THE EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON ONION BULB GROWTH AND DEVELOPMENT

J.M. de Ruiter

Plant Physiology Division, DSIR, Palmerston North

ABSTRACT

A thermal-time model of the change in diameter of onion (*Allium cepa* L.) bulbs, which describes the responses of six cultivars of varying maturities, is presented. A common response was obtained for multiple sowing dates, although cultivars behaved differently. Initial growth rates of an early cultivar, Yozui Yellow (YY), were higher than in a late maturing one such as Pukekohe Longkeeper (PLK). Growth rates of Early Longkeeper, Gladalan Brown, Braeside Golden Globe and Porters Early Globe were intermediate. Leaf development was a useful indicator for the initiation of bulb growth. Estimated photoperiods at initiation of the last-emerged leaf of YY were significantly shorter than for PLK, although significant interactions with temperature were evident. Bulbing in the early cultivar (YY) appeared to depend more on temperature than photoperiod, although the reverse was true for the remaining cultivars.

Additional Key Words: Allium cepa *L., Pukekohe Longkeeper, Early Longkeeper, Gladalan Brown, Braeside Golden Globe, Porters Early Globe, Yozui Yellow, sowing date, early maturation*

INTRODUCTION

The production of early maturing onion (*Allium cepa* L.) cultivars is a priority for breeders in New Zealand, with the long term objective of securing a stable export market (Grant, 1983). Early cultivars with resistance to bolting are available but do not have the desirable keeping qualities and shape of the commonly grown Pukekohe Longkeeper (PLK) and Early Longkeeper (ELK) cultivars.

Bulb growth and development are both influenced by temperature and photoperiod (Brewster, 1977), bulb formation being promoted by long days and high temperatures (Heath, 1945; Kato, 1964; Magruder and Allard, 1943). These responses are modified by interactions with cultivar, daylength and temperature (Steer, 1980a). Little is known of the combinations of temperature and photoperiod which control bulb development and maturation, especially in cultivars important for breeding early maturing, high quality onions for New Zealand conditions.

Onions have a determinate growth habit. Therefore, the rate of leaf development and number of leaves formed influence the duration from seedling emergence to crop maturity measured as 'top down'. An adequate period of bulb growth is essential if bulbs of desirable size are to be attained. Early planting ensures an extended period of bulb growth and the maintenance of optimum leaf area until top down. However, bolting can be induced by low temperatures during early growth.

This study was conducted to identify the important environmental responses which relate to earliness in onions. The main objective was to describe the physiology of New Zealand cultivars (PLK, ELK, Porters Early Globe), Australian cultivars (Gladalan Brown and Braeside Golden Globe) and an early maturing Japanese cultivar (Yozui Yellow). A knowledge of the responses of these cultivars to temperature and photoperiod would assist in the design of a breeding programme to produce a high quality, early maturing onion cultivar.

MATERIALS AND METHODS

Plant material and field sampling

Six cultivars, Pukekohe Longkeeper (PLK), Early Longkeeper (ELK), Gladalan Brown (GB), Braeside Golden Globe (BGG), Yozui Yellow (YY), and Porters Early Globe (PEG) were grown at Palmerston North (lat. 40°12') on a Manawatu silt loam. The genetic origin of the Australian cultivars, GB and BGG, were described by Steer (1980a) and the New Zealand cultivars by Grant (1983). Yozui Yellow is a Japanese line noted for its early maturation but poor shape and keeping quality.

The trial was a split plot randomized complete block design with three replications. The main plots were sowing dates (14 May, 4 June, 26 June, 17 July, 7 August and 28 August 1985) and cultivars, which were randomized in 2 m rows, constituted the split plots.

Seeds were sown directly into the field except for sowing 4 (17 July). At this date, seeds were germinated in trays and transplanted at the first true leaf stage. Seeds were dusted at sowing with Thiram to prevent damping off. Plants were thinned at the second leaf stage to an average spacing of 10 cm within the rows. All plots were hand weeded. A basal dressing of 4.0 t/ha of 30% potassic superphosphate was applied before the first sowing and three split applications of urea (3 x 108 kg/ha) were applied at 8 week intervals beginning at sowing 1.

Leaf tips of five plants per plot were marked with paint at 2 week intervals throughout growth, beginning at the appearance of the second true leaf. The total number of emerged leaves and the total number of leaves per plant were recorded at similar intervals. Bulb and neck diameters were measured with a micrometer at 2 weekly intervals on the same marked plants.

Daily maximum, minimum and hourly mean temperatures for air and soil (2, 5 and 10 cm depth) were recorded for the duration of the experiment. Photoperiods were calculated by the method of Keisling (1982) using a critical light intensity of 1.54 W/m².

Top down was defined as the time when 50% of the tops had fallen over. At top down, plants were harvested and measurements made of the bulb size, total number of emerged leaves, total leaves and bulb scales initiated. In addition, five previously unlabelled plants from each plot were marked so that bulb growth after top down could be monitored. For convenience, the duration of bulb growth was calculated for the period from field emergence to top down.

Glasshouse experiment

Leaf initiation rates were determined from a glasshouse experiment. Forty plants of each cultivar were sown in pots of 4 cm diameter in a 5:2:1 mix of Opiki silt loam, pumice and sand. These were sown on 27 May 1986. Hourly mean temperatures were recorded in a glasshouse set to a 25/10 °C max/min for venting and heating. Four plants of each cultivar were harvested at weekly intervals and dissected to determine the number of leaves initiated. Counts were made of the number of emerged leaves. A relationship between glasshouse initiation rate and leaf emergence rate was used to predict leaf initiation of field grown plants. It was assumed that field initiation rates in response to thermal time (base 5 °C) were the same as for glasshouse grown plants. Field leaf initiation rates were then used to calculate photoperiods at the initiation of the last-emerged leaf. The photoperiod at initiation of this leaf was assumed to be an important environmental event facilitating the initiation of bulbing.

Data analysis

A degree-day sum was calculated according to

$$\sum_{i=1}^{n} [Tmax_i + Tmin_i)/2 - T_b]$$

and only included days when mean temperature exceeded the base temperature (T_b), for the period from emergence to top down (day n). A minimum variance method (Arnold, 1955) for leaf appearance rate of leaves 3 to 9 of plants from serial sowings was used to select the appropriate base temperature. A linear rate of leaf appearance was assumed in calculating the base temperature.

RESULTS AND DISCUSSION

Field growth

From sowing until mid August mean air temperatures at 10-day intervals were approximately one degree higher than soil temperatures. For the period of the experiment, soil temperatures were, on average, two degrees warmer than air temperatures. Air temperature was chosen for the degree-day growth responses because it is more commonly used in degree-day studies. Also, there was little difference between air (5 °C base) and soil (7 °C base) coefficients of variation for thermal time of the appearance of leaves 3 to 9

among sowings. Field emergence occurred on average 23 ± 2.7 days after sowing and was equivalent to a thermal time of 124 ± 29 degree days.

There were no observable disease problems during growth except for a minor incidence of damping off which reduced seedling numbers. Seed treatment with Thiram appeared to be effective in controlling this problem.

Cultivar and sowing date influenced both the total number of leaves initiated at top down and the number of bulb scales initiated (Table 1). In all cultivars except YY, approximately four more leaves were initiated in the early sown crops (mid May) compared to the late sowings (early September). In Yozui Yellow, sowing date had little effect on the number of leaves produced. There was no effect of sowing date on the number of bulb scales at top down, although there was a strong cultivar effect. PLK produced, on average, two more scales than YY, while the other cultivars were intermediate.

TABLE 1: Mean cumulative number of leaves and bulb scales initiated at maturity (top down).

Cultivar*	Sowing (date)					
	1(14/5)	2(4/6)	3(26/6)	4(17/7)	5(7/8)	6(28/8)
			Leaves			
PLK	16.7	15.4	15.3	15.9	13.1	12.9
ELK	16.0	14.7	13.1	12.7	12.3	10.9
BG	14.8	15.7	13.7	13.1	12.8	10.7
BGG	14.4	14.5	12.7	13.5	10.7	12.2
PEG	—	14.9	13.7	13.6	12.6	11.7
YY	—	8.5	8.5	9.5	9.7	8.6

LSD (p≤0.05) sowing x cultivar = 2.1
LSD (p≤0.05) within sowing level = 2.0

			Scales			
PLK	10.4	9.8	11.2	10.3	11.3	10.9
ELK	9.7	10.2	9.7	10.1	10.3	10.5
BG	9.5	8.6	9.5	9.7	10.0	10.5
BGG	9.2	9.2	9.4	9.5	9.5	9.5
PEG	—	8.6	10.2	10.3	10.5	9.9
YY	—	8.9	9.1	8.4	8.8	9.7

LSD (p≤0.05) sowing x cultivar = 0.8
LSD (p≤0.05) within sowing level = 0.8

*PLK = Pukekohe Longkeeper, ELK = Early Longkeeper, GB = Gladalan Brown, BGG = Braeside Golden Globe, PEG = Porter Early Globe, YY = Yozui Yellow.

Some of the above effects may be explained in terms of the duration of bulb growth. The relative difference in the period from emergence to top down between sowing 2 and sowing 6 was remarkably consistent in all cultivars (Table 2). This ranged from 62% (YY and PEG) to 68% (PLK). On average, PLK took 44 days longer to mature than YY.

Thermal durations (base 5 °C) for bulb growth did not significantly differ with successive plantings, but cultivar differences were significant. An average of 1617 and 1046 degree-days were required for bulb development to top down in PLK and YY, respectively (Table 2). Bulb size at

TABLE 2: Mean number of days and degree-days from emergence to top down.

Cultivar*	Sowing (date)					
	1(14/5)	2(4/6)	3(26/6)	4(17/7)	5(7/8)	6(28/8)
	Days					
PLK	218	205	188	172	155	140
ELK	204	191	169	152	141	124
BG	203	191	165	154	134	120
BGG	200	192	165	157	135	128
PEG	—	189	164	153	136	117
YY	—	164	138	126	110	101

LSD (p$\leqslant$0.05) sowing x cultivar = 6.8
LSD (p$\leqslant$0.05) within sowing level = 6.5

	Degree-days†					
PLK	1798	1673	1659	1626	1582	1547
ELK	1570	1515	1362	1305	1368	1321
GB	1614	1527	1376	1376	1318	1303
BGG	1495	1510	1375	1418	1355	1414
PEG	—	1147	1045	1007	1010	1019
YY	—	1494	1391	1362	1384	1256

*Cultivar abbreviations as for Table 1.
†Calculated from air temperature (base 5 °C) for the period from emergence to mean date of top down.

top down was positively related to duration of bulb growth (r = 0.78**[a]) and the thermal time (base 5 °C) from emergence to top down (r = 0.59**). The duration of bulb growth has been shown in other studies to be important in determining final bulb size (Watson, 1951; Abe et al., 1955; Brewster, 1982; Khan, 1981). Factors which limit the duration of bulb growth and the potential transport of photosynthate from leaves to developing scales (Mann, 1983) are therefore important in not only determing earliness but also final size.

There was only a minor incidence of bolting among the cultivars evaluated. Gladalan Brown (GB) was the most susceptible with 20% of the plants sown on 14 May producing flower heads. There was no bolting in sowings later than mid July and no bolting at any planting for BGG or YY. The incidence of bolting was less than 5% for sowings of PLK, ELK, GB, BGG and PEG before mid July. Bolting can be a significant problem with early sowing. Bolting is promoted by low temperature and generally affected less by daylength (Holdsworth and Heath, 1950). Another report by Brewster (1983) showed that bolting was accelerated by long photoperiods (20 h), but there was little evidence that bolting resistant types were more likely to mature earlier.

Variability

Onions are an open pollinated species and considerable variation exists within cultivars. Variability within onion
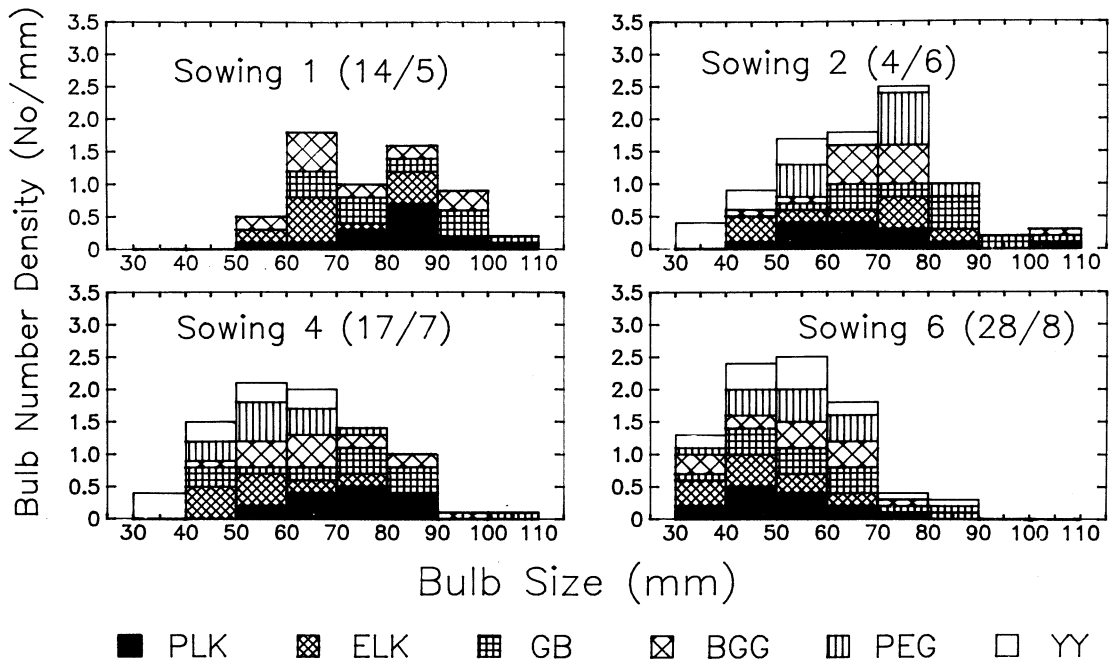

Figure 1: Bulb size distributions at top down for six onion cultivars at four sowings.

[a] Significant at p$\leqslant$0.01

cultivars in response to temperature and photoperiod is useful when selecting for better cultivars, but interactions with the environment have proved to be a major obstacle to devising efficient selection techniques for earliness.

Plant processes are usually described in terms of mean responses. An alternative approach is to accept the inherent variability in the populations and attempt to model growth and development in terms of distributions. An example is the prediction of the distribution of final bulb size from a distribution of size at some earlier stage in bulb development. The initial bulb size tended to influence the size later in development (data not shown), although some crossovers in growth trajectories occurred. This growth pattern was consistent in other combinations of cultivar and sowing date. It should be possible to predict final bulb size from initial bulb size as a base. Use of such a model for screening of specific bulb characteristics depends on uniform growth of all bulbs and would require considerable refinement and testing.

The variability in bulb size at top down is demonstrated in Fig. 1. In later plantings the distribution changes from a right to left skew and the average bulb size becomes significantly smaller. Mean bulb size was 82 mm in sowing 1 (14 May) compared with 52 mm from sowing 6 (22 August). All cultivars except YY showed significant reductions in bulb size with later sowings. Also, in all
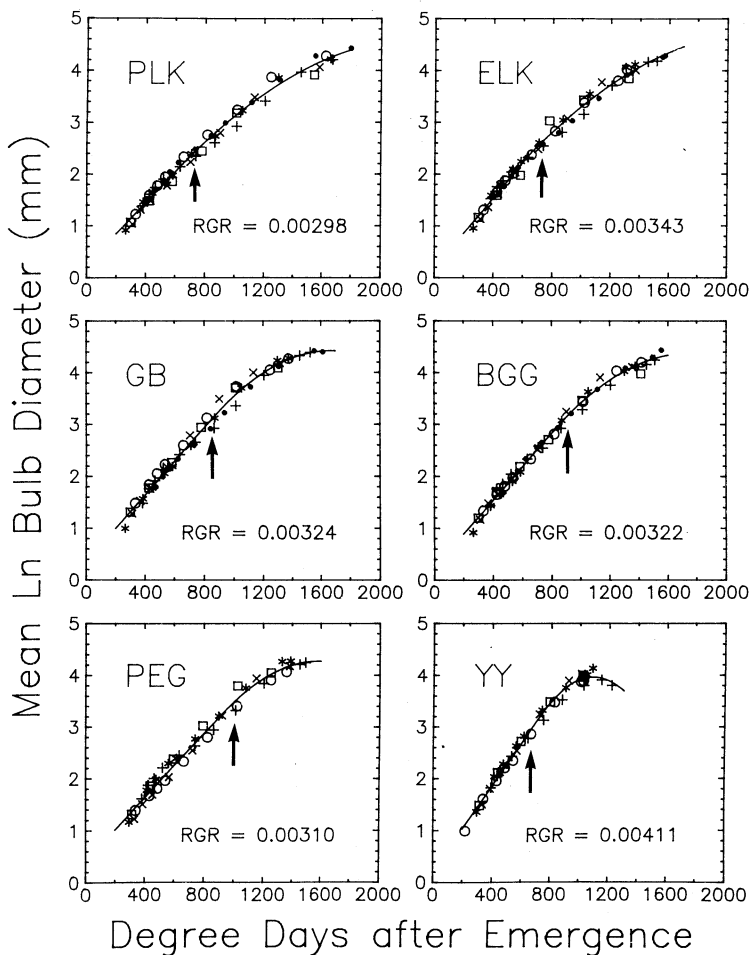

Figure 2: Relationship between mean log bulb diameter and thermal time for six onion cultivars (PLK = Pukekohe Longkeeper, ELK = Early Longkeeper, GB = Gladalan Brown, BGG = Braeside Golden Globe, PEG = Porters Early Globe, YY = Yozui Yellow) until top down. A break point was estimated in a non-linear routine by fitting a linear and quadratic segmented function to log transformed bulb diameters. RGR = relative growth rate for the initial growth phase terminated by ↑; (●, +, *, ○, ×, □ = sowings 1 to 6; respectively).

sowings except sowing 6, the size distribution of YY was skewed to the left of that for PLK. Top down occurred much earlier in YY than PLK and bearing in mind the shorter period in which photosynthate was transported from leaves to developing bulbs, it was not surprising that YY bulbs were smaller at top down than in later maturing cultivars.

Bulb growth model

For convenience the pattern of bulb growth was separated into two phases, separated by top down. Top down was chosen because it is a convenient and precise ontogenetic event in bulb development. Before top down there was little generalised pattern for bulb growth which could be used predictively in relation to days after sowing or Julian day. Use of a thermal time response for bulbing

did, however, normalise the sowing date responses, at least within cultivar.

Linear relationships were found for log transformed bulb diameter versus thermal time accumulation (base 5 °C). This could be useful for making comparison among cultivars of bulb diameter growth rates in the early growth stages. In this model, the initial bulb growth rates were exponential; however, the rates declined as the plant approached top down. The point of departure from an exponential relationship is indicated by arrows in Figure 2, defining a change from a linear to quadratic fit. During the phase of declining bulb growth rate, as described by the quadratic curve fit, limitations to the photosynthate supply to the bulb scales may have occurred as a result of leaf senscence and a declining rate of leaf appearance. Leaf
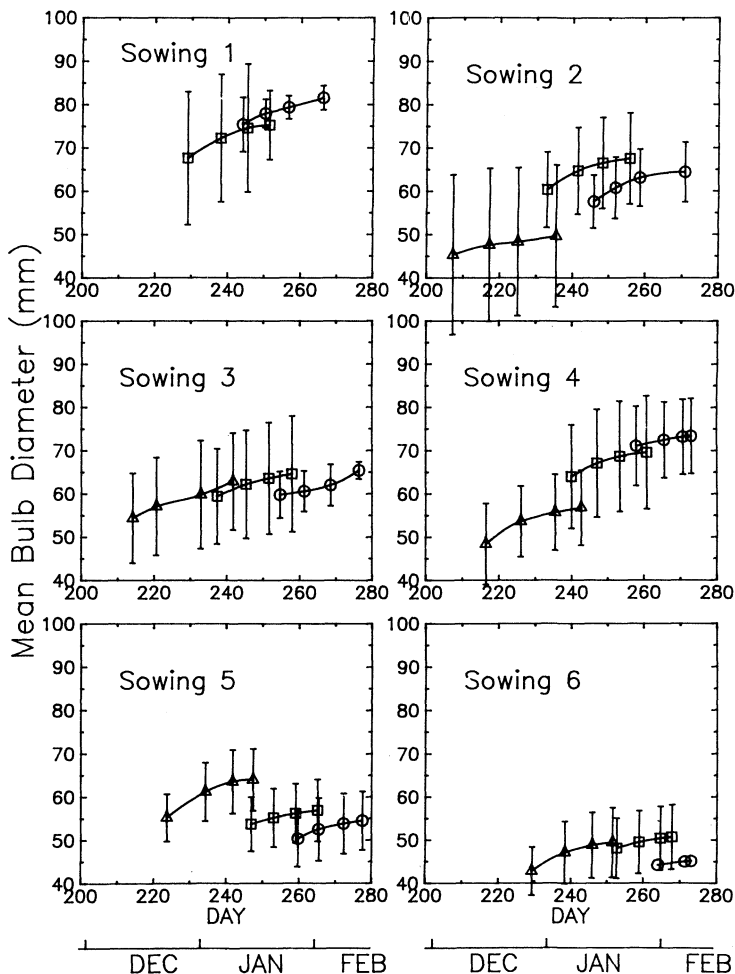

Figure 3: Growth of onion bulbs after top down at successive sowings (O = PLK; □ = combined intermediate maturity cultivars ELK, GB, BGG and PEG; △ = YY).

development is described in the following section.

The responses relating bulb growth to degree-days are useful as the various sowing date effects are explained by single functions. Top down in the later sowings occurs after a greater accumulation of thermal time from emergence. The problem of predicting top down still remains. In YY this occurs in all sowings before the accumulation of 1200 degree-days and around 1600 degree-days for PLK, with the remaining cultivars being intermediate. For YY the initial rate of change in bulb size was significantly different (p≤0.05) from the other cultivars. The initial relative growth rate may be an important and potentially useful diagnostic characteristic for early maturing genetic material. Selection of bulbs with a relative growth rate

greater than a predefined critical value may form the basis for a modified population of earlier maturing bulbs.

Bulb growth after top down is shown in Fig. 3. For the purposes of comparison, the data for cultivars of intermediate maturity (ELK, GB, BGG and PEG) were combined. Considerable variation in bulb size was evident. A consistent trend emerged with a gradual fall off with time. Even though the tops had fallen, there was still a substantial increase in size and probable translocation of reserves into the developing bulb for a period of at least 30 days after top down. Final mean bulb sizes for YY were lower than PLK until sowings 5 and 6. These two cultivars were quite different in their maturation dates (3-18 January for YY, and 7-15 February for PLK).
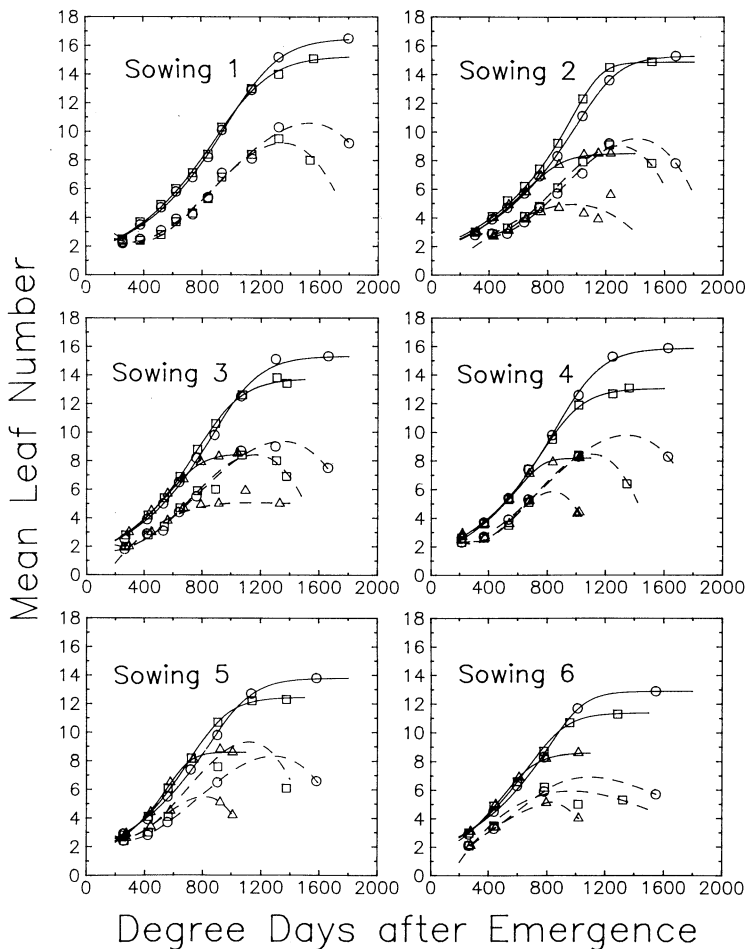

Figure 4: Leaf growth (——— = total emerged leaves, – – – = net leaf number per plant) of early (= YY); intermediate (□ = ELK, GB, BGG and PEG) and late (= PLK) cultivars. Curves for cumulative leaf numbers were fitted using a non-linear Richards function (Causton and Venus, 1981). A cubic function was fitted to net leaf numbers.

Leaf development

The relationship of leaf development to thermal time is shown in Fig. 4. Unlike the model for bulb growth (Fig. 2), a linear response relating leaf numbers to thermal time was inappropriate although the initial rates of leaf appearance were close to linear. More complex functions were required to fit the data for the period until top down. This was partly a result of significant planting date effects on the number of emerged leaves and a significant reduction in the rate of leaf emergence as the plants approached top down. In addition, there were significant cultivar differences in the number of leaves produced at top down, although leaf production patterns were similar within sowings in the early developmental stages. Leaf production appears to be under close genetic control as the final leaf numbers were related to cultivar earliness. Simpler, more generalised responses could possibly be found if the number of leaves up to and including the last leaf appearance was related to thermal time. The responses of the intermediate cultivars were again combined. At top down, considerable leaf senescence had occurred.

Photoperiodic effects

Under New Zealand conditions, PLK and ELK are known to bulb in response to daylengths greater than 12 hours (D. Grant, personal communication). The relative importance of temperature is unknown, although high night temperatures have been shown to promote bulb formation in PLK and Gladalan Brown (Steer, 1980b). Little mention has been made of the photoperiodic requirements for bulb initiation. At bulb initiation, it has been suggested that leaf initials switch to form bulb scales rather than new leaf blades (Brewster, 1982). Initiation of the last leaf also appears to coincide with the photoperiodic stimulus for bulbing. Leaf initiation and appearance rates were calculated from a glasshouse experiment (Fig. 5), and applied to field data. These calculations assumed that the difference in initiation and appearance rates were similar in
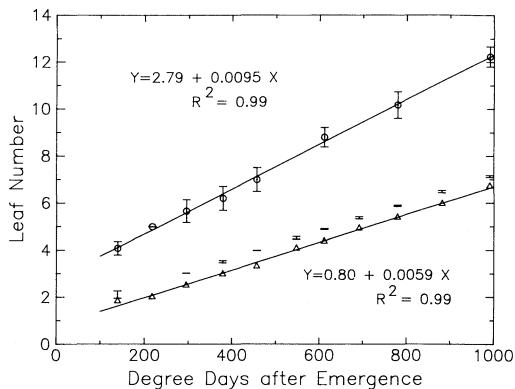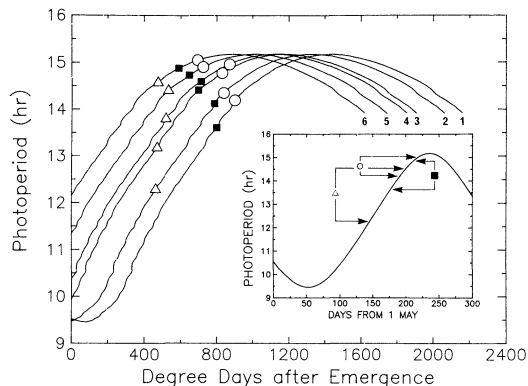
Figure 6: Photoperiod vs degree-day (base 5 °C) trajectories for sowings 1-6. Data points indicate initiation of the last-emerged leaf (○ = PLK; ■ = combined ELK, GB, BGG and PEG; △ = YY). Figure insert demonstrates the range of photoperiods for initiation of last-emerged leaves.

the differing environments, and that initiation of the last-emerged leaf occurred at photoperiods ranging from 12.3 to 14.6 hours for YY and 14.2 to 15.1 hours for PLK (Fig. 6). With the above assumptions these photoperiods will facilitate bulb initiation under the specific temperature prehistory of this study.

In the bulb growth model, it was assumed that temperature had a dominating influence on growth and that photoperiods were of sufficient length to facilitate bulb development. Interactions between plant size, temperature and photoperiod were not examined in detail and can only be satisfactorily elucidated in a controlled environment. Some indications of the interactions occurring are shown in Fig. 6. Yozui Yellow appears to be more temperature than photoperiod dependent in terms of the approximate time to onset of bulbing. Last-leaf initiation occurred at similar thermal times after emergence irrespective of the photoperiod. Conversely, there was a definite photoperiod and temperature influence on the time to initiation of the last-emerged leaf in the remaining cultivars. Photoperiods for initiation of the last leaf of PLK occurred near the upper limits of photoperiods received at Palmerston North (Fig. 6), while the range of photoperiods indicated for the intermediate and early maturing cultivars was significantly shorter.

Figure 5: Leaves initiated (○) and emerged (△) in relation to thermal time (base 5 °C) for glasshouse grown plants. Upper vertical bars are ± standard deviations, and lower bars are standard errors for cultivar means.

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