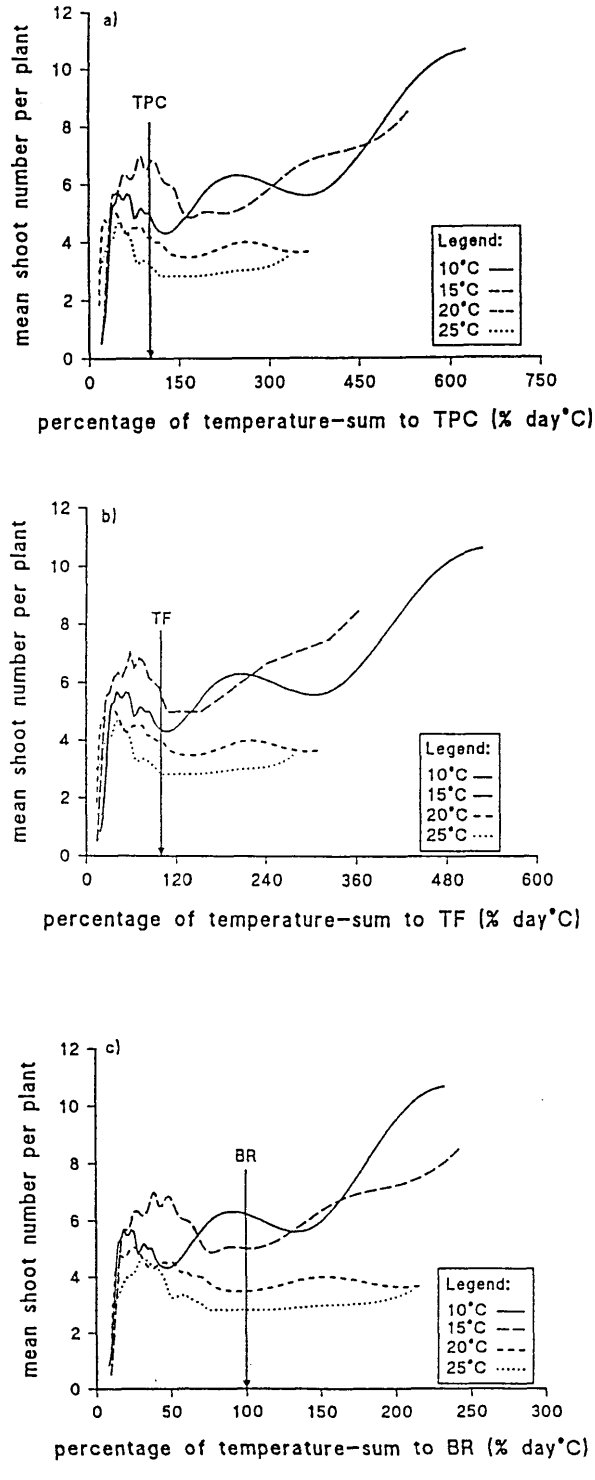


Figure 6.11a - c The relationship between shoot number and developmental stage of the first shoot to emerge (expressed as a percentage of the temperature-sum to a given stage). a) P → TPC, b) P → TF, c) P → BR

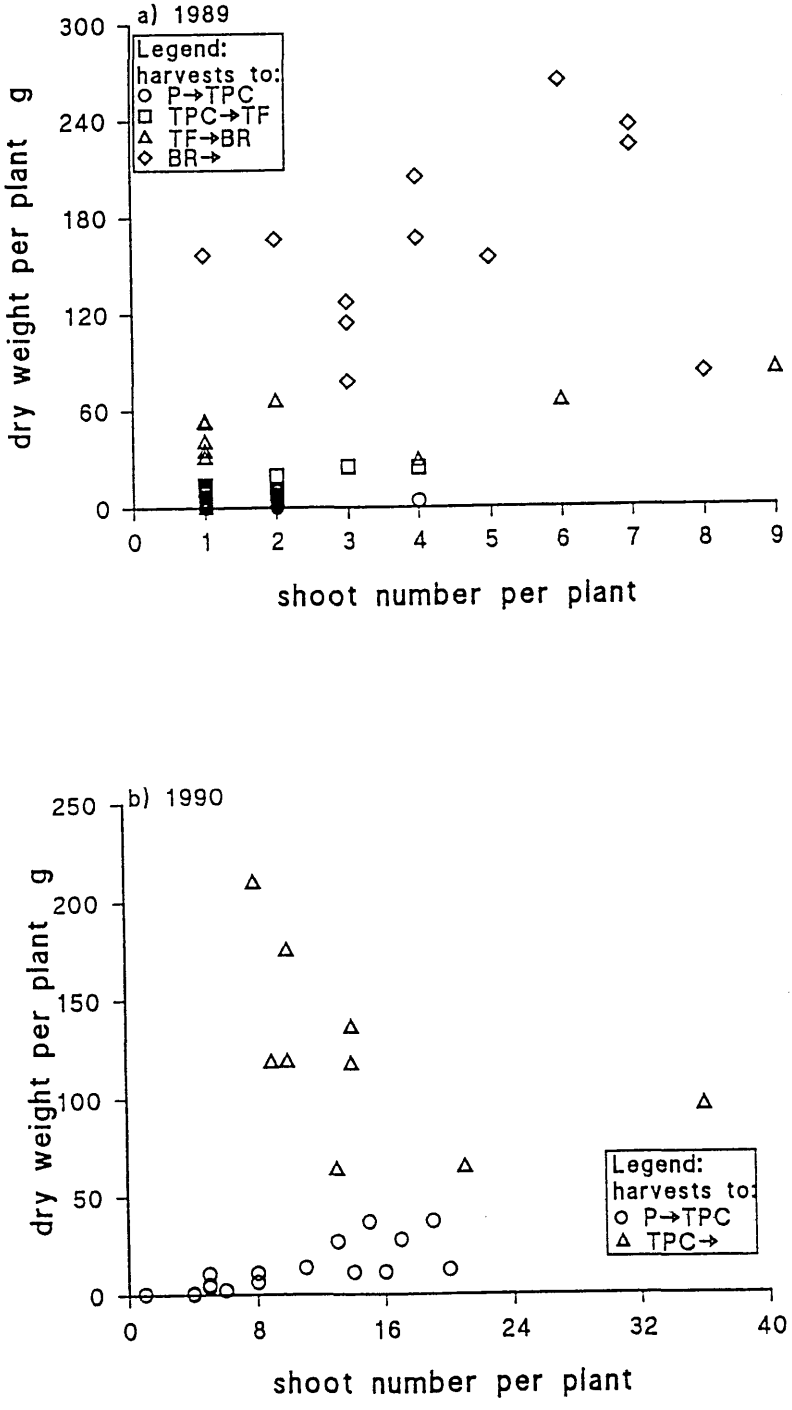


Figure 6.12a - b The relationship between the total dry weight per plant and shoot number for field grown plants. a) 1989 field data (one year old stools), b) 1990 field data (two year old stools)

6.5 DISCUSSION AND CONCLUSIONS

The model is effective in predicting the timing of developmental phases up to cane maturity in individual shoots for the four data sets employed. In theory, the point of maximum rate of node production is equivalent to floral initiation, the release of correlative inhibition, and hence lateral formation. The rate of change of node production first reaches a maximum after E and the first cohort of shoots is established. Shoot population reaches a maximum prior to the maximum rate of node production, and then decreases until the second maximum rate of change of node production at TF. The second cohort of shoots then establishes after TF, as the first cohort canes fruit and senesce. Berry ripening occurs some time after TF and is best predicted from 500 - 700 day°C after TF.

The implications of the model in elucidating plant development in cv. "Autumn Bliss" are:

i) The logistic relationship between node number and day degree accumulation provides a model for individual shoot development.

ii) The development of first cohort shoots influences the timing of new shoot production and growth.

This gives it a distinct advantage over the alternative Threshold model alone, where temperature-sums are used empirically. The model encompasses the absolute sum **h** required for a given shoot to proceed in predefined developmental stages towards maturity. Further to this, and arguably more importantly, the model pinpoints key physiological events in terms of *changes in rate* of node production in thermal time.

The reasons for these relationships are concerned primarily with apical dominance, which occurs within the root system as well as the shoot system (Robinson, 1975). Experiments on detached roots of apple (Robinson and Schwabe, 1977a, 1977b) showed that preferential bud initiation occurred at the proximal end of vertically planted cuttings, due to depletion of IAA via rapid, acropetal movement. Takeda (1990) demonstrated basal bud suppression using NAA. This polarity was exhibited to a lesser extent in raspberry root cuttings when planted horizontally (Hudson, 1954). Hudson also found that half of the cuttings produced only one

shoot and proportionately fewer produced 2 - 6 shoots. Wareing (1982) hypothesised that loss of apical dominance, releasing upper buds in horizontally trained branches of fruit trees, was due to differential movement of auxin. He suggested the involvement of cytokinins.

In *Rubus*, stem base shoots are inhibited by upper buds from the vertical axis of the developing first cohort cane. As successive axillary buds are released to form laterals, inhibition is lost in these subterranean buds. Williams (1959a) showed that no new suckers were produced during the period of maximum elongation of existing shoots. Vasilakakis and Dana (1978) found that inflorescence removal from existing shoots resulted in the production of a number of suckers compared with a single sucker produced from intact plants. This adequately explains the timing of development of second cohort shoots.

However, 4 - 5 shoots were able to establish from one year old stools in the data modelled. This implies that these buds were not subordinate to the first basal bud. Possibly a critical distance exists between successive subterranean buds which enforces correlative inhibition to a reduced extent compared with upper buds. Alternatively, expansion of buds from laterally orientated roots explains this phenomenon.

The apical meristem of the first shoot to emerge therefore exerts some dominance over the development of the whole plant. Buds are thought to be inhibited as a result of hormone directed metabolite transport (Zraly, 1978; Waister and Barritt, 1980). This theory is backed up by the following:

i) Auxin synthesis or release occurs at active meristems or related tissues,

ii) Nutrients and growth factors accumulate in these areas,

iii) Auxin induces long distance metabolite transport.

(Hillman, 1984).

In a model of *Chrysanthemum* floral development cited by Lyndon (1990), floret primordia and bracts are assumed to compete with the apical dome for assimilates, whereas leaf primordia do not. Thus, the apical meristem is inactivated and is no longer dominant.

The deviance of the "10°C" cabinet data from the model implies that shoots

of these plants developed at a faster rate per day degree accumulated. Possibly the temperature range experienced by plants in this cabinet had a facultative vernalizing effect. Root buds responded facultatively to chilling at 5°C (for up to 35 days)(Chapter 3). Further to this, there is evidence (Williams, 1960) that as node number increases, receptivity to cold temperature inductive treatment increases in obligate cultivars such as "Malling Promise".

By increasing the accuracy of temperature recording, it would be possible to achieve some improvement on the estimates for base temperature. Although the base temperature for node production obtained from field data was in approximate agreement with that obtained from cabinet data.

In conclusion, the model catalogues the timing of developmental events in the first shoot to emerge per plant and it indicates the mechanisms which are involved in whole plant development. Ideally, the ultimate aim in crop modelling is to produce a model, which can be applied to the field situation under a range of environmental conditions. More research is required in this crop, areas of which are discussed in Chapter 7. Most importantly this model gives a clearer understanding of the mechanisms involved.

CHAPTER 7
GENERAL DISCUSSION

Jackson (1989) summarised areas of research for manipulating commercial crops to improve yield into: i) modification of the cropping season, ii) manipulation of the balance between fruiting and vegetative growth, iii) modification of the perennial habit and iv) increase in fruit set. The above experiments on the effect of temperature on the rate of shoot development in cv. "Autumn Bliss" highlight areas for the manipulation of plant growth in two of these aspects.

Firstly, cropping season was contracted when plants were cultivated in glasshouse and polytunnel environments. This was due to higher rates of shoot development compared with outdoor-grown plants. However, plants from polytunnel and outside plots produced similar yields. This pattern was also shown for plants treated at 10°C and 25°C in temperature control cabinets. Yield was expected to decrease linearly with temperature or to form a curve with a maximum at approximately 25°C. The inverse relationship expected depends on the duration of photosynthesis. Rapidly developing shoots have a reduced period in which to produce photosynthates for growth and storage. More rapidly developing shoots have an increased demand for assimilates, forming strong sinks (Farrar, 1988). In cereals, this period is limited to the time from shoot emergence to ear emergence (Kirby, 1985). In raspberry, lateral (secondary) leaf development supports fruit development during cropping. Assessing the timing of lateral expansion as a result of terminal floral primordia appearance is therefore important in: i) The formation of the lateral meristems as sinks, as opposed to the developing terminal meristem alone, and ii) The amount of assimilate available to the developing fruit. High yields in plants treated at 25°C were probably achieved as a result of increased sink activity, where assimilate utilisation would be expected to exceed fixation leading to mobilisation and depletion of storage carbohydrates from the stool and roots. However, plants were removed from temperature treatments prior to lateral expansion and no differences were seen in total plant dry weight to account for this depletion. Although, it is

important to bear in mind that plant dry weight was assessed only after cropping had been completed. Root and stool dry weights were not accounted for, but stem dry weights were reduced. This indicated that early temperature treatment had a lasting effect on subsequent fruiting cane productivity, causing assimilate depletion, despite lateral canopy photosynthesis. This was indicated by low shoot number in the second cohort.

High temperatures throughout the growing season (in the range of 20°C) in the commercial cultivation of cv. "Autumn Bliss" would result in depletion of storage carbohydrate in the roots and stool, reducing the growth and yield in the proceeding year. Therefore, continuous protected cultivation under plastic may lead to a decline in yield in successive years. The slower rate of shoot development for plants treated at "10°C" accounted partly for the high yields in these plants.

Although the model estimated rates of development, these were expressed in day°C, making the assumption that plants accumulated the same total temperature for flower initiation over differing periods of time. Therefore the temperature-sum obtained gave no information on the duration from emergence to flower initiation and no indication of differences in yield. The model did show that plants treated at "10°C" (taking longer to develop in time) accumulated lower temperature-sums, in terms of day°C developing at a higher rate than plants treated at "25°C". This indicates that the actual temperatures experienced by these plants were responsible for low temperature promotion of shoot development. Evidence that this cultivar is sensitive to low temperature promotion of development was supplied by a positive linear trend in emergence and ripening rates with chilling time at 5°C. Yield and above ground dry matter content also increased with chilling time.

Minimum temperatures experienced by plants treated at "10°C" and in the outside plot (7 and -4°C respectively) suggest that low temperatures in the range of 1 - 7°C promote shoot development and increased yield.

Accumulation of Fructan, an important storage carbohydrate (next to starch and sucrose) in higher plants (Kühbauch and Schnyder, 1989) arises when carbon fixation exceeds utilisation in cold temperatures (2 - 10°C) in monocotyledonous crops (Pontis, 1989; Chatterton *et al.*, 1989). Fructans accumulate in wheat (*T. aestivum*

L.) up to and after anthesis. Degradation occurs when current photosynthate production is insufficient to support the developing grain (Kühbauch and Thome, 1989). Similar processes occurring in this plant species explain the differences observed.

Secondly, it is difficult to assess quantitatively the interaction between individual shoots, in terms of their physiological dominance over each other. Generally, there is good evidence that apical dominance exists between individual shoots so shoots were studied in terms of their age. The number of shoots in the initial population depended on the fresh weight of the mother plant (stem base and stool). Field-grown and potted plants from one year old stools produced 3 - 5 shoots in comparison to chilled plants (35 days chilling) which produced a maximum of 15 in the first cohort. Evidence from research on over-wintering canes indicates that dormancy of the apical meristem, as well as physical injury (field data, 1990), releases inhibition of basal buds (Champagnat, 1978; Jennings, 1988). Temperatures below the base temperature for node production of 5.84°C in this cultivar may bring about this release.

The first cohort appeared to prevent further shoot development in all experiments and, importantly, served as the fruiting cane population for the current year's crop. Subsequent shoot production after terminal flower bud appearance in this cohort served as competition (although possibly providing a late season crop) for assimilates and light (Wright and Waister, 1984). This competition is a considerable problem in commercial cultivation. The paradox that the size of a shoot population is a major yield component and yet can reduce yield in individual canes needs careful consideration and further research to find the equilibrium between population and yield.

The model highlights the important stages of shoot development at:

i) the cellular level - changes in the rate of node production point to important ontogenetic changes at the apex, which are indicative of changes at

ii) the shoot level - the timing of the appearance of the terminal floral primordia complex relates to the release of lateral buds and basal buds from apical dominance.

iii) the plant level - terminal flower appearance marks the timing of the production of the second cohort of shoots.

Figure 7.1 summarises the model and its implications in elucidating the developmental processes in plants of cv. "Autumn Bliss".

Further research on chilling plants at different developmental stages over a range of temperatures would provide a chilling index for incorporation into the model. Plants are assumed to be day-neutral; however, rosetting was shown in plants held at lower temperatures and is indicative of day length sensitivity (Wareing and Phillips, 1981).

Work on the effect of day length at low temperatures and low light intensities may provide a further index for the model. The model could then be tested in field conditions.

More precise measurement of dry matter accumulation, incorporating the roots and stem base is essential to a fuller understanding of the effect of temperature on partitioning. A means of overcoming the problems of the measurement of root dry weight would be to cultivate plants in Nutrient Film.

Plant development and resource allocation rests on the manipulation of ontogenesis (Waister and Wright, 1989) of the first shoots to emerge. The effect of removal of the apex at different stages of shoot development may provide useful information on the relationship between allocation of assimilates to plant growth and fruit yield.

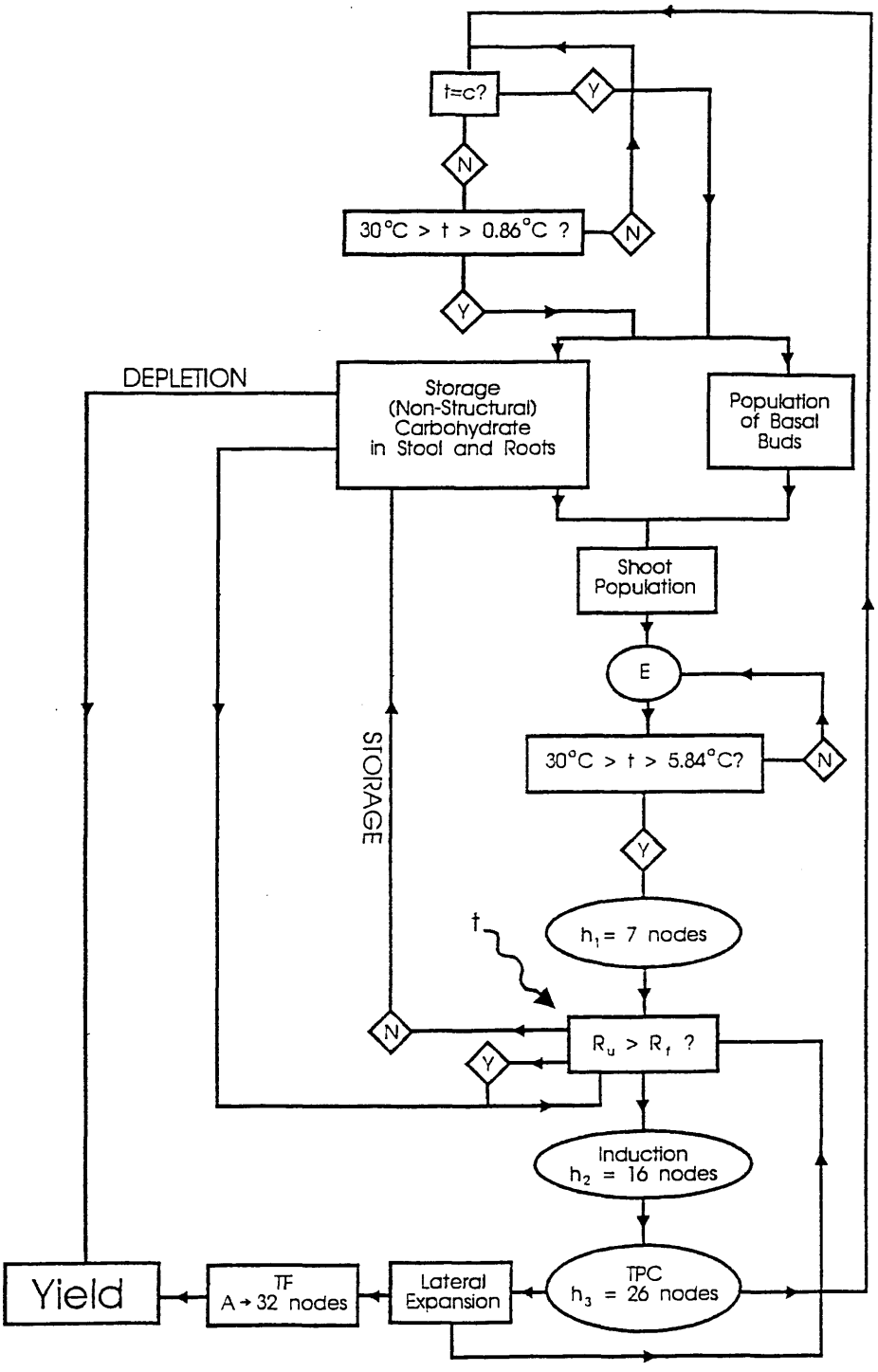


Figure 7.1 Flow diagram to show the effect of temperature on shoot development and plant growth of cv. "Autumn Bliss", as determined by base and upper threshold temperatures for emergence, node production and chilling temperature (where: 7°C>C>0.86°C = probable range).

LEGEND: t - air temperature, C - chilling temperature, E,TPC,TF - stages of shoot development, R_u - rate of assimilate utilisation and R_f - rate of carbon fixation. Model derivatives: h_1 - h_3 modelled stages of shoot development, A absolute node number.

REFERENCES

Anderson, H.M., Guttridge, C.G. (1982). Strawberry truss morphology and the fate of high-order flower buds. *Crop Res. (Hort. Res.)*, **22**, 105-122.

Anon. (1988). Sunfleck Ceptometer User's Manual, Decagon Devices Inc., Delta-T Devices Ltd., 128, Low Road, Burwell, Cambridge, CB5 OEJ, 27p.

Arnold, C.Y. (1959). The determination and significance of the base temperature in a linear heat unit system. *Proc. Amer. Soc. Hort. Sci.*, **74**, 430-445.

Ayala, F.J., Kiger, J.A., Jr. (1980). Modern Genetics, The Benjamin/Cummings Publishing Company, Inc., California, 844p.

Baker, C.K., Gallagher, J.N. (1983). The development of winter wheat in the field 2. The control of primordium initiation rate by temperature and photoperiod. *J. Agric. Sci., Camb.*, **101**, 337-344.

Baskerville, G.L., Emin, P. (1969). Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology*, **50**, 514-517.

Ben-Tal, Y. (1986). Flowering: Its control by vegetative growth inhibition. *Acta Hortic.*, **179**, 329-335.

Bradshaw, A.D. (1965). Evolutionary significance of phenotypic plasticity. *Adv. in Genetics*, **13**, 115-155.

Braun, J.W., Garth, J.K.L. (1984a). Growth and fruiting of "Heritage" primocane fruiting red raspberry in response to Daminozide and Ethepon. *J. Amer. Soc. Hort. Sci.*, **109**(2), 207-209.

Braun, J.W., Garth, J.K.L. (1984b). Intracane yield compensation in the red raspberry. *J. Amer. Soc. Hort. Sci.*, **109**(4), 526-530.

Braun, J.W., Garth, J.K.L. (1986). Growth and fruiting of "Heritage" primocane fruiting red raspberry in response to Paclobutrazol. *HortSci.*, **21**(3), 437-439.

Braun, J.W., Garth, J.K.L., Brun, C.A. (1989). Distribution of foliage and fruit in association with light microclimate in the red raspberry canopy. *J. Hort. Sci.*, **64**(5), 565-572.

Brierley, W.G. (1931). Effects of height of pruning on size of berries and yield in the Latham raspberry.

Minn. Agric. Expt. Sta. Bull., **281**, 20.

Burgess, C.M. (1986). Personal communication.

Buszard, D.J.I. (1986). The effect of management system on winter survival and yield of raspberries in Quebec. *Acta Hort.*, **183**, 175-181.

Causton, D.R., Elias, C.O., Hadley, P. (1978). Biometrical studies of plant growth. *Plant, Cell and Enviro.*, **1**, 163-184.

Champagnat, P. (1978). Formation of the trunk in woody plants, pp401-422. In: Tomlinson, P.B., Zimmermann, M.H. (eds), Tropical Trees as Living Systems, Proc. 4th Cabot Symposium, Cambridge University Press, London, 675p.

Chatterton, N.J., Harrison, P.A., Bennett, J.H., Asay, K.H. (1989). Carbohydrate partitioning in 185 accessions of *Graminae* grown under warm and cool temperatures. *J. Plant Physiol.*, **134**(2), 169-179.

Clapham, A.R., Tutin, T.G., Warburg, E.F. (1968) (2nd ed). Excursion Flora of the British Isles, Cambridge University Press, Cambridge, 586p.

Cline, R.A. (1964). Factors affecting leaf-nutrient content of raspberry. *Rep. Ont. Hort. Expt. Sta. Prod. Lab.*, 49-54.

Collins, W.J., Wilson, J.H. (1974). Node of flowering as an index of plant development. *Ann. Bot.*, **38**, 175-180.

Cormack, M.R., Lawson, H.M., Waister, P.D. (1976). Comparisons of four methods of establishing raspberry plantations from spawn canes. *Hort. Res.*, **16**, 1-17.

Crandall, P.C., Chamberlain, J.D. (1972). Effects of water stress, cane size and growth regulators on floral primordia development in red raspberries. *J. Amer. Soc. Hort. Sci.*, **97**(3), 418-419.

Crandall, P.C., Allmendinger, D.F., Chamberlain, J.D., Biderbost, K.A. (1974). Influence of cane diameter, irrigation and carbohydrate reserves on the fruit number of red raspberries. *J. Amer. Sci. Hort. Sci.*, **99**(6), 524-526.

Crandall, P.C., Chamberlain, J.D., Biderbost, K.A. (1974). Cane characteristics associated with berry number of red raspberry. *J. Amer. Soc. Hort. Sci.*, **99**(4), 370-372.

Crandall, P.C., Chamberlain, J.D., Garth, J.K.L. (1980). The effects of chemical primocane suppression on growth, yield and chemical composition of red raspberries. *J. Amer. Soc. Hort. Sci.*, **105**(2), 194-196.

Crandall, P.C., Garth, J.K.L. (1981). Yield and growth response of "Heritage" raspberry to Daminozide and Ethephon. *HortSci.*, **16**(5), 654-655.

Cross, H.Z., Zuber, M.S. (1972). Prediction of flowering dates in maize based on different methods of estimating thermal units. *Agron. J.*, **64** (May-June), 351-355.

Dale, A. (1979). Varietal differences in the relationships between some characteristics of red raspberry fruiting laterals and their position on the cane. *J. Hort. Sci.*, **54**(4), 257-265.

Dale, A. (1986). Some effects of the environment on red raspberry cultivars. *Acta Hort.*, **183**, 155-161.

Dale, A. (1988). Relationships between some yield components of the red raspberry (*Rubus idaeus L.*) and the fruiting season: a multivariate approach. *Crop Res.*, **28**, 123-135.

Dale, A. (1989). Productivity in red raspberries. *Hort. Rev.*, **11**, 185-228.

Dale, A., Daubeny, H.A. (1985). Genotype-environment interactions involving British and Pacific Northwest red raspberry cultivars. *HortSci.*, **20**(1), 68-69.

Dale, A., Daubeny, H.A. (1987). Notes and comments. Flower bud initiation in red raspberry (*Rubus idaeus L.*) in two environments. *Crop Res. (Hort. Res.)*, **27**, 61-66.

Dale, A., Jarvis, B.C. (1983). Studies on germination in raspberry (*Rubus idaeus* L.). *Crop Res. (Hort. Res.)*, **23**, 73-81.

Dale, A., Topham, P.B. (1980). Fruiting structure of the red raspberry: multivariate analysis of lateral characteristics. *J. Hort. Sci.*, **55**(4), 397-408.

Dalman, P. (1989). Within-plant competition and carbohydrate economy in the red raspberry. *Acta Hort.*, **262**, 269-276.

Dana, M.N. (1983). New system for fall raspberries. *Fruit Grower*, June, 30&32.

Darrow, G.M., Waldo, G.F. (1933). Raspberry and blackberry cane measurements. *Proc. Amer. Soc. Hort. Sci.*, **30**, 269-274.

Dawkins, H.C. (1981). The misuse of t-tests, LSD and multiple-range tests. *British Ecol. Soc. Bull.*, November, 112-115.

Dijkstra, J., Van Oosten, A.A. (1984). Culture experiments with raspberries and currants. *Rep. Wilhelminadorp Res. Sta. for Fruit Growing*, 43-49.

Doughty, C.C., Crandall, P.C., Shanks, C.H., Jr. (1972). Cold injury to red raspberries and the effect of premature defoliation and mite damage. *J. Amer. Soc. Hort. Sci.*, **97**(5), 670-673.

Durner, E.F., Poling, E.B. (1985). Comparison of three methods for determining the floral or vegetative status of strawberry plants. *J. Amer. Soc. Hort. Sci.*, **110**(6), 808-811.

Erasmus, D.J., Staden, J. Van (1983). Seasonal translocation of assimilates in the weed, *Rubus cuneifolius*. *S. African J. of Botany*, **2**(3), 187-190.

Farrar, J.F. (1988). Temperature and the partitioning and translocation of carbon, p203-235. In: Long, S.P., Woodward, F.I. (eds), Plants and Temperature, Symposia of the Society for Experimental Biology, Number XXXXII, The Company of Biologists Limited, Cambridge, 415p.

Fejer, S.O. (1977). Inheritance of yield, yield components and fall-fruiting habit in red raspberry diallel crosses. *Can. J. Genet. Cytol.*, **19**, 1-13.

Fejer, S.O., Spangelo, L.P.S. (1974). Three generations of inbreeding and s_2 factorial test crosses in red raspberry cultivars. *Can. J. Genet. Cytol.*, **16**, 419-432.

Ford, E.B. (1975). Ecological Genetics, Chapman and Hall, London, 422p.

France J., Thornley, J.H.M. (1984). Mathematical Models in Agriculture: a quantitative approach to problems in agriculture and related sciences, Butterworths, London, 335p.

Freeman, J.A., Eaton, G.W., Baumann, T.E., Daubeny, H.A., Dale, A. (1989). Primocane removal enhances yield components of raspberries. *J. Amer. Soc. Hort. Sci.*, **114**(1), 6-9.

Geense, C. (1983). Visit of commission for cane (woody) soft fruit to Belgium. *De Fruitteelt*, no. 39, 1034-1036.

Gibson, J. (1987). A blissful autumn crop. *The Fruit Grower*, 3 December, 38-39.

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

Goulart B.L. (1989a). Growth and flowering of greenhouse-grown red raspberry treated with plant growth regulators. *HortSci.*, **24**(2), 296-298.

Goulart, B.L. (1989b). Influence of three soil water levels on micropropagated greenhouse grown red raspberry. *Acta Hort.*, **262**, 277-283.

Grace, J. (1988). Temperature as a determinant of plant productivity, pp91-107. In: Long, S.P., Woodward, F.I. (eds), Plants and Temperature, Symposia of the Society for Experimental Biology, Number XXXXII, The Company of Biologists Limited, Cambridge, 415p.

Grant, R.F. (1989). Simulation of maize phenology. *Agron. J.*, **81**, 451-457.

Hackett, W.P. (1980). Control of phase change in woody plants, pp257-272. In: Control of Shoot Growth in Trees, Proceedings of the Joint Workshop of IUFRO Working Parties on Xylem and Shoot Growth Physiology, Fredericton, New Brunswick, 357p.

Hackett, W.P. (1985). Juvenility, maturation and rejuvenation in woody plants. *Hort. Rev.*, **7**, 109-155.

Haltvick, E.T., Struckmeyer, B.E. (1965). Blossom bud differentiation in red raspberry. *Proc. Amer. Soc. Hort. Sci.*, **87**, 234-237.

Harper, J.L. (1977). Population Biology of Plants, Academic Press, London, 892p.

Hillman, J.R. (1984). Apical dominance, pp127-146. In: Wilkins, M.B. (ed.), Advanced Plant Physiology, Pitman, London, 514p.

Hoover, E., Luby, J., Bedford, D. (1986). Yield components of primocane-fruiting red raspberries. *Acta Hort.*, **183**, 163-166.

Hoover, E., Luby, J., Bedford, D. (1988). Vegetative and reproductive yield components of primocane-fruiting red raspberries. *J. Amer. Soc. Hort. Sci.*, **113**(6), 824-826.

Hoover, E., Luby, J., Bedford, D., Pritts, M., Hanson,E., Dale, A., Daubeny, H. (1989). Temperature influence on harvest date and cane development of primocane-fruiting red raspberries. *Acta Hort.*, **262**, 297-303.

Hudson, J.P. (1954). Propagation of plants by root cuttings, I. Regeneration of raspberry root cuttings. *J. Hort. Sci.*, **29**, 27-43.

Hudson, J.P. (1956). The regeneration of plants from roots. *Rep. XIVth Inter. Hort. Congr.*, 1165-1172.

Hudson, J.P. (1959). Effects of environment on *Rubus idaeus L.*, I. Morphology and development of the raspberry plant. *J. Hort. Sci.*, **34**, 163-169.

Hudson, J.P., Williams, I.H. (1961). Effects of environment and age on flowering in raspberries. *Proc. Linn. Soc. Lond.*, **172**, 101-108.

Jackson, J.E. (1989). The manipulation of fruiting, pp3-10. In: Wright, C.J. (ed), Manipulation of Fruiting, Butterworths, London, 414p.

Jahn, O.L., Dana, M.N. (1970). Crown and inflorescence development in the strawberry, *Fragaria ananassa. Am. J. Bot.*, **57**(6), 605-612.

Jefferies, R.L. (1984). The Phenotype: its development, physiological constraints and environmental signals, pp347-358. In: Dirzo, R., Sarukhán, J., (eds), Perspectives on Plant Population Ecology, Sinauer Associates Inc., Sunderland, Massachusetts, 478p.

Jennings, D.L. (1964a). Some evidence of population differentiation in *Rubus idaeus L.*. *New Phytol.*, **63**, 153-157.

Jennings, D.L. (1964b). Two further experiments on flower-bud initiation and cane dormancy in the red raspberry (cv. "Malling Jewel"). *Hort. Res.*, **4**, 14-21.

Jennings, D.L., (1966). The manifold effects of genes affecting fruit size and vegetative growth in the raspberry I. Gene L_1. *New Phytol.*, **65**, 176-187.

Jennings, D.L. (1979a). Genotype-environment relationships for ripening time in blackberries and prospects for breeding an early ripening cultivar in Scotland. *Euphytica*, **28**, 747-750.

Jennings, D. L. (1979b). The occurrence of multiple fruiting laterals at single nodes of raspberry canes. *New Phytol.*, **82**, 365-374.

Jennings, D.L. (1987). Some effects of correlative inhibition on the development of lateral buds of raspberry canes (*Rubus idaeus* L.). *Crop Res. (Hort. Res.)*, **27**, 119-129.

Jennings, D.L. (1988). Raspberries and Blackberries; Their Breeding, Diseases and Growth, Academic Press, London, 230p.

Jennings, D.L., Dale, A. (1982). Variation in the growth habit of red raspberries with particular reference to cane height and node production. *J. Hort. Sci.*, **57**(2), 197-204.

Jennings, D.L., McGregor, G.R., Wong, J.A., Young, C.E. (1986). Bud suppression ("blind bud") in raspberries. *Acta Hort.*, **183**, 285-290.

Jennings, D.L., McGregor, G.R. (1989). Some genetic factors which control number and size of raspberry fruits produced on a raspberry cane, pp315-327. In: Wright, C.J., (ed.), Manipulation of Fruiting, Butterworths, London, 414p.

Johnson, I.R., Thornley, J.H.M. (1985). Temperature dependence of plant and crop processes. *Ann. Bot.*, **55**, 1-24.

Keep, E. (1961). Autumn-fruiting in raspberries. *J. Hort. Sci.*, **36**, 174-185.

Keep, E. (1988). Primocane (autumn)-fruiting raspberries: a review with particular reference to progress in breeding. *J. Hort. Sci.*, **63**(1), 1-18.

Keep, E., Parker, J.H., Knight, V.H., (1984). Autumn-fruiting or primocane selections. *Rep. E. Malling Res. Stn. for 1983(1984)*, 165 & 237.

Khanmai, M.A., Brown, W.S. (1940). Correlations between leaf area and leaf weight and between leaf weight and fruit production of red raspberries. *Proc. Amer. Soc. Hort. Sci.*, **7**, 589-592.

Kirby, E. J. M. (1985). Significant stages of ear development in Winter Wheat, pp7-24. In: Day W.,

Atkin, R. K. (eds), Wheat Growth and Modelling, NATO ASI Series, Plenum Press, London, 407p.

Knight, V.H. (1986). Recent progress in raspberry breeding at East Malling. *Acta Hort.*, **183**, 67-75.

Knight, V.H., Jennings, D.L., M^{c}Nicol, R.J. (1989). Progress in the UK raspberry breeding programme. *Acta Hort.*, **262**, 93-103.

Kühbauch, W., Schnyder, H. (1989). Preface. In: Kühbauch, W., Schnyder, H. (eds), Fructan (special issue). *J. Plant Physiol.*, **134**(2), 123-124.

Kühbauch, W., Thome, U. (1989). Nonstructural carbohydrates of wheat stems as influenced by sink-source manipulations. *J. Plant Physiol.*, **134**(2), 243-250.

Landsberg, J.J. (1974). Apple fruit bud development and growth; analysis and an empirical model. *Ann. Bot.*, **38**, 1013-1023.

Lawrence, F.J. (1981). Another look at "day-neutral" strawberries and "primocane-fruiting" raspberries. *Ann. Rep. Oregon Hort. Soc.*, **72**, 108-112.

Lawson, H.M., Waister, P.D. (1972). The response to nitrogen of a raspberry plantation under contrasting systems of management of weed and sucker control. *Hort. Res.*, **12**, 43-55.

Ljones, B., Sakshaug, K. (1967). Nitrogen effects on composition and yield components of raspberry cultivars. *Meld. Norges Landbr. Høgskole*, **46**(12), 1-19.

Lockshin, L.S., Elfving, D.C. (1981). Flowering response of "Heritage" red raspberry to temperature and nitrogen. *HortSci.*, **16**(4), 527-528.

Lovelidge, B. (1988). Blissful raspberries. *The Fruit Grower*, October 20th, 29 & 31 & 33.

Lyndon, R.F. (1990). Meristem functioning: formation of branches, leaves and floral organs, pp39-57. In: Lyndon, R.F., Plant Development: The Cellular Basis. Topics in Plant Physiology: 3. Unwin Hyman, London, 320p.

MacArthur, R.H., Connell, J.H., (1966). Biology of Populations. John Wiley and Sons Inc., London, 200p.

MacDaniels, L. H. (1922). Fruit bud formation in *Rubus* and *Ribes*. *Proc. Amer. Soc. Hort. Sci.*, **19**, 194-200.

MacKerron, D.K.L. (1978). Spawn cane production in raspberry: The response to shelter from wind and the consequences of grading. *Hort. Res.*, **18**, 93-100.

MacKerron, D.K.L. (1982). Growth and water use in the red raspberry (*Rubus idaeus* L.), I. Growth and yield under different levels of soil moisture stress. *J. Hort. Sci.*, **57**(3), 295-306.

Mason, D.T., Topham, P.B. (1981). Measurements and evaluation of the crop components of a raspberry harvest model. *Hort. Res.*, **21**, 19-28.

Mathers, B.A. (1952). A study of fruit-bud development in *Rubus idaeus* L.. *J. Hort. Sci.*, **27**, 266-272.

Monteith, J.L. (1965). Light distribution and photosynthesis in field crops. *Ann. Bot.*, **29**(113), 17-37.

Nehrbas, S.R., Pritts, M.P. (1988). Effect of pruning system on yield components of two summer-bearing raspberry cultivars. *J. Amer. Soc. Hort. Sci.*, **113**(3), 314-321.

Newby, J.C. (1980). Mathematics for the Biological Sciences, Clarendon Press, Oxford, 319p.

Nonnecke, G.R., Taber, H.G. (1989). Effects of row cover on vegetative and reproductive growth of "Heritage" red raspberry. *Acta Hort.*, **262**, 391-394.

Ong, C.K., Baker, C.K. (1985). Temperature and leaf growth, pp175-200, In: Baker, N.R., Davis, W.J., Ong, C.K. (eds) Control of Leaf Growth, Cambridge University Press, Cambridge, 350p.

Orkney, G.D., Martin, L.W. (1980). Fruiting potential and flower truss characteristics of select "Willamette" red raspberry canes. *Acta Hort.*, **112**, 195-203.

Ourecky, D.K. (1975). Brambles, pp98-129, In: Janick, J., Moore, J.N. (eds), Advances in Fruit Breeding, Purdue University Press, W. Lafayette, Indiana, 623p.

Ourecky, D.K. (1976). Fall-bearing red raspberries, their future and potential. *Acta Hort.*, **60**, 135-144.

Oydvin, J. (1969). Repeatabilities for measures of cane production and scores of yield characters in the raspberry (*Rubus idaeus L.*). *Hort. Res.*, **9**, 103-111.

Palmer, J.W., Jackson, J.E., Ferree, D.C. (1987). Light interception and distribution in horizontal and vertical canopies of red raspberries. *J. Hort. Sci.*, **62**(4), 493-499.

Partis, J. (1987). Personal communication.

Payne, R.W. (Chairman), Lane, P.W. (Secretary), Ainsley, A.E., Bicknell, K.E., Digby, P.G.N., Harding, S.A., Leech, P.K., Simpson, H.R., Todd, A.D., Verner, P.J., White, R.P., Gower, J.C., Tunnicliffe Wilson, G., Paterson, L.J. (Technical writer) (1988). Genstat 5 Reference Manual, Oxford Science Publications, Clarendon Press, Oxford, 740p.

Phillips, I.D.J. (1975). Apical dominance. *Ann. Rev. Plant Physiol.*, **26**, 341-367.

Pontis, H.G. (1989). Fructans and cold stress. *J. Plant Physiol.*, **134**(2), 148-150.

Porter, J.R., Delecolle, R. (1988). Interaction of temperature with other environmental factors in controlling the development of plants, pp133-157, In: Long, S.P., Woodward, F.I., Plants and Temperature, Symposia of the Society for Experimental Biology, Number XXXXII, The Company of Biologists Limited, Cambridge, 415p.

Ratkowsky, D.A. (1983). Non-linear Regression Modelling: A unified approach, Marcel Dekker, Inc., New York, 276p.

Redalen, G. (1980). Effect of Ethephon on cane development, flowering and fruiting of the fall-bearing red raspberry cultivar "Heritage". *Acta Hort.*, **112**, 211-216.

Redalen, G. (1986). Winter survival, variation in bud burst and fruit ripening, and some yield components in raspberry cultivars and selections. *Acta Hort.*, **183**, 199-206.

Rice, R.P., Duna, N., (1986). The effect of initial plant size on yield components of winter-planted strawberries in coastal Lebanon. *J. Hort. Sci.*, **61**(2), 210-203.

Roberts, E.H., Summerfield, R.J. (1987). Measurement and prediction of flowering in annual crops, pp17-50, In: Atherton, J.G. (ed), Manipulation of Flowering, Butterworths, London, 438p.

Robertson, M. (1957). Further investigations of flower-bud development in the genus *Rubus*. *J. Hort. Sci.*, **32**, 265-273.

Robinson, J.C. (1975). The regeneration of plants from root cuttings with special reference to the apple. *Hort. Abs.*, **45**(6), 305-315.

Robinson, J.C., Schwabe, W.W. (1977a). Studies on the regeneration of apple cultivars from root cuttings, I. Propagation aspects. *J. Hort. Sci.*, **52**, 205-220.

Robinson, J.C., Schwabe, W.W. (1977b). Studies on the regeneration of apple cultivars from root cuttings, II. Carbohydrate and auxin relations. *J. Hort. Sci.*, **52**, 221-233.

Roy, S.K., Gallagher, J.N. (1985). Production and survival of wheat tillers in relation to plant growth and development, pp59-67, In: Day, W., Atkin, R.K. (eds), Wheat Growth and Modelling, NATO ASI Series, Plenum Press, London, 407p.

Russell, W.K., Stuber, C.W. (1984). Prediction of tassel initiation in Corn. *Crop Sci.*, **27**, May-June, 507-510.

Ruxton, J.P., Modlibowska, I. (1954). Preliminary studies on the resistance of raspberry varieties to spring frosts. *Rep. E. Malling Res. Stn. for 1953(1954)*, 111-117.

Snir, I. (1986). Growing raspberries under subtropical conditions. *Acta Hort.*, **183**, 183-190.

Snyder, J.C. (1936). Flower bud formation in the Latham raspberry. *Proc. Amer. Soc. Hort. Sci.*, **33**, 417-429.

Steel, R.G.D., Torrie, J.H. (1980) (2nd Ed.) Principles and Procedures of Statistics with Special Reference to the Biological Sciences, M^{c}Graw-Hill, New York, 633p.

Sullivan, J.A., Dale, A. (1989). Intensive management of red raspberry in Eastern Canada. *Acta Hort.*, **262**, 405-410.

Takeda, F. (1990). Growth control in Eastern Thornless blackberry with NAA. *HortSci.*, **26**(1), 37-38.

Thomas, B., Vince-Prue, D. (1984). Juvenility, photoperiodism and vernalization, pp408-436, In: Wilkins, M.B. (ed.). Advanced Plant Physiology, Pitman, London, 514p.

Thornley, J.H.M. (1987). Modelling flower initiation, pp67-79, In: Atherton, J.G. (ed), Manipulation of Flowering, Butterworths, London, 438p.

Thornley, J.H.M., Johnson, I.R. (1990). Plant and Crop Modelling: A mathematical approach to plant and crop physiology, Clarendon Press, Oxford, 669p.

Tollenaar, M., Daynard, T.B., Hunter, R.B. (1979). Effect of temperature on rate of leaf appearance and flowering date in maize. *Crop Sci.*, **19**, May-June, 363-366.

Tomlinson, P.B. (1978). Branching and axis differentiation in tropical trees, pp187-207, In: Tomlinson, P.B., Zimmermann, M.H. (eds). Tropical Trees as Living Systems, Proc. 4th Cabot Symposium, Cambridge University Press, London, 675p.

Vasilakakis, M.D., Dana, M.N. (1978). Influence of primocane inflorescence removal on number of inflorescences and suckers in "Heritage" red raspberry. *HortSci.*, **13**(6), 700-701.

Vasilakakis, M.D., M^{c}Cown, B.H., Dana, M.N. (1979). Hormonal changes associated with growth and development of red raspberries. *Physiol. Plant*, **45**, 17-22.

Vasilakakis, M.D., McCown, B.H., Dana, M.N. (1980). Low temperature and flowering of primocane-fruiting red raspberries. *HortSci.*, **15**(6), 750-751.

Vasilakakis, M.D., Struckmeyer, B.E., Dana, M.D. (1979). Temperature and development of red raspberry flower buds. *J. Amer. Soc. Hort. Sci.*, **104**(1), 61-62.

Verwijs, D.L. (1983). Advancing the date of harvesting small fruit (raspberries and redcurrants) in a plastic greenhouse. *De Fruitteelt*, no. 9, 222-223.

Waister, P.D. (1970). Effects of shelter from wind on the growth and yield of raspberries. *J. Hort. Sci.*, **45**, 435-445.

Waister, P.D., Barritt, B.H. (1980). Compensation in truss numbers following loss of lateral buds in the red raspberry. *Hort. Res.*, **20**, 25-31.

Waister, P.D., Cormack, M.R., Sheets, W.A. (1977). Competition between fruiting and vegetative phases in the red raspberry. *J. Hort. Sci.*, **52**, 75-85.

Waister, P.D., Gill, P.A. (1979). Plant hardiness, and its significance for the raspberry crop in Scotland. *Sci. Horticult.*, **30**, 59-68.

Waister, P.D., Wright, C.J. (1989). Dry matter partitioning in cane fruits, pp51-61, In: Wright, C.J. (ed), Manipulation of Fruiting, Butterworths, London, 414p.

Waldo, G.F. (1934). Fruit bud formation in brambles. *Proc. Amer. Soc. Hort. Sci.*, **30**, 263-267.

Wareing, P.F. (1982). A plant physiological odyssey. *Ann. Rev. Plant Physiol.*, **33**, 1-26.

Wareing, P.F., Phillips, I.D.J. (1981)(3rd Ed.). Growth and Differentiation in Plants, Pergamon Press, Oxford, 343p.

Warrington, I.J., Kanemasu, E.T. (1983a). Corn growth response to temperature and photoperiod. I Seedling emergence, tassel initiation and anthesis. *Agron. J.*, **75**, Sept-Oct, 749-754.

Warrington, I.J., Kanemasu, E.T. (1983b). Corn growth response to temperature and photoperiod II. Leaf initiation and leaf appearance rates. *Agron. J.*, **75**, Sept-Oct, 755-761.

White, J. (1979). The plant as a metapopulation. *Ann. Rev. Ecol. Syst.*, **10**, 109-145.

White, J. (1984). Plant metamerism, pp15-47, In: Dirzo, R., Sarukhán, J. (eds), Perspectives on Plant Population Ecology, Sinauer Associates Inc., Sunderland, Massachusetts, 478p.

Whitney, G.G. (1982). The productivity and carbohydrate economy of a developing stand of *Rubus idaeus*. *Can. J. Bot.*, **60**(12), 2697-2703.

Williams, I.H., Hudson, J.P. (1956). Effect of environment upon the growth and development of raspberry canes. *Nature*, **177**, 798-799.

Williams, I.H. (1959a). Effects of environment on *Rubus idaeus* L., II. Field observations on the variety "Malling Promise". *J. Hort. Sci.*, **34**, 170-175.

Williams, I.H. (1959b). Effects of environment on *Rubus idaeus* L., III. Growth and dormancy of young shoots. *J. Hort. Sci.*, **34**, 210-218.

Williams, I.H. (1959c). Effects of environment on *Rubus idaeus* L., IV. Flower initiation and development of the inflorescence. *J. Hort. Sci.*, **34**, 219-228.

Williams, I.H. (1960). Effects of environment on *Rubus idaeus* L., V. Dormancy and flowering of the

mature shoot. *J. Hort. Sci.*, **345**, 214-220.

Wood, C.A., Anderson, M.M., Freeman, G.H. (1961). Studies on the cultivation of raspberries I. Effects of planting distances and of the winter tipping of canes. *Hort. Res.*, **1**, 3-24.

Wood, C.A., Robertson, M. (1957). Observations on the fruiting habit of the red raspberry (*Rubus idaeus* L.) and on the occurrence of cane "die-back" in Scotland. *J. Hort. Sci.*, **32**, 172-183.

Wright, C.J., Waister, P.D. (1982a). Within-plant competition in the red raspberry, I. Primocane growth. *J. Hort. Sci.*, **57**(4), 437-442.

Wright, C.J., Waister, P.D. (1982b). Within-plant competition in the red raspberry, II. Fruiting cane growth. *J. Hort. Sci.*, **57**(4), 443-448.

Wright, C.J., Waister, P.D. (1984). Light interception and fruiting cane architecture in the red raspberry grown under annual and biennial management systems. *J. Hort. Sci.*, **59**(3), 395-402.

Wright, C.J., Waister, P.D. (1986). Canopy structure and light interception in the red raspberry. *Acta Hort.*, **183**, 273-283.

Zraly, B. (1978). Effect of apical dominance on outgrowth of flower buds on raspberry canes; attempt to release apical dominance by treatment with Benzyladenine and Gibberellic acid. *Fruit Sci. Rpt.*, **5**(4), 15-22.

APPENDIX 4.1

Table 4.1.1 Mean rates of terminal berry ripening (TB, days^{-1}) for the first shoot to emerge per plant, to show the interaction between environment and grading treatments.

environment treatment	mean ripening rate (days^{-1} to TB) per plant for each grading treatment			
	A	B	C	D
glasshouse	0.0080	0.0094	0.0096	0.0092
polytunnel	0.0075	0.0073	0.0078	0.0077
outside	0.0064	0.0074	0.0057	0.0064

Note: sed = 0.0004, se = 0.0005, cv% = 6.8, P = 0.005, $LSD_{0.05}$ = 0.00073.

Table 4.1.2 Mean total shoot height per plant for each environmental treatment

days from planting	mean total shoot height (cm) per plant for each environmental treatment			P	sed
	glasshouse	polytunnel	outside		
0	0	0	0	-	-
8	3.33	3.40	3.85	ns	1.97
15	7.00	5.65	4.20	ns	2.05
32	25.80	14.70	6.20	<0.001	3.07
51	60.40	43.40	20.60	<0.001	6.06
79	195.10	158.40	61.50	<0.001	17.70
100	191.60	214.60	125.90	<0.001	18.80
112	200.60	247.10	157.80	<0.001	21.27
129	215.40	252.60	216.40	ns[17]	24.48
146	-	270.00	283.00	ns	29.70
161	-	290.00	313.00	ns	33.40
181	-	316.00	363.00	ns	39.60

[17]no significant difference between treatments.

Table 4.1.3 Mean total shoot height (cm) for each grading treatment

days from planting	grading treatment means (cm)				P	sed
	A	B	C	D		
0	0	0	0	0	-	-
8	0.13	3.40	5.07	5.50	ns	2.28
15	1.50	4.53	8.20	8.23	0.017	2.37
32	8.3	11.6	16.0	26.3	<0.001	3.55
51	25.5	34.7	46.1	59.6	<0.001	6.99
79	105.3	141.3	137.2	169.6	0.028	20.44
100	144.5	170.9	189.9	204.1	0.049	21.71
112	162.3	187.3	215.0	242.7	0.013	24.56
129	175.1	217.5	243.3	276.7	0.007	28.27
146[18]	192.0	286.0	300.0	326.0	0.018	42.0
161	216.0	306.0	310.0	373.0	0.022	47.3
181	251.0	343.0	337.0	428.0	0.032	55.9

Table 4.1.4 Mean rate of shoot elongation (centimetres of total shoot height per plant per day) for each environmental treatment.

days from planting	mean rate of shoot elongation (cm day^{-1}) for each environmental treatment			P	sed
	glasshouse	polytunnel	outside		
0	0	0	0	-	-
8	0.42	0.42	0.48	ns	0.25
15	0.53	0.32	0.05	0.002	0.12
32	1.11	0.53	0.10	<0.001	0.11
51	1.82	1.52	0.71	<0.001	0.200
79	4.81	4.11	1.35	<0.001	0.55
100	-0.71	2.68	2.90	<0.001	0.85
112	0.75	2.71	2.43	0.027	0.76
129	0.87	0.32	3.28	<0.001	0.78

[18]only for comparison of polytunnel and outside-plot plants at 146, 161 and 181 days from planting.

Table 4.1.5 Mean rate of shoot elongation (centimetres of total shoot height per day) for each grading treatment

days from planting	grading treatment means (cm day^{-1})				P	sed
	A	B	C	D		
0	0	0	0	0	-	-
8	0.02	0.43	0.63	0.69	ns	0.29
15	0.20	0.16	0.45	0.39	0.15 (ExG, 0.03)	0.14
32	0.40	0.41	0.44	1.06	<0.001	0.13
51	0.91	1.22	1.51	1.75	0.005	0.23
79	2.85	3.81	3.10	3.93	ns	0.64
100	1.87	1.41	2.28	1.64	ns	0.98
112	1.48	1.37	1.79	3.22	ns	0.88
129	0.76	1.77	1.44	2.00	ns	0.90

Note: Where ExG - significant interaction between grading and environmental treatments.

Table 4.1.6 Mean shoot height per plant (cm) for each environmental treatment

days from planting	mean shoot height (cm) per plant for each environmental treatment			P	sed
	glasshouse	polytunnel	outside		
0	0	0	0	-	-
8	2.21	1.90	2.56	ns	1.05
15	3.93	3.15	2.96	ns	1.04
32	12.49	6.90	2.62	<0.001	1.50
51	32.70	21.40	7.10	<0.001	2.70
79	80.60	65.80	22.00	<0.001	5.67
100	98.30	100.40	43.40	<0.001	6.92
112	100.40	102.20	54.30	<0.001	6.72
129	96.20	110.90	64.80	<0.001	8.42

Table 4.1.7 Mean shoot height per plant (cm) for each grading treatment

days from planting	grading treatment means (cm)				P	sed
	A	B	C	D		
0	0	0	0	0	-	-
8	0.13	3.17	2.48	3.11	ns	1.22
15	0.99	3.85	4.28	4.26	0.023	1.20
32	5.04	7.56	6.91	9.82	ns	1.73
51	15.4	21.0	21.9	23.2	ns	3.12
79	57.7	62.2	56.0	48.7	ns	6.55
100	89.4	84.8	79.0	69.7	ns	7.99
112	95.0	91.7	82.4	73.3	0.033	7.76
129	95.9	97.1	90.2	79.3	ns	9.72

Table 4.1.8 Mean shoot number per plant for each environmental treatment

days from planting	mean shoot number per plant for each environmental treatment			P	sed
	glasshouse	polytunnel	outside		
0	0	0	0	-	-
8	0.40	0.60	0.75	ns	0.28
15	1.55	1.25	0.85	ns	0.29
32	2.25	2.40	1.59	ns	0.36
51	1.90	2.25	2.68	ns	0.35
79	2.60	2.60	2.91	ns	0.37
100	2.15	2.40	3.11	ns	0.40
112	2.20	2.70	3.06	ns	0.40
129	2.60	2.55	3.86	0.024	0.52
146[19]	-	2.95	5.12	0.003	0.68
161	-	3.20	5.56	0.004	0.75
181	-	3.60	6.80	0.006	1.08

[19]for comparison of polytunnel and outside-plot data only.

Table 4.1.9 Mean shoot number per plant for each grading treatment

days from planting	mean shoot number per plant for each grading treatment				P	sed
	A	B	C	D		
0	0	0	0	0	-	-
8	0.07	0.53	0.87	0.87	ns	0.32
15	0.73	1.13	1.60	1.40	ns	0.34
32	1.47	1.67	2.18	3.00	0.003	0.42
51	1.60	2.07	2.50	2.93	0.011	0.40
79	1.73	2.53	2.88	3.67	<0.001	0.43
100	1.67	2.40	2.82	3.33	0.006	0.46
112	1.73	2.33	2.95	3.60	0.002	0.47
129	2.33	2.60	3.02	4.07	0.032	0.60

Table 4.1.10 Mean leaf number per plant for each environmental treatment

days from planting	mean leaf number for each environmental treatment			P	sed
	glasshouse	polytunnel	outside		
0	0	0	0	-	-
8	1.30	1.30	0.30	ns	0.73
15	3.35	1.85	0.40	0.001	0.76
32	13.60	8.65	2.20	<0.001	1.15
51	17.70	14.65	10.20	<0.001	1.59
79	34.05	27.20	21.56	<0.001	2.29
100	71.60	42.90	30.50	<0.001	4.84
112	105.60	62.40	37.40	<0.001	5.13
129	39.80	39.70	39.30	ns	4.50

Table 4.1.11 Mean leaf number per plant for each grading treatments

days from planting	grading treatment means				P	sed
	A	B	C	D		
0	0	0	0	0	-	-
8	0.20	0.80	1.40	1.47	ns	0.84
15	1.13	1.40	2.47	2.47	ns	0.87
32	5.60	7.07	8.27	11.67	<0.001	1.33
51	9.73	12.07	15.00	19.93	<0.001	1.84
79	20.20	24.33	30.35	35.53	<0.001	2.65
100	35.8	48.3	53.4	55.6	0.004	0.11
112	57.1	63.3	71.1	82.2	<0.001	5.93
129	29.9	38.0	39.3	51.2	0.002	5.19

Table 4.1.12 Mean rate of shoot production per plant for each environmental treatment

days from planting	mean rate of shoot production (ln (shoot number + 1) day^{-1}) for each environmental treatment			P	sed
	glasshouse	polytunnel	outside		
0	0	0	0	-	-
8	0.033	0.045	0.054	ns	0.018
15	0.087	0.050	0.009	0.001	0.019
32	0.016	0.026	0.015	ns	0.010
51	-0.006	-0.002	0.021	<0.001	0.005
79	0.007	0.004	0.002	ns	0.003
100	-0.007	-0.003	0.003	0.008	0.003
112	0.001	0.007	-0.001	0.042	0.003
129	0.005	-0.003	0.01	ns	0.005

Table 4.1.13 Mean rate of shoot production per plant for each grading treatment

days from planting	grading treatment means ln (shoot no +1) day^{-1}				P	sed
	A	B	C	D		
0	0	0	0	0	-	-
8	0.006	0.050	0.060	0.061	0.036	0.020
15	0.057	0.039	0.058	0.041	ns	0.023
32	0.023	0.011	0.009	0.033	ns	0.011
51	0.005	0.011	0.004	-0.001	ns	0.006
79	0.002	0.006	0.003	0.007	ns	0.003
100	-0.001	-0.003	-0.001	-0.005	ns	0.003
112	0.002	-0.001	0.003	0.005	ns	0.004
129	0.008	0.004	0.001	0.004	ns	0.006

APPENDIX 5.1

ESTIMATION OF ACTUAL LEAF AREA FROM NON-DESTRUCTIVE MEASUREMENTS OF LEAF LAMINA DIMENSIONS

Leaf samples were collected over a year from one-year old spawn cane planted in a field plot at 0.4m spacing. Linear regression was carried out to find a relationship between lamina length x breadth measurements and actual leaf area, in order to estimate actual area from non-destructive measurements of the leaf.

Non-destructive measurements were recorded as:

$$\mathbf{LD = L \times W}$$

Where:

LD = area calculated from lamina dimensions,

L = length of pinnate compound leaf from tip of terminal leaflet to the midrib of the basal leaflets,

D = width of pinnate compound leaf from tip of the left basal leaflet to the tip of the right basal leaflet.

Actual area was measured using a Leaf Area Meter[20]. These figures included the area of the Rhachis (Clapham, Tutin and Warburg, 1968), however as this was green it was assumed to be photosynthetically active.

Leaves were divided into five morphologically distinct groups:

i) SIMPLE LEAVES - (area calculated as the length from tip to base of leaf and width as the widest part of the leaf).

ii) BIFOLIATE LEAVES - leaves composed of 2 leaflets (area calculated as the length from tip of longest leaf and width as the widest point across both leaflets).

iii) TRIFOLIATE LEAVES - leaves composed of 3 leaflets.

iv) FOUR-FOLIATE LEAVES - leaves composed of 4 leaflets.

v) FIVE-FOLIATE LEAVES - leaves composed of 5 leaflets.

[20]Delta - T Devices, 128, Low Road, Burwell, CAMBRIDGE.

Table 5.1.1 Regression coefficients of the linear model for calculating actual leaf area (L_A) from leaf lamina dimensions (LD)

leaf morphology	regression equation	degrees of freedom	R^2 Statistic
general	$L_A = 0.501LD - 0.138$	434	95.3
simple leaf	$L_A = 0.608LD + 0.25$	90	97.1
bifoliate leaf	$L_A = 0.355LD + 4.95$	13	82.5
trifoliate leaf	$L_A = 0.492LD - 1.630$	148	95.2
four-foliate leaf	$L_A = 0.497LD - 1.670$	39	93.4
five-foliate leaf	$L_A = 0.524LD - 2.620$	136	94.3

WHERE: LD - lamina dimensions = length (cm) x breadth (cm), L_A = actual leaf area (cm^2).

APPENDIX 5.2

GENERAL NOTE TO TABLES:

i) where treatment means are followed by figures in brackets, these refer to the weighted number of replicates.

ii) sed*/RSE* is for comparison of treatment means with maximum and minimum numbers of weighted replicates.

iii) Where there is significance for trends in partitioned sum of squares (SS), other than linear then; Q - refers to quadratic SS, N - other.

Table 5.2.1 Mean rates of shoot development for different phenological stages (for the first shoot per plant to reach a given stage)

stage[21]	mean rate of development $(days)^{-1}$ for each temperature treatment				variation		
	10°C	15°C	20°C	25°C	significance of linear sum of squares	sed	%cv
E	0.1280	0.1080	0.1760	0.2500	<0.001	0.0309	32.2
TPC	0.0129	0.0201	0.0152	0.0167	0.025N	0.0021	23.0
TF	0.0105	0.0125	0.0123	0.0132	ns	0.0012	17.8
BR	0.0074	0.0088	0.0088	0.0097	<0.001	0.0005	10.2

[21]Where; E- emergence, TPC - terminal floral primordia complex appearance, TF - "green bud" stage and BR - berry ripening.

Table 5.2.2 Residuals of the time for the first shoot per plant to reach TPC (for replicates within each temperature treatment).

replicate	time to TPC (days) for each temperature treatment				equivalent residual[22]			
	10°C	15°C	20°C	25°C	10°C	15°C	20°C	25°C
1	77	64	59	54	-1.0	8.5	-6.8	-6.7
2	81	79	75	54	3.0	23.5	9.2	-6.7
3	81	38	69	54	3.0	-17.5	3.2	-6.7
4	69	76	64	64	-9.0	20.5	-1.8	3.3
5	69	38	64	69	-9.0	-17.5	-1.8	8.3
6	91	38	64	69	13.0	-17.5	-1.8	8.3

NOTE: High residuals obtained for plants treated at 15°C.

[22]residual standard error = 10.70

Table 5.2.3 Mean node number per shoot (of samples of first cohort shoots per plant)

days from planting	mean node number temperature treatment				significance of linear sum of squares	sed*
	10°C	15°C	20°C	25°C		
18	2.73(15)	3.79(19)	4.94(21)	6.75(19)	0.002	1.19
23	4.61(19)	5.48(23)	7.14(21)	7.77(22)	0.026	1.46
28	5.19(21)	6.71(24)	8.52(21)	8.83(24)	<0.001	0.89
33	7.14(21)	7.83(24)	9.52(21)	10.00(23)	0.001	0.87
38	8.38(21)	9.29(24)	11.45(20)	12.30(20)	0.001	1.14
43	9.57(21)	10.51(22)	12.85(20)	14.00(20)	0.002	1.37
48	11.43(21)	11.92(24)	14.10(21)	15.95(19)	0.002	1.33
53	12.80(21)	13.60(23)	16.00(21)	17.60(19)	0.004	1.64
58	15.00(21)	15.20(23)	17.90(21)	19.3(19)	0.01	1.71
63	16.00(21)	16.60(23)	19.8(21)	21.8(18)	0.003	1.91
68	18.00(21)	18.60(22)	21.5(21)	24.9(17)	0.004	2.26
73	20.6(21)	20.5(22)	23.6(20)	27.8(16)	0.005	2.38
78	22.3(21)	21.9(21)	25.2(20)	28.3(16)	0.009	2.26
84	24.20(21)	23.50(21)	28.30(19)	29.40(16)	0.007	2.14
89	25.8(21)	24.6(21)	29.4(19)	30.10(16)	0.013	2.05
102	29.70(16)	27.4(20)	31.2(18)	31.1(16)	ns	1.86
116	32.40(16)	28.80(19)	31.50(17)	31.60(16)	ns	1.90
163	32.60(20)	30.30(17)	30.2(18)	31.80(16)	ns	2.33
214	19.82(17)	19.68(17)	19.86(19)	19.19(16)	ns	0.99
243	19.04(19)	18.64(18)	16.61(19)	19.47(16)	0.025Q	0.96

Table 5.2.4 Residuals and variation in mean node number per shoot (of samples of first cohort shoots per plant)

days from planting	residual standard error RSE*	max-min weighted treatment means[23]	outlying residuals[24]	
			maximum	minimum
18	1.609 - 3.218	4,1	-	6.75 (23)
23	2.144 - 3.032	4,1	-	7.23 (22), 7.77 (23)
28	1.354 - 1.915	4,1	2.81 (1)	3.83 (23)
33	1.331 - 1.882	4,1	-	4.25 (23)
38	1.715 - 2.425	4,1	-	-
43	2.022 - 2.860	4,1	-	6.00 (19), 5.75 (23)
48	1.983 - 2.804	4,1	-	6.05 (19), 5.95 (23)
53	2.410 - 3.410	4,1	-	8.40 (19)
58	2.520 - 3.560	4,1	-	7.40 (19)
63	2.770 - 3.920	4,1	-	8.50 (19), 8.20 (23)
68	3.200 - 4.52	4,1	-	9.10 (19), 9.90 (23)
73	3.310 - 6.620	4,2	-	-
78	3.110 - 6.230	4,2	-	-
84	2.950 - 5.890	4,2	-	-
89	2.820 - 5.640	4,2	-	-
102	2.530 - 5.050	3,2	-	-
116	2.550 - 5.100	1,2	-	-11.4 (3)
163	3.180 - 6.350	1,3	-9.2 (16)	-
214	1.330 - 2.660	3,4	4.81 (22)	-
243	1.293 - 2.586	4,3	2.89 (17)	-

[23]Where treatments 1-4 refer to temperature treatments 10-25^{0}C respectively.

[24]Outlying residuals: defined as residuals which lie outside range, (2 x RSE).

Table 5.2.5 Mean shoot number per plant

days from planting	mean shoot number per plant for each temperature treatment				significance of the linear sum of squares	sed
	10°C	15°C	20°C	25°C		
8	0.83	0.50	1.83	3.00	0.003	0.74
11	1.33	2.00	4.00	3.17	0.01	0.84
18	3.67	5.50	4.67	4.00	ns	0.95
23	5.17	5.67	5.00	4.17	ns	0.96
28	5.33	6.17	5.00	4.67	ns	1.19
33	5.67	6.33	4.67	4.50	ns	1.12
38	5.50	6.17	4.33	4.33	ns	1.09
43	5.50	6.50	4.33	4.00	ns	1.05
48	5.67	7.00	4.50	3.33	0.016	1.14
53	5.50	6.50	4.50	3.33	0.046	1.26
58	4.83	6.83	4.50	3.33	ns	1.19
63	5.00	6.67	4.17	3.17	0.049	1.20
68	5.17	6.17	4.17	3.00	0.029	1.14
73	5.00	6.00	4.00	2.83	0.019	1.06
78	5.00	5.83	4.00	2.83	0.013	0.96
84	4.67	5.33	3.83	2.83	0.025	0.92
89	4.50	5.00	3.67	2.83	0.020	0.79
102	4.50	5.00	3.50	2.83	0.026	0.86
116	5.83	5.00	3.50	2.83	0.002	0.94
163	5.67	6.67	4.00	3.00	0.005	1.07
214	9.67	7.50	3.67	3.17	<0.001	1.31
243	10.67	8.50	3.67	3.50	<0.001	1.61

Table 5.2.6 Residuals and variation in mean shoot number per plant

days from planting	%cv	stratum standard error (SSE)	residual standard error (RSE)	outlying residuals[25]
8	83.5	1.288	1.176	3.00 (24)
11	55.3	1.452	1.325	3.00 (11)
18	36.9	1.646	1.502	3.33 (1)
23	33.2	1.658	1.514	4.00 (14)
28	39.1	2.068	1.887	5.00 (14)
33	36.7	1.943	1.774	-
38	37.1	1.884	1.720	3.67 (23)
43	35.8	1.821	1.662	-
48	38.6	1.977	1.805	5.00 (10)
53	44.1	2.189	1.998	5.50 (10)
58	42.2	2.055	1.876	6.17 (10)
63	43.9	2.086	1.904	6.33 (10)
68	42.8	1.981	1.809	5.83 (10)
73	41	1.828	1.669	5.00 (10)
78	37.8	1.668	1.523	4.17 (10)
84	38.1	1.586	1.448	3.67 (10)
89	34.3	1.372	1.253	-
102	37.4	1.480	1.351	3.00 (10)
116	38.0	1.630	1.488	3.00 (10)
163	38.3	1.853	1.691	-
214	37.8	2.269	2.072	5.33 (5) 4.50 (10)
243	42.4	2.790	2.547	6.33 (5) 5.50 (10)

[25]Outlying residuals: defined as residuals lying outside range, (2 x RSE). Plant number in brackets as an identifier.

Table 5.2.7 Mean shoot diameter per shoot (of samples of first cohort shoots per plant)

days from planting	mean shoot diameter (cm) for each temperature treatment				significance of the linear sum of squares	sed*
	10°C	15°C	20°C	25°C		
43	0.20(21)	0.25(22)	0.51(20)	0.31(20)	ns	0.16
48	0.32(21)	0.46(24)	0.60(21)	0.33(19)	ns	0.16
53	0.42(21)	0.57(23)	0.54(21)	0.42(19)	ns	0.12
58	0.64(21)	0.61(23)	0.56(21)	0.47(19)	0.017	0.07
63	0.65(21)	0.62(23)	0.56(21)	0.47(18)	0.01	0.07
68	0.66(21)	0.64(22)	0.59(21)	0.49(17)	0.02	0.07
73	0.64(21)	0.59(22)	0.60(20)	0.52(16)	ns	0.06
78	0.67(21)	0.63(21)	0.62(20)	0.53(16)	ns	0.06
84	0.71(21)	0.64(21)	0.63(19)	0.54(16)	ns	0.06
89	0.71(21)	0.65(21)	0.60(19)	0.57(16)	0.032	0.07
102	0.78(16)	0.67(20)	0.65(18)	0.63(16)	0.024	0.06
116	-	-	-	-	-	-
163	0.81(20)	0.73(17)	0.71(18)	0.78(16)	ns	0.05
214	0.84(17)	0.72(17)	0.74(19)	0.79(16)	0.019Q	0.05
243	0.81(19)	0.71(18)	0.73(19)	0.83(16)	0.016Q	0.05

Table 5.2.8 Residuals and variation in mean shoot diameter per shoot (of samples of first cohort shoots per plant)

days from planting	residual standard error RSE*	maximum and minimum weighted treatment means[26]	outlying residuals[27]	
			maximum	minimum
43	0.237-0.335	3,1	0.5(4)	-
48	0.232-0.328	3,1	-	-
53	0.180-0.255	2,4	0.417(24)	-
58	0.098-0.138	1,4	-	-
63	0.096-0.138	1,4	-	-
68	0.102-0.144	1,4	-	-
73	0.080-0.161	1,4	-	-
78	0.086-0.172	1,4	0.182(19)	-
84	0.086-0.172	1,4	-	-
89	0.092-0.184	1,4	-0.185(23)	-
102	0.078-0.155	1,4	-0.156(23)	-
116	-	-	-	-
163	0.074-0.148	1,3	0.196(17)	-
214	0.064-0.128	1,2	-	-
243	0.073-0.146	4,2	-	-

[26]Where treatments 1-4 refer to temperature treatments 1-25^{0}C respectively.

[27]Outlying residuals: defined as residuals which lie outside range, (2 x RSE).

Table 5.2.9 Mean total above ground dry weight (minus fruit weight) and stem dry weight per shoot (of samples of first cohort shoots per plant) and per plant

variable		mean dry weight (g) for each temperature treatment				significance of linear sum of squares	sed*
		10°C	15°C	20°C	25°C		
total above ground dry matter (g)	per plant	81.0	59.1	78.6	75.9	ns	13.07
	per shoot	25.6(19)	20.3(18)	24.8(19)	28.5(16)	ns	6.01
stem dry weight (g)	per plant	50.8	28.9	21.2	16.1	<0.001	6.20
	per shoot	16.1(19)	9.9(18)	6.7(19)	6.0(16)	<0.001	2.02

Table 5.2.10 Mean number of laterals expanded per shoot (of samples of first cohort shoots per plant)

days from planting	mean lateral number for each temperature treatment				significance of linear sum of squares	sed*
	10°C	15°C	20°C	25°C		
63	0.00(21)[28]	2.68(22)	0.33(21)	1.09(17)	-	1.31
68	0.00	1.64	1.14	4.41	-	1.43
73	0.00	2.00	2.90	7.80	-	2.04
78	1.00(21)	3.80(22)	4.70(21)	8.50(17)	0.006	2.38
84	2.50(21)	5.40(22)	7.60(21)	11.80(17)	<0.001	2.16
89	4.00(21)	6.60(22)	8.60(21)	12.10(17)	<0.001	2.01
102	9.80(21)	9.80(22)	10.30(21)	13.10(17)	ns	1.83
116	13.70(21)	9.70(22)	9.20(21)	14.90(17)	<0.001Q	1.75
163	4.07(16)	2.50(16)	6.10(17)	7.41(17)	0.005	1.37
214	1.50(16)	2.96(16)	5.18(17)	3.06(17)	0.002Q	0.71
243	0.63(16)	2.06(16)	5.00(17)	2.65(17)	<0.001	0.65

[28]Value of weighted replicate for analysis of lateral number at 63-116 days respectively.

5.2.11 Mean fruit bud number per shoot (of samples of first cohort shoots per plant)

days from planting	mean fruit bud number for each temperature treatment				significance of linear sum of squares	sed*
	10°C	15°C	20°C	25°C		
63	0.00	1.00	1.10	10.80	-	3.18
68	0.10(21)	3.50(22)	2.80(21)	19.80(17)	0.006	5.63
73	0.40(21)	6.10(22)	7.40(21)	31.50(17)	0.003	8.32
78	1.80(21)	8.90(22)	11.40(21)	38.60(17)	0.002	9.67
84	4.30(21)	14.10(22)	22.20(21)	46.50(17)	<0.001	11.03
89	9.00(21)	25.10(22)	31.10(21)	62.80(17)	<0.001	11.98
102	39.00(21)	45.00(22)	45.00(21)	60.00(17)	ns	15.80
116	71.00(21)	59.00(22)	45.00(21)	65.00(17)	ns	16.00
163	20.30(16)	41.00(16)	44.00(17)	23.30(17)	0.004Q	7.58
214	8.90(16)	18.30(16)	22.00(17)	17.90(17)	ns	7.42
243	5.30(16)	11.40(16)	12.60(17)	7.40(17)	0.039	3.68

Table 5.2.12 Mean percentage of fruiting nodes per shoot (of samples of first cohort shoots per plant)

days from planting	mean percentage of fruiting nodes (transformed[29]) for each temperature treatment				significance of linear sum of squares	sed*
	10°C	15°C	20°C	25°C		
63	0.00	8.30	2.80	12.90	-	5.35
68	0.00	11.50	9.90	17.40	-	5.42
73	0.00	14.10	18.30	25.50	-	6.59
78	9.20(21)	20.60(22)	24.80(21)	29.80(17)	0.007	8.36
84	14.40(21)	27.50(22)	30.70(21)	38.00(17)	<0.001	6.73
89	19.70(21)	30.70(22)	32.60(21)	38.70(17)	0.002	6.48
102	34.90(21)	36.90(22)	35.00(21)	40.00(17)	ns	5.13
116	40.70(21)	35.30(22)	32.40(21)	43.40(17)	<0.001	4.69
163	19.20(16)	16.20(16)	27.20(17)	27.80(17)	0.004	4.44
214	13.80(16)	23.00(16)	30.70(17)	22.60(17)	0.007	3.49
243	6.90(16)	18.90(16)	32.90(17)	20.40(17)	<0.001	3.29

[29]Data transformed using an angular transformation (Payne *et. al.*, 1988).

Table 5.2.13 Summary of yields and length of cropping for plants in each temperature treatment

variable	mean for each temperature treatment				significance of linear sum of squares	cv%	sed
	10°C	15°C	20°C	25°C			
total fruit fresh weight/shoot (g)	183(17)	80(17)	78(16)	113(16)	0.005Q	-	30.9*[30]
total fruit fresh weight/plant (g)	669	364	296	449	<0.001Q	30.3	77.7
total berry number/cane	68.5(17)	39.3(17)	33(16)	69.2(16)	0.003Q	-	13.90*
total berry number/plant	258	177	116	191	0.003	30.5	32.7
berry size/cane (g)	2.76(17)	2.09(17)	2.25(16)	1.92(16)	0.045	-	0.35*
berry size/plant (g)	2.60	2.06	2.65	2.38	ns	21.7	0.304
% fruit set/cane	93(17)	67(17)	69(16)	108(16)	0.032Q	-	19.7*
length of cropping period (days)	98	113.8	129.8	136.2	0.001	15.9	10.95

[30]sed* - for comparison of means with maximum and minimum numbers of replicates.

Table 5.2.14 Fraction of incident radiation (f) [31] absorbed by the crop canopy (means of individual plants) for plants held in temperature control cabinets

days from planting	mean f for each temperature treatment				significance of linear sum of squares	cv%	sed
	10°C	15°C	20°C	25°C			
53	0.9593	0.9810	0.9805	0.8620	0.003	5.0	0.0271
63	0.9760	0.9760	0.9760	0.7140	<0.001	12.0	0.0632
73	0.9750	0.9740	0.9680	0.7830	<0.001	7.1	0.0377
78	0.9848	0.9837	0.9538	0.9192	<0.001	2.5	0.0138
83	0.9780	0.9570	0.8730	0.4660	<0.001	21.0	0.0994
89	0.9660	0.9470	0.8100	0.5690	<0.001	19.2	0.091

Table 5.2.15 Fraction of incident radiation (f) [31] absorbed by the canopy (means of individual plants) after removal to the glasshouse

days from planting	(f) sample means[32]			
	10°C	15°C	20°C	25°C
107	0.878	0.763	0.701	0.679
118	0.913	0.875	0.843	0.913

[31] Where; f=(1-t), t is the fraction of PAR not absorbed by the canopy and is calculated by dividing the amount of PAR at the soil surface (T) by the amount of PAR immediately above the crop canopy (S) (Anon., 1988; after Monteith, 1965).

[32]Means of ten samples (each sample in turn is an average of 80 line sensor readings) taken, averaged and stored by the Sunfleck Ceptometer.

APPENDIX 5.3

Calculus to determine the turning points of the Richards Function

The Richards function can be expressed as:

$$N=\frac{A}{(1\pm e^{b-kt})^{1/n}} \qquad (5.3.1)$$

Substituting with q:

$$N=A[1+q]^{-\frac{1}{n}}$$

$$q=e^{b-kt}$$

$$\frac{dq}{dt}=-kq$$

Therefore:

$$\frac{dN}{dt}=-\frac{1}{n}A[1+q]^{-1/n-1}(-kq)$$

from which is obtained the gradient or rate of node production:

$$=\frac{kAq}{n}[1+q]^{-1/n-1} \qquad (5.3.2)$$

Deriving the function again indicates where the points occur at which the rates of change of gradient (node number) are zero:

$$\frac{d^2N}{dt^2} = \left[\left(\frac{kAq}{n}\right) \left[-\left(\frac{n+1}{n}\right) \right] (1+q)^{-1/n-2} + (1+q)^{-1/n-1} \left(\frac{kA}{n}\right) \right] - kq$$

$$= \frac{k^2Aq}{n} (1+q)^{-1/n-2} \left[\left(\frac{n+1}{n}\right) q - (1+q) \right]$$

$$= \frac{k^2Aq}{n} (1+q)^{-1/n-2} \left(\frac{q}{n} - 1\right)$$

$$= \frac{k^2Aq^2}{n^2} (1+q)^{-1/n-2} - \frac{k^2Aq}{n} (1+q)^{-1/n-2} \qquad (5.3.3)$$

The final third derivative locates the actual turning points themselves, by solving this equation an estimate of the maximum or minimum rate of change of gradient can be made:

$$\frac{d^3N}{dt^3} = \frac{d}{dq} \cdot \left(\frac{d^2N}{dt^2}\right) \cdot \frac{dq}{dt}$$

$$\frac{d}{dq} \cdot \left(\frac{d^2N}{dt^2}\right) = \frac{k^2Aq^2}{n^2} \left(-\frac{1}{n} - 2\right) (1+q)^{-1/n-3} + (1+q)^{-1/n-2} \left(\frac{2qk^2A}{n^2}\right)$$

$$- \frac{k^2Aq}{n} \left(-\frac{1}{n} - 2\right) (1+q)^{-1/n-3} - (1+q)^{-1/n-2} \left[\frac{k^2A}{n}\right]$$

$$= \frac{k^2A}{n} (1+q)^{-1/n-3} \left[\frac{q^2}{n} \left(-\frac{1}{n} - 2\right) + (1+q) \frac{2q}{n} - q\left(-\frac{1}{n} - 2\right) - (1+q) \right]$$

$$\therefore \frac{d^3N}{dt^3} = -\frac{k^2Aq}{n}(1+q)^{-1/n-3} \times \frac{1}{n^2}\left[q^2(-1-2n) + (1+q)2qn - q(-n-2n^2) - (1+q)n^2\right]$$

is =0 if:

$$q^2 - (n^2+3n)q + n^2 = 0 \qquad (5.3.4)$$

When n=1 then:

$$q^2 - 4q + 1 = 0$$

$$\therefore q = \frac{4 \pm \sqrt{16-14}}{2}$$

as q > 0:

$$q = \frac{4 \pm 3.464}{2}$$

q= 0.536, 3.732

$$\therefore e^{b-kt} = 0.536$$

$$\therefore b - kt = \log_e 0.536 = -0.624$$

$$\therefore t_2 = \frac{b+0.624}{k} \qquad (5.3.5)$$

$$e^{b-kt}=3.732$$

$$b-kt=\log_e 3.732=1.317$$

$$\therefore t_1=\frac{b-1.317}{k} \qquad (5.3.6)$$

APPENDIX 5.4

Weighted mean estimates for the Richards function

Initial estimates of **b**, **k** were made with the actual mean value of **A** from the raw data. These were fitted to the Richards function for values of **n** (-1 to -0.5 and 0.5 to 5.0, in 0.25 steps). RSS refers to the residual sum of squares.

1) 10°C

RSS = 5.092 (minimum 17 iterations)

F ratio = 4488.83 ($P<0.001$)

Initial values **A**=32.60, **b**=2.7040, **k**=0.0507, **n**=1.25

Stable estimates **A**=33.4859, **b**=3.9482, **k**=0.0542, **n**=1.4051

(standard error) (0.6258) (0.8186) (0.0069) (0.3508)

2) 15°C

RSS = 1.1935 (minimum 16 iterations)

F ratio = 17834.21 ($P<0.001$)

Initial values **A**=30.30, **b**=2.3779, **k**=0.0487, **n**=1.25

Stable estimates **A**=30.6702, **b**=3.0295, **k**=0.0477, **n**=1.1938

(standard error) (0.3129) (0.4191) (0.0033) (0.1895)

3) 20°C

RSS = 6.3730 (minimum 24 iterations)

F ratio = 4334.71 ($P<0.001$)

Initial values **A**=31.50, **b**=3.2240, **k**=0.0728, **n**=1.50

Stable estimates **A**=31.2540, **b**=8.0925, **k**=0.1027, **n**=3.9490

(standard error) (0.4806) (1.9112) (0.0211) (1.0710)

4) 25°C

RSS = 3.090 (minimum 16 iterations)

F ratio = 10169.88 ($P<0.001$)

Initial values **A**=31.80, **b**=3.3232, **k**=0.0779, **n**=1.75

Stable estimates **A**=31.5226, **b**=8.4820, **k**=0.1163, **n**=4.1713

(standard error) (0.2913) (1.3158) (0.0157) (0.7440)

APPENDIX 6.1

Table 6.1.1 Harvest means from analysis of variance for the rate of node production at different mean ambient air temperatures

Mean air temperature from planting to harvest date (°C)	6.9215	7.0630	7.3100	7.5726	8.1117	8.2727	8.3196
mean rate of node production (nodes per day)	0.1136	0.1058	0.1431	0.1407	0.1630	0.1713	0.1976
95% confidence interval	0.1136± 0.0913	0.1058± 0.0368	0.1430± 0.0358	0.1407± 0.0356	0.1630± 0.0595	0.1713± 0.0701	0.1976± 0.0323

Table 6.1.2 Treatment means from analysis of variance for the rate of the first shoot to emerge at five mean air temperatures (1990 data)

Mean air temperature (°C) from planting to emergence	28.94	26.13	17.17	13.40	13.10
mean rate of emergence (days $^{-1}$)	0.0804	0.0810	0.0665	0.0694	0.0557
95% confidence interval	0.0804± 0.0191	0.0810± 0.0127	0.0665± 0.0145	0.0694± 0.0156	0.0557± 0.0236
Mean air temperature (°C) from emergence to the end of the experiment	28.34	24.83	17.50	13.60	13.56
rate of node production (nodes per day)[33]	0.5029	0.4475	0.2584	0.2132	0.1446
95% confidence interval	0.5029± 0.0625	0.4475± 0.0559	0.2584± 0.0837	0.2132± 0.0542	0.1446± 0.0265

[33]Significant linear sum of squares.

Table 6.1.3 Treatment means from analysis of variance for the rate of the first shoot to emerge per plant, at four mean air temperatures (1989 data)

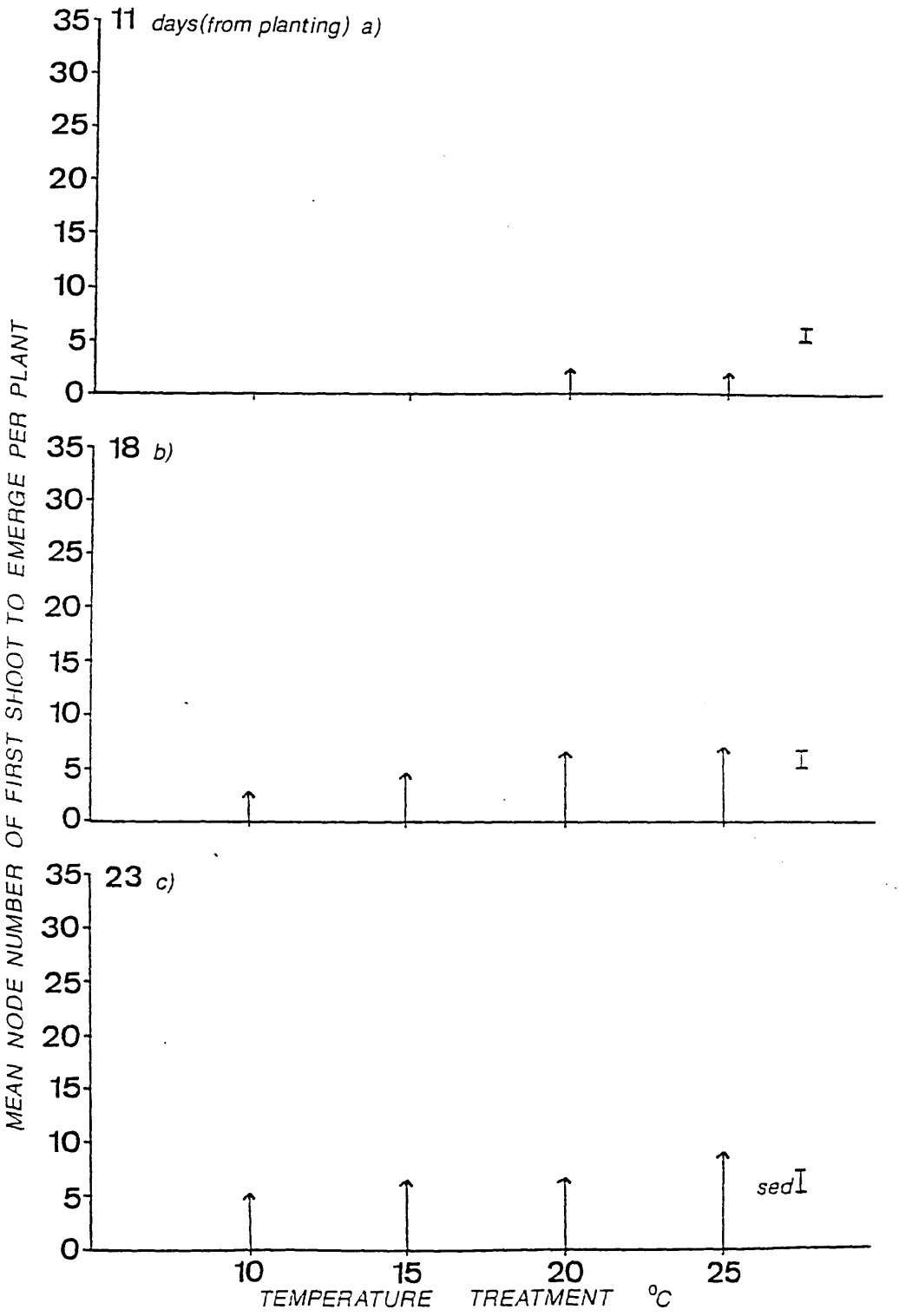
mean air temperature from planting to emergence (°C)	10.91	14.38	19.34	23.85
mean rate of emergence ($days^{-1}$)[34]	0.1280	0.1080	0.1760	0.2500
95% confidence interval for treatment means	0.1280± 0.0688	0.1080± 0.0200	0.1760± 0.0860	0.2500± 0

Table 6.1.4 Comparison of observed (H) and estimated (h) temperature-sums (and the corresponding node number at each stage) for phases of shoot development from planting.

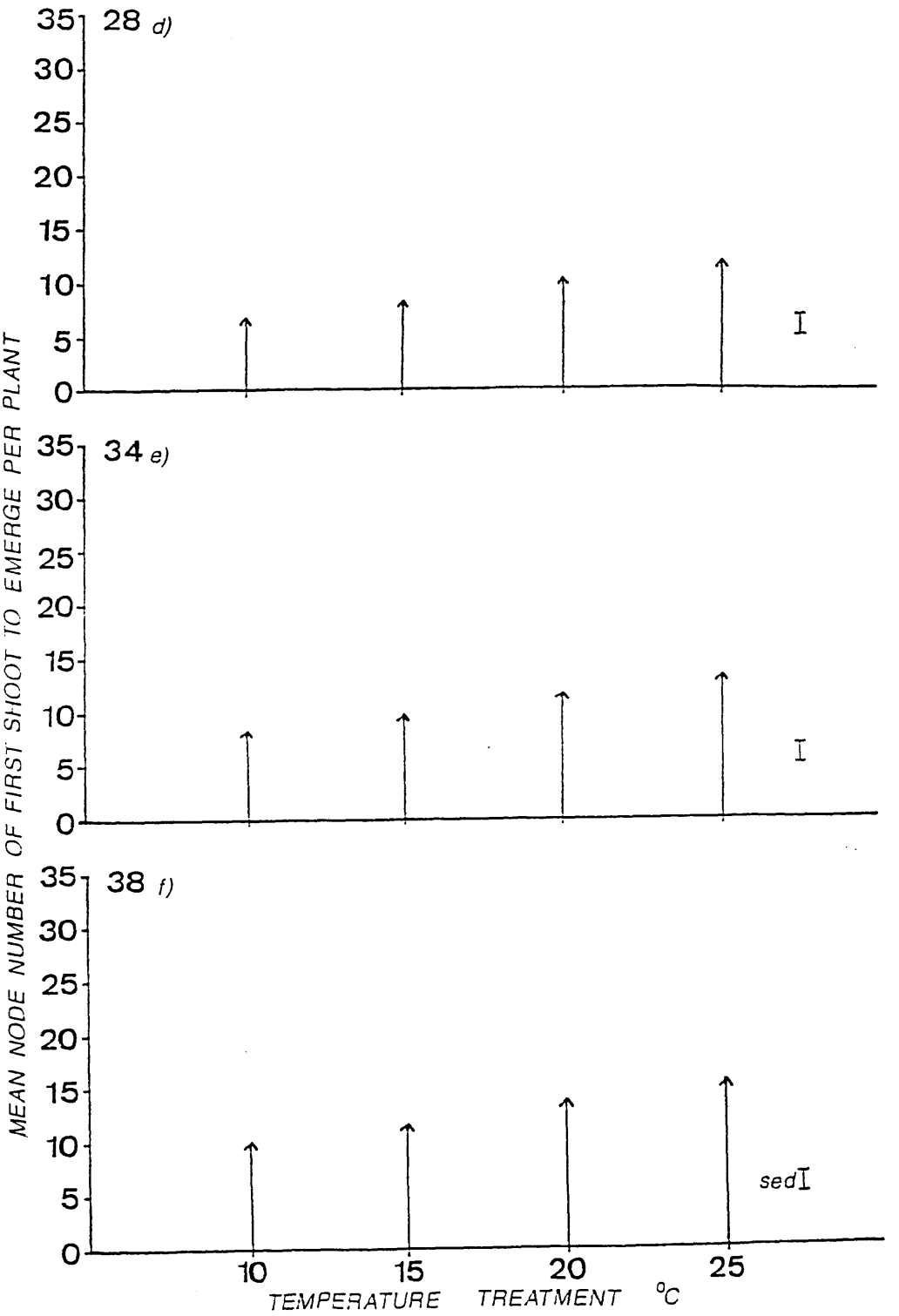
phase	temperature -sum	temperature-sum for each treatment (day°C)				estimated node number[35] for each treatment			
		10°C	15°C	20°C	25°C	10°C	15°C	20°C	25°C
P → E	H_1	104.61	144.31	142.89	109.97	2.69	2.90	2.60	2.77
	h_1	199	309.22	392.75	413.01	6.91	6.66	7.02	6.90
P → TPC	H_2	420.89	585.17	950.33	1152.6	25.45	18.19	25.83	25.51
	h_2	312.53	532.44	679.06	789.29	16.34	15.76	16.62	16.33
P → TF	H_3	502.45	859.17	1126.4	1381.2	29.44	27.52	29.48	29.01
	h_3	426.07	755.66	965.36	1165.6	25.78	24.86	26.22	25.76
P → BR	H_4	1138.8	1289.0	1617.3	1819.4	32.69	31.17	32.81	31.81
	-								

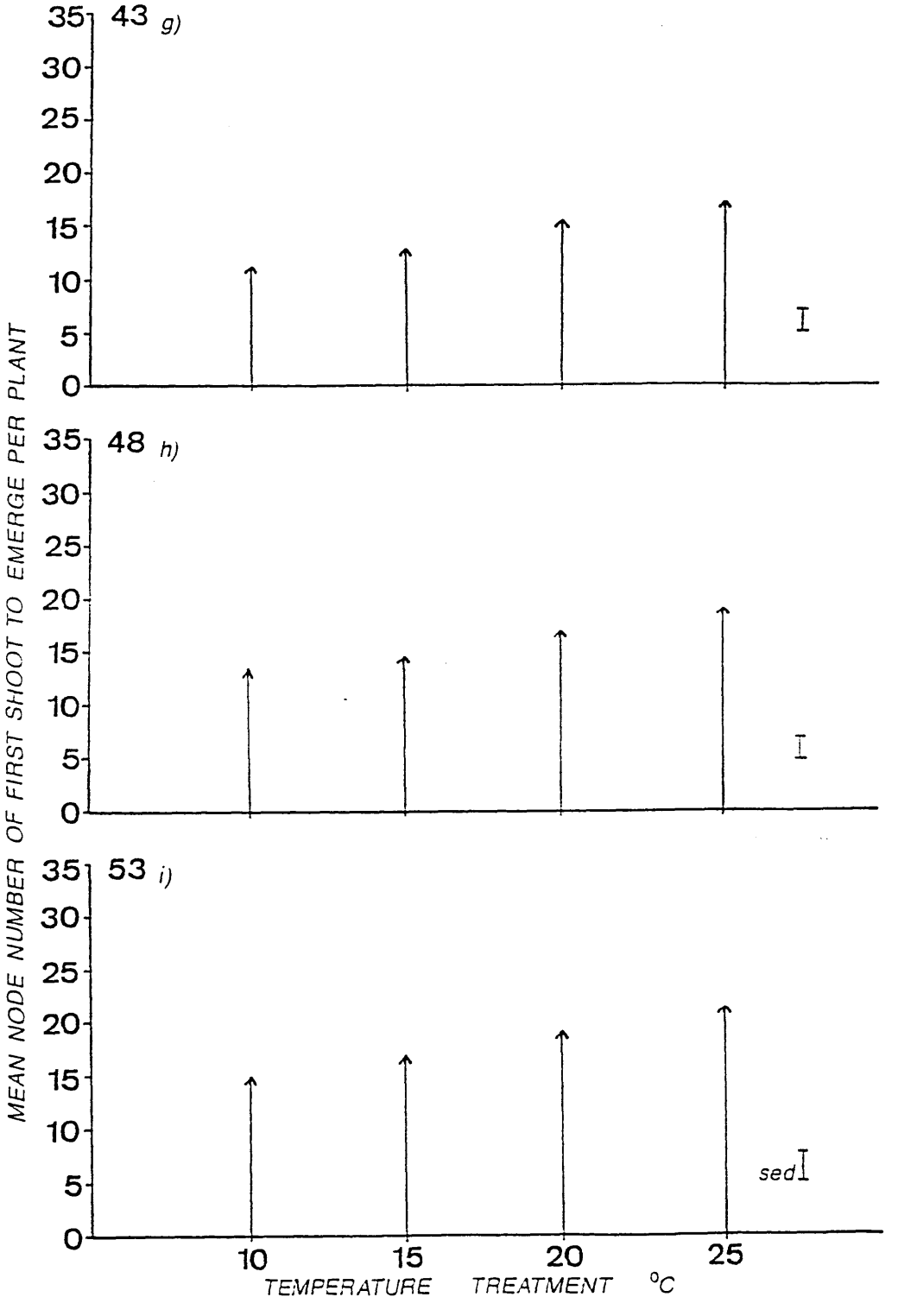
[34]Significant linear sum of squares.

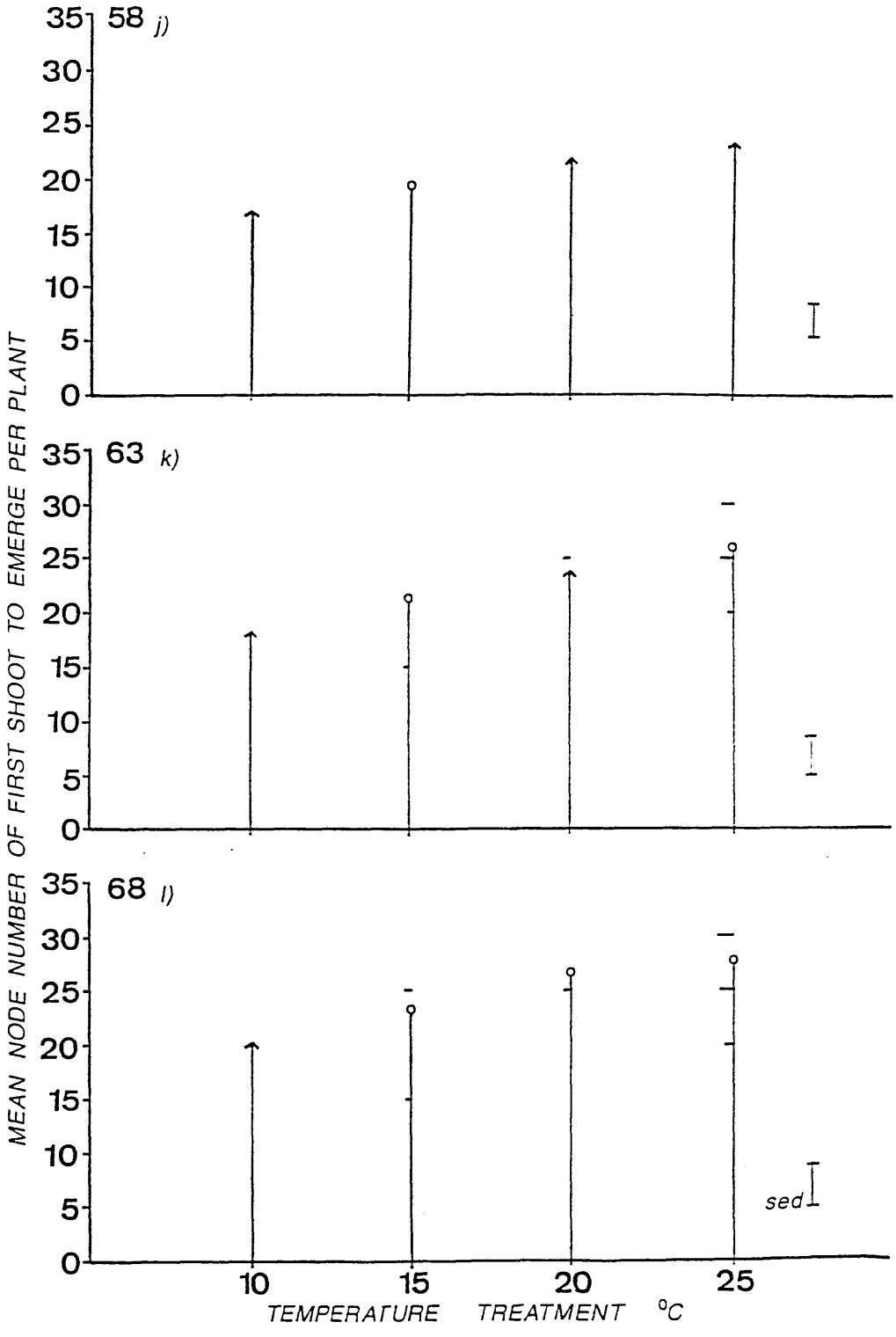
[35]Calculated by substitution into equation 6.4

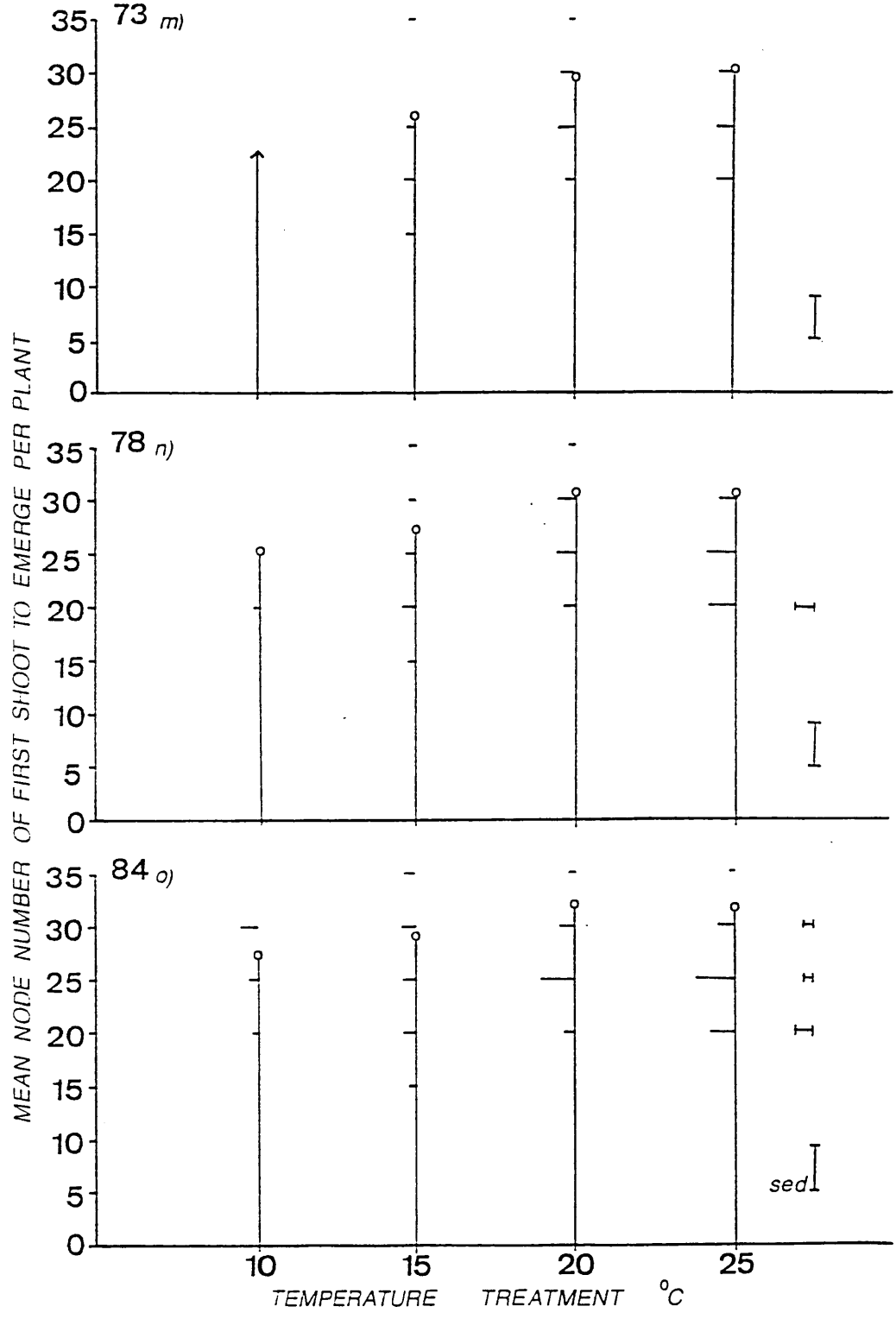


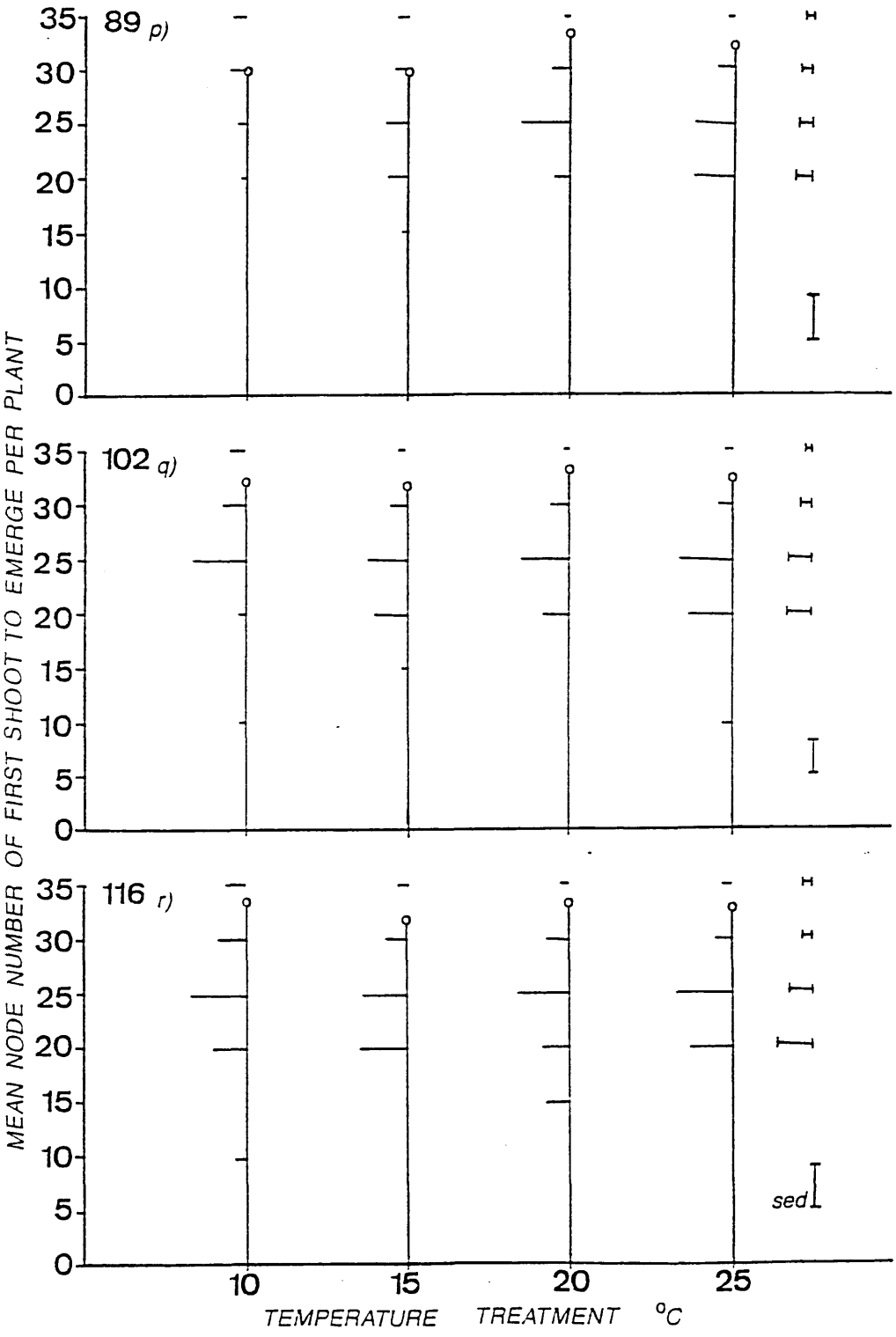
Figures 6.2.1 a - u Development of the first shoot to emerge per plant to show the relationship between node production (and the timing of lateral development) and temperature treatment. Units expressed in mean node number per plant and seds are shown for node number (vertical axis) and lateral node number (horizontal axis).

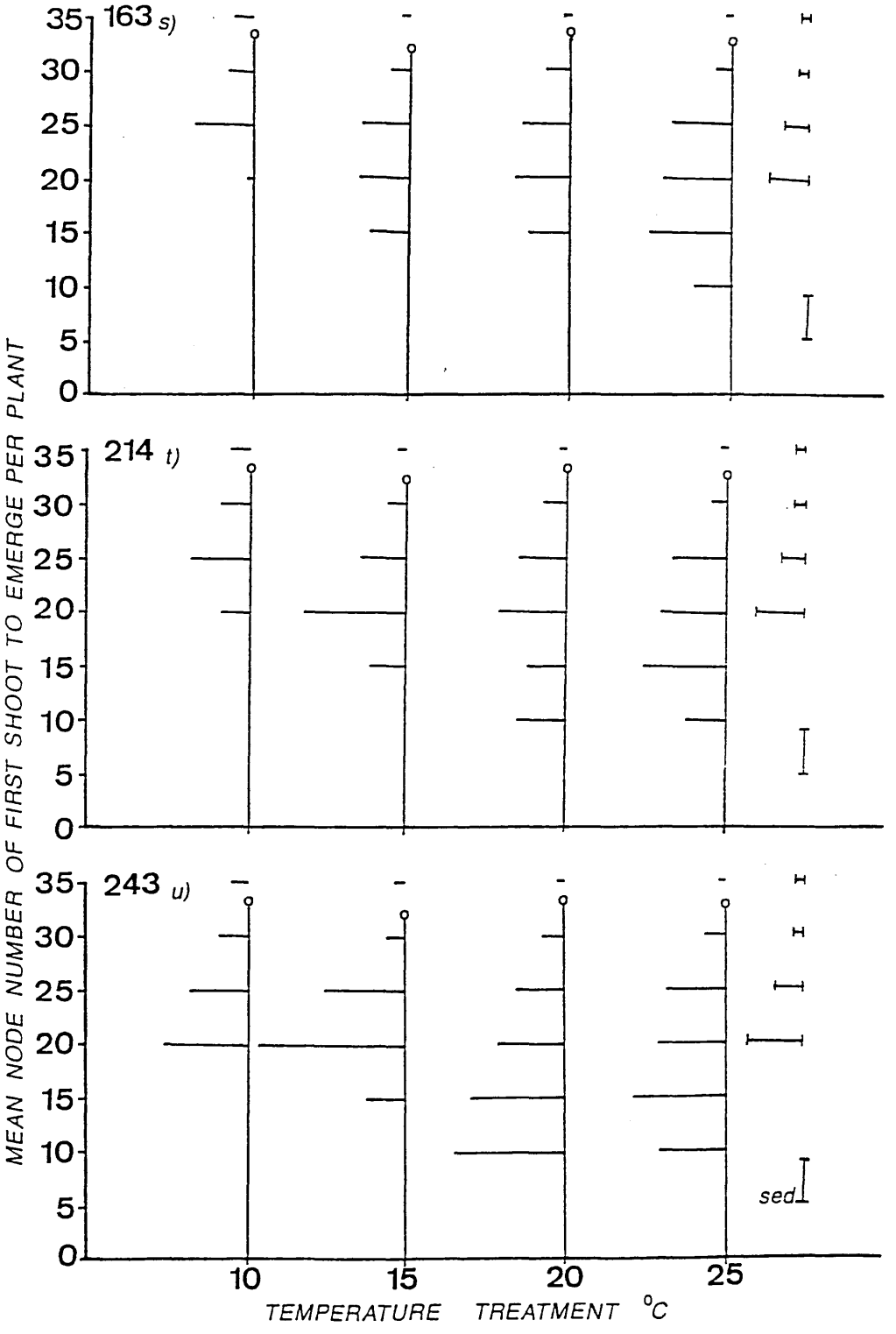

28 d)
34 e)
38 f)
35
30
25
20
15
10
5
0
I
sedI
MEAN NODE NUMBER OF FIRST SHOOT TO EMERGE PER PLANT
10
15
20
25
TEMPERATURE TREATMENT °C


43 g)
48 h)
53 i)
35
30
25
20
15
10
5
0
I
sed I
MEAN NODE NUMBER OF FIRST SHOOT TO EMERGE PER PLANT
10
15
20
25
TEMPERATURE TREATMENT °C


58 j)
63 k)
68 l)
35
30
25
20
15
10
5
0
MEAN NODE NUMBER OF FIRST SHOOT TO EMERGE PER PLANT
sed
10
15
20
25
TEMPERATURE TREATMENT °C


73 m)
78 n)
84 o)
35
30
25
20
15
10
5
0
MEAN NODE NUMBER OF FIRST SHOOT TO EMERGE PER PLANT
sed
10
15
20
25
TEMPERATURE TREATMENT °C


89 p)
102 q)
116 r)
MEAN NODE NUMBER OF FIRST SHOOT TO EMERGE PER PLANT
0
5
10
15
20
25
30
35
sed
10
15
20
25
TEMPERATURE TREATMENT °C


163 s)
214 t)
243 u)
35
30
25
20
15
10
5
0
MEAN NODE NUMBER OF FIRST SHOOT TO EMERGE PER PLANT
sed
10
15
20
25
TEMPERATURE TREATMENT °C

APPENDIX 6.3

Derivation of the model for node production to locate the point of maximum slope and maximum rate of change of slope

For:

$$N=\frac{A}{1+be^{-kh}} \qquad (6.2.1)$$

$$A(1+be^{-kh})^{-1}$$

1) then:

$$\frac{dN}{dh}=A(-1)\ (1+be^{-kh})^{-2}\times(-bke^{-kh})$$

$$=Abke^{-kh}(1+be^{-kh})^{-2}$$

and:

$$\frac{d^2N}{dh^2}=Abk[e^{-kh}(-2)\ (1+be^{-kh})^{-3}(-kb)\ e^{-kh}+(1+be^{-kh})^{-2}(-k)\ e^{-kh}]$$

$$=\frac{Abk^{-2}e^{-kh}}{(1+be^{-kh})^3}[2be^{-kh}-(1+be^{-kh})]$$

therefore:

$$\frac{d^2N}{dh^2}=\frac{Abk^2e^{-kh}}{(1+be^{-kh})^3}[be^{-kh}-1] \qquad (6.2.2)$$

Therefore the rate of change of slope = 0, if

$$be^{-kh}=1$$

$$\therefore e^{-kh}=b^{-1}\therefore -kh=-1\log_e b$$

Thus the value of h when the slope is a maximum is:

$$h=\frac{1}{k}\log_e b$$

2) When h = 0, then:

$$\frac{A}{1+b}$$

3) To find

$$\frac{d^3N}{dh^3}$$

Let

$$q=1+be^{-kh}$$

so

$$be^{-kh}=(q-1)$$

and

$$1-be^{-kh}=2-q$$

and

$$\frac{dq}{dh} = -kbe^{-kh} = -k(q-1)$$

then

$$\frac{d^2N}{dh^2} = \frac{Ak^2}{q^3}(2-q)(1-q)$$

call this V, so

$$\frac{d^3N}{dh^3} = \frac{dV}{dh}$$

$$\frac{dV}{dh} = \frac{dV}{dq}.\frac{dq}{dh}$$

$$= Ak^2\left[q^{-3}(-3+2q) + (2-3q+q^2)(-3)q^{-4}\right](-k)(q-1)$$

as

$$(2-q)(1-q) = 2-3q+q^2$$

as

$$\frac{dV}{dh} = \frac{d^3N}{dh^3}$$

$$\frac{d^3N}{dh^3} = \frac{Ak^3}{q^4}\left[q(-3+2q) - 3(2-3q+q^2)\right](1-q)$$

$$= \frac{Ak^3}{q^4} [6(q-1) - q^2] [1-q]$$

$$= \frac{Ak^3}{(1+be^{-kh})^4} [6be^{-kh} - (1+be^{-kh})^2] (-b) e^{-kh}$$

$$= \frac{-bAk^3 e^{-kh}}{(1+be^{-kh})^4} [4be^{-kh} - 1 - b^2 e^{-2kh}] \qquad (6.2.3)$$

= 0, if

$$b^2x^2 - 4bx + 1 = 0$$

where:

$$x = e^{-kh}$$

$$\therefore x = \frac{+4b \pm \sqrt{16b^2 - 4b^2}}{2b^2}$$

$$= \frac{4b \pm \sqrt{12b^2}}{2b^2}$$

$$= \frac{4b \pm 2b\sqrt{3}}{2b^2}$$

$$\therefore e^{-kh} = \frac{2 \pm \sqrt{3}}{b}$$

$$\therefore e^{-kh} = b^{-1}(2 \pm \sqrt{3})$$

$$\therefore -kh = -1 \log_e b + \log_e (2 \pm \sqrt{3})$$

Therefore, the rate of change of slope is a maximum when:

$$h = \frac{\log_e b}{k} - \frac{\log_e (2+\sqrt{3})}{k}$$

$$= \frac{\log_e b - 1.317}{k} \qquad (6.2.4)$$

or

$$h = \frac{\log_e b - \log_e (2-\sqrt{3})}{k}$$

$$= \frac{\log_e b + 1.317}{k} \qquad (6.2.5)$$