

# THE EFFECTS OF LIGHT ON BULBING IN ONIONS

D.S. Bertaud

Plant Physiology Division, DSIR, Palmerston North

## ABSTRACT

Growth and development of onions bulbs is affected by daylength, light quality and light interception. In short days, no bulbs are formed; in long days, large bulbs are formed, but take some time to mature; and in very long days, small bulbs are formed and mature quickly. The effect of daylength depends on the quality of the light; bulb growth requires a high level of far-red light.

In conditions favourable for bulbing, sucrose and oligosaccharides accumulate in the bulb. Bulb growth and carbohydrate accumulation depend on current environmental conditions and cease if conditions are no longer favourable. High light intensity and leaf area enhance bulb growth. These results are consistent with the concept of bulb growth as a process that depends on the partitioning of available photosynthates. The results are summarised as a conceptual model for leaf extension involving a partitioning function A, the fraction of photosynthate available to a leaf which is used in leaf extension, and a growth function G, which is the amount of photosynthate available to a leaf. The implications of this model for physiologists and breeders are discussed.

*Additional Key Words: photomorphogenesis, light interception, phytochrome, red/far-red ratio, plant growth models, Allium cepa L.*

## INTRODUCTION

Onions are widely grown in New Zealand for the domestic market and for export. At present almost all exports go to Japan, leaving the industry vulnerable to fluctuations in demand. To stabilise the industry, and develop new markets, we must be able to respond to market demands, either by breeding new varieties or by managing crops to meet shipping requirements. Breeding and management of crops are complicated by the varying responses of different cultivars to daylength (Magruder and Allard, 1937; Austin, 1972; Brewster, 1977), and other environmental factors such as temperature (e.g. de Ruiter, 1986). These environmental responses control the rate of growth of a bulb, and its time of maturity. An understanding of the way in which onions respond to environment would be useful to physiologists, breeders and growers interested in meeting the demands of particular markets.

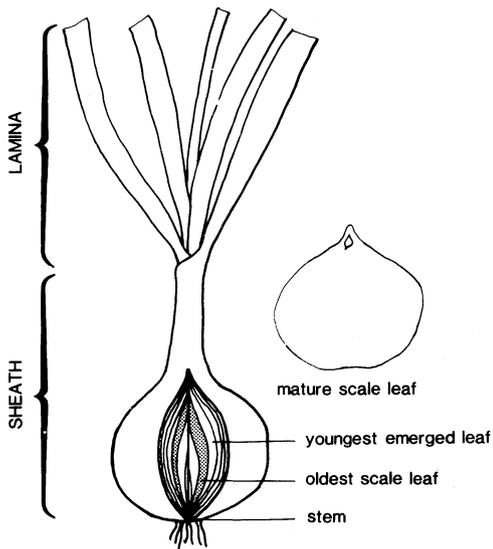
Onion physiology was reviewed comprehensively by Brewster (1977). Bulbing in onions was reported to be affected by daylength (Magruder and Allard, 1937) and light quality (Austin, 1972), and to be reversible; bulbing plants transferred to short days resumed leaf growth, or sprouted (Kedar *et al.*, 1975). In this paper, I shall develop the hypothesis that bulbing is a result of partitioning of photosynthate in growing cells in response to current daylength. This hypothesis is based upon information reviewed by Brewster and more recent work on carbohydrate metabolism (Lercari, 1982a,b, 1983), light interception (Brewster, 1982) light quality and planting density (Mondal *et al.* 1986a,b,c; Brewster *et al.*, 1986) and growth rates (de Ruiter, 1986). The hypothesis will be expressed as a model for leaf growth.

I shall start by examining what an onion is and how it grows, to see how the description of its growth can be reduced to a manageable problem. The simplified picture of an onion thus developed will be used to analyse the results of physiological studies on the effects of daylength, light quality and light interception on bulb growth. A model for bulb growth and leaf extension will be sketched; predictions from this model provide a physiological input into New Zealand breeding and research programs, and suggest tests of the hypothesis expressed by the model.

## STRUCTURE OF AN ONION

Onions (*Allium cepa* L.) are monocotyledonous plants, and may be placed in either Liliaceae or Amaryllidaceae families (Rabinowitch, 1985). The genus *Allium* has also been placed in a separate family, the Alliaceae (Willis, 1966). Leaves arise from a very short, flat stem (Fig. 1.) The outermost leaves are the oldest, and new leaves arise from the apical meristem at the tip, in the centre of the stem.

Onions produce two kinds of leaves; green foliage leaves each with a long, cylindrical sheath and a hollow blade that grows from one side of the cylinder, and non-green scale leaves, where the blade does not develop and the hollow sheath is thickened as storage tissue (Fig. 1). Younger leaves emerge through the hole at the top of the sheath (where the ligule would be on a grass leaf). There is a high turnover of leaves on a growing onion (de Ruiter, 1986). Older leaves die and are sloughed off and the diameter of the stem increases as successive leaves are formed. Some of the scales on a mature onion bulb are thickened leaf bases (the lower parts of the sheaths) and some are scale-leaves (Fig. 1). These organs store carbohydrate in the form of sucrose and more complex



**Figure 1: An onion plant, showing growth habit and (inset) a scale leaf. The two outermost leaves on the bulb appear as a single line on this scale.**

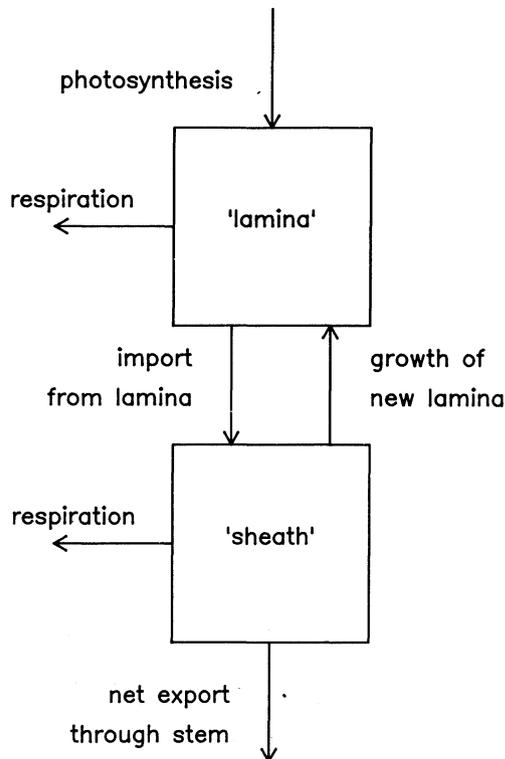
oligosaccharides (mainly fructans of various degrees of polymerisation). Growth of the bulb is a result of thickening of leaf-bases and scale-leaves. There are generally 4 - 8 scales on a mature bulb, plus a number of immature leaves and primordia. The proportion of the bulb made up of scale leaves varies between cultivars and between plants (de Ruiter, pers. comm.). Generally, most of the bulb is made up of leaf-bases; however, scale leaves may comprise up to 74% of the fresh weight (Bertaud, unpublished work).

When conditions are suitable for bulbing to occur, the growing bases of leaf sheaths thicken as cells expand and fill with complex sugars (Abdalla and Mann, 1963). The apex begins to produce scale leaves, which do not extend above the top of the bulb; this means that the last green leaves, when fully grown, are not supported by emerging new leaves. Eventually the remaining green leaves fall over, and the onion is said to be 'top down', or mature.

Onion leaves mature first at the tip (Bertaud, unpublished work); we assume that mature leaf tissue is continuously pushed up by growth at the leaf base until the leaf is mature, as in grass leaves. This assumption is supported by the work of Denne (1960) in *Narcissus*, a bulb-forming plant which also produces foliage leaves and scale leaves. Patterns of leaf growth and cell elongation in *Narcissus* were the same for both foliage and scale leaves that were 0.5-1 mm long. In foliage leaves, the intercalary meristem present in the primordium was maintained and enlarged, though it never extended more than 50 mm up the lamina, even when the lamina was 250 mm long (Denne, 1960). When the lamina was nearly mature, cell division became restricted to the sheath. In scale leaves, however,

leaf growth and cell division were restricted to the sheath very early in development, without the intervening stage of lamina growth (Denne, 1960). This difference in growth suggests that partitioning of photosynthates between sheath and lamina is the process that is affected by environmental conditions causing bulbing.

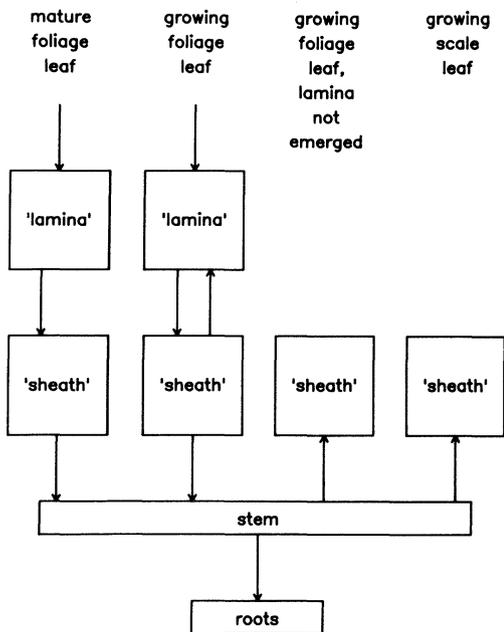
In a discussion of partitioning, it is useful to picture the leaf as having two notional compartments (Fig. 2). The 'lamina' compartment, comprising emerged, photosynthesising lamina, is a net source of photosynthate; non-structural carbohydrates produced in the lamina by photosynthesis are exported to the 'sheath' compartment, consisting of sheath and unemerged lamina. The boundary between the two compartments is the point in space at which the lamina emerges from the uppermost sheath. Most cell division and expansion takes place in the 'sheath' compartment; in monocotyledonous plants leaf tissue is largely mature by the time it emerges.



**Figure 2: A compartment model for an onion leaf, showing inputs, outputs and transfers of dry matter.**

An onion plant can be considered as a series of leaves at various stages of development, interconnected through the stem (Fig. 3). The relative importance of the different inputs and outputs changes as a leaf matures. In a growing leaf, the 'sheath' is the major sink for photosynthates. If

the plant is not bulbing, they are used as structural carbohydrates for leaf extension; if the plant is bulbing, they are used as storage carbohydrates in scale tissue. Leaves that are no longer growing export carbohydrates through the stem to supply the youngest leaves (Mann, 1983), while in very young leaves, or scale leaves with no photosynthesising lamina, all carbohydrates are imported through the stem from older, photosynthesising leaves (Fig. 3).

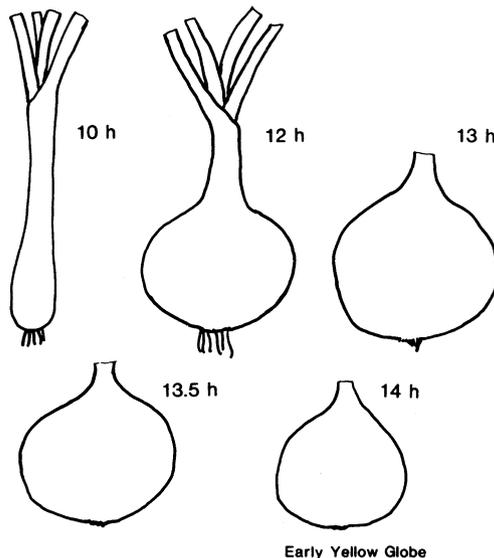


**Figure 3:** Simplified model of an onion plant, showing different kinds of leaves. Not all types of leaves would be expected to be present on a plant at the same time. This schematic representation shows two photosynthesising leaves, one foliage leaf with no emerged lamina (which therefore does not photosynthesise), and one scale leaf, which produces a rudimentary lamina that never emerges. Arrows indicate movement of dry matter as in Fig. 2; respiration losses are omitted for simplicity.

### DAYLENGTH

Bulbing in onions has been known to depend on daylength since the work of Garner and Allard (1920). Magruder and Allard (1937) studied the effects of daylengths ranging from 10h to 14.25h, and naturally increasing daylengths on a range of cultivars. Only one cultivar produces bulbs that eventually dried down normally in 10h days; most produced good bulbs in 14h days. A typical pattern of response was that exhibited by

the variety Early Yellow Globe (Fig. 4), which showed very little evidence of bulbing in 10h days. In 12h days, bulbs formed, but the plants continued producing green leaves and the tops did not fall. In 13h and 13.5h days, the plants produced large bulbs; in 14h and 14.25h days, maturity was earlier and bulbs were progressively smaller. The size of bulb decreased with increasing daylength, as plants reached top down earlier. There was a considerable range in response to photoperiod within each cultivar, as well as between cultivars. Austin (1972) using a number of cultivars, found that bulbs formed in continuous light in a glasshouse (14h days extended by low intensity incandescent light) had weights of 1-5 g, which was about the size of a large bean.



**Figure 4:** Effect of daylength on shape and size of onion bulbs. Redrawn from Magruder and Allard, 1937.

This pattern could be explained by a gradient in partitioning of photosynthates in response to daylength. In short days, most photosynthates go to leaf extension, and a higher proportion goes to bulb growth as days lengthen. Bulbs will form under some daylength conditions as a result of thickening of the leaf bases, but scale leaves are not produced, so bulb tops never fall. By contrast, in very long days, all photosynthates go to the bulb, leaving none for leaf growth; leaf production stops and bulbs mature early, so the period for bulb growth is short, and bulbs are small. However, bulbing does not require increasing daylengths; bulbs can be grown in decreasing daylengths if the daylength requirements of the cultivar are met (Kedar *et al*, 1975).

The possibility that bulbing depends on total photosynthate rather than on daylength per se was investigated by Wright and Sobeih (1986). Plants exposed

to 67.5 E/m<sup>2</sup>/s during 16h days bulbed; those given 135 E/m<sup>2</sup>/s during 8h days did not, though the total amount of photosynthetically active radiation was the same in the two treatments. However, plants exposed to the high light intensity for 16h days bulbed faster than those exposed to the low light intensity. Extending an 8h daylength with low intensity (11 W/m<sup>2</sup>) light was also effective in producing bulbing (Wright and Sobeih, 1986).

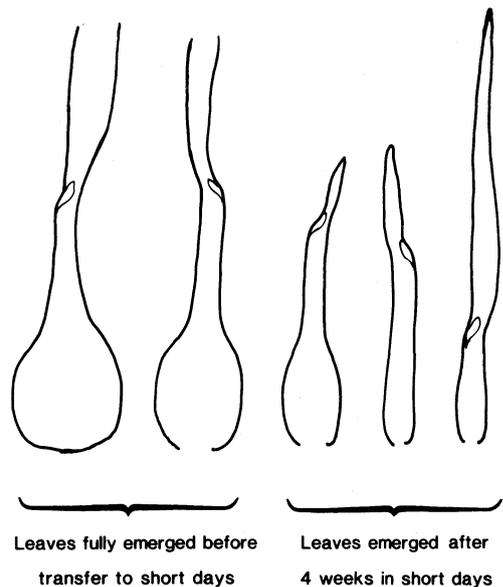
Bulb growth can be stopped or reversed by transferring bulbing plants to short days. The growth in bulb diameter slows and stops, green leaves are produced, and the diameter of the bulb decreases as scales senesce. Renewed production of green leaves and reversal of bulbing can occur even after the tops have fallen (Kedar *et al.* 1975; Bertaud, unpublished results). An immature, bulbing onion, transferred from long days to short days with mature, or near mature, green leaves, stopped bulb development, and produced instead new green leaves of atypical form (Fig. 4). Since onion leaves mature first at the tip, the shapes of these leaves provide further information. Evidently leaves which started maturing as scales (their laminae had nearly matured as the residual points observed on scale leaves [Fig. 1]) have changed partway through their development to produce short green laminae with normal sheaths. Under some conditions (e.g., low temperatures) mature scale-leaves were observed between the last leaf emerged before transfer and the first leaf emerged after transfer. The plasticity of the leaf tissue is probably responsible for the phenomenon observed during bulb growth, where long leaves with green blades finish development at the sheath base with a region of white, thickened scale tissue. Thus it seems that green or scale leaves are not initiated as such, but that a more general 'leaf' is initiated (c.f. Denne, 1960) which has the potential to develop as a green leaf, as a scale leaf, or with an intermediate form. The path of development taken is determined by the environmental conditions which prevail at the time cells are growing and maturing.

These results indicate that bulbing is a continuous response to a current daylength; it is not triggered by a short exposure to long days. This is a different phenomenon from the classic flowering response to daylength, where flowering may be induced irreversibly by a short exposure to inductive conditions (Salisbury, 1982). It also suggests that a term like 'onset of bulbing' (Mondal *et al.* 1986a) or 'start of bulb growth' would be preferable to 'bulb initiation', since a bulb is not an organ to be initiated in the same way as, for instance, a flower.

### LIGHT QUALITY

A number of authors (e.g. Austin, 1972; Lercari, 1982; Mondal *et al.*, 1986b,c) have reported that bulbing in onions requires far-red light (FR). A higher proportion of FR in the available light will increase the rate of bulbing (Austin, 1972), while R:FR ratios of about 3.5 required 18h days to produce bulbs comparable with those produced in sunlight (R:FR = 1.1) in normal daylengths of 14h.

Lercari (1982a) also found that the rate of bulbing increased with the proportion of far-red light (Fig. 5).

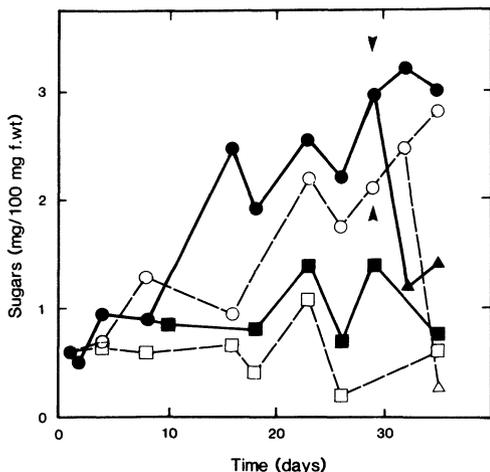


**Figure 5: Schematic drawing of successive leaves from an immature, bulbing onion transferred from long to short days (Bertaud, unpublished work).**

There is possibly circadian rhythm in this response; far-red light applied alone for 3h in the middle of the day was more effective than that applied at the beginning or end of the day; red light and blue light were ineffective at all times. A 3h dark break in the middle of an inductive photoperiod of 18h also prevented bulbing. Since the results for red and blue light were similar to those for darkness, while that for far-red light was different, this is probably a photoperiodic effect rather than a total photosynthate effect. As such it may reflect a circadian rhythm in the response to the light, or disruption of the phytochrome photoequilibrium.

Bulbing may be reversed by changing light quality as well as by changing daylength (Lercari 1982a). The accumulation of reducing sugars in the leaf blades and bulb observed under conditions of long days with a high level of far-red light is also reversible, and there appears to be no lag when conditions are changed (Fig. 5) (Lercari 1982b). Oligosaccharides and sucrose also increase in the bulb under these conditions — this is reversible, but there is a lag between the change of conditions and a drop in oligosaccharides. The action spectrum of the response suggests that phytochrome may be involved; possibly because the phytochrome photoequilibrium affects carbohydrate metabolism in some way (Lercari 1982b). The responses are observed very soon after conditions are changed.

Mondal *et al.* (1986b,c) have demonstrated an effect of light quality on bulb growth and maturity. Light transmitted through leaves is known to be enhanced in far-red light relative to red light. Onions grown under a canopy



**Figure 6: Effect of light quality on levels of oligosaccharides and reducing sugars in onion bulbs (Redrawn from Lercari, 1982). Solid symbols: reducing sugars. Open symbols: oligosaccharides and sucrose. ■, □ 18h days, R:FR 1.2; ●, ○ 18h days, R:FR 6.7. ▲, △ transferred to 10h days at arrow.**

of leaves (climbing peas and beans) matured about 10 days earlier than those grown under neutral shade or in sunlight. Similar effects were observed for plants in very high density plantings (400 plants/m<sup>2</sup>). In both cases, leaf appearance ceased earlier and fewer leaves were produced. Unfortunately they did not record the sizes of the resulting bulbs. Mondal *et al.* (1986b) also reported some evidence of the effect of fluence rate, as did Lercari (1983). Wright and Sobeih (1986) reported that for a given daylength, bulbing is delayed by low light intensity.

Bulbing appears to be a classic, fluence-rate dependant, "high irradiance response" (e.g. Lercari 1982a, 1983). This suggests that it is analogous to the daylength responses reported for internode elongation, which have been demonstrated to involve phytochrome.

## LIGHT INTERCEPTION

Brewster (1982) showed that total shoot dry matter yields of onion crops were linearly related to the total radiation intercepted during bulb growth. On average, the onion crop planted at a density of 100 plants/m<sup>2</sup>, intercepted 49% of the total radiation. The maximum observed was 65% for early sowings of late maturing cultivars which had time to establish a larger leaf area.

Maturity date decreased linearly with the fraction of light intercepted. Brewster *et al.* (1986) showed that crops which established a high leaf area index (LAI) early in growth matured early. They achieved this by very high density (400 plants/m<sup>2</sup>) plantings, irrigated and fertilised to minimise competition for water and nutrients. However,

the duration of bulb growth was reduced by high light interception, at least in high density planting. The difficulty with this method of achieving high light interception is that the results could also be affected by changes in light quality under the canopy.

The longer duration of bulbing in autumn-sown crops, which led to bigger bulbs, may have occurred because the LAIs established over winter were lower. Spring-sown crops, sowings made earlier within a season, and later-maturing cultivars, which intercepted a higher proportion of the incident radiation, had a shorter duration of bulbing. A cold winter, which resulted in smaller plants in spring, delayed maturity of normally early-maturing cultivars (Brewster, 1982).

It appears that in some cultivars development of scales in the bulb may be delayed by low LAI (Brewster *et al.*, 1986). Early maturing cultivars appear to respond more to photoperiod or temperature and begin bulbing at a low LAI. This tends to reduce yield, probably because the bulb scales compete more strongly with the new laminae as sinks for photosynthate, reducing the later development of leaf area. As the daylength increases, the leaf bases become stronger sinks, until eventually no laminae are formed, and scale leaves are produced. These results suggest that final yield is the result of a trade-off between leaf area during bulbing, and duration of bulbing.

Sobeih and Wright (1986) found that bulbing was delayed by reducing the leaf area of the plants. The ages of the remaining leaves were also important; later formed leaves seemed to be more sensitive to photoperiod, regardless of leaf area.

## A MODEL FOR THE EFFECTS OF LIGHT ON BULBING

Bulbing in onions involves preferential growth of sheaths at the expense of laminae, rather than the initiation of a discrete organ. Formation, growth and maturity of bulbs must therefore depend on the production of translocatable photosynthate, and the partitioning of this photosynthate between leaf blades and sheaths. In this section partitioning of photosynthate is discussed, and a model for onion growth involving light-controlled partitioning of photosynthate is presented.

The two compartment model of a leaf (Fig. 2) shows inputs and outputs of dry matter. The growth rate, considered as rate of increase in dry matter, of either 'lamina' or 'sheath' can be obtained by summing the rates if input and output. Bulb growth is the result of growth of the component parts of the bulb, the leaf-bases and scale-leaves. The rate of bulb growth, measured as rate of increase in dry matter,  $W'$ , can be approximated by the sum of the rates of input and output of all 'sheaths'. This can be written as an equation

$$W' = \sum_{\text{all 'sheaths'}} (I' - E' - L' - R') \quad (1)$$

Where

$I'$  is the rate of import from the lamina,

$E'$  is the net rate of export through the stem,

$L'$  is the rate of loss of dry matter through leaf extension, and

$R'$  is the rate of loss of dry matter through respiration.

For the whole plant,  $\Sigma I'$  is closely related to the net rate of photosynthesis.  $E'$  for a leaf may be positive or negative in sign, depending on whether the leaf is exporting photosynthate (as mature green leaves must) or importing it (as very young leaves and scales do). For the whole bulb, net exports by leaves cancel out, so  $\Sigma E'$  is positive, the net loss of dry matter to the roots.

Daylength, or light quality, must affect at least one of the terms in equation (1) to produce the responses observed in onions. The rate of import of photosynthate from the lamina,  $I'$ , depends on intercepted radiation, which is a function of previously developed leaf area. Daylength could well affect  $I'$ , but there is no obvious reason why either  $I'$ ,  $E'$  or  $R'$  should be affected by light quality. However,  $L'$  is clearly affected; in scale leaves  $L'$  is zero, because no lamina is produced.

The results reviewed suggest that the rate of leaf growth  $L'$  is controlled by two factors: partitioning of photosynthate, which is a function of light quality, daylength and temperature, and  $\Sigma I'$ , the total rate of increase in available dry matter for the bulb, which is a function of temperature, intercepted radiation (which depends on leaf area), and time. These observations may be summarised in a model for the rate of leaf growth which, by making a few assumptions, incorporates the observed results as explicit functional relationships. Partitioning of photosynthate is described by the partitioning function  $A(z,D,T)$  where

$z$  is the ratio of red to far-red light,

$D$  is the daylength, and

$T$  is temperature.

The total rate of increase in dry matter available to a leaf  $l$  may be described by a growth function  $G_l(S,T,t)$ , where

$S$  is intercepted solar radiation,

$T$  is temperature, and

$t$  is time.

$G_l$  is the part of  $\Sigma I'$  which is available to leaf  $l$ , and is a function of time.

Such a model may be expressed in terms of an equation. Since the form of the interaction between partitioning and rate of increase in dry matter is unknown, the form of the equation, as well as the functional relationships, is a matter of hypothesis. One form of the equation would be

$$L' = A(z,D,T) \times G_l(S,T,t) \quad (2)$$

The partitioning function,  $A$ , has values ranging between 1 (no photosynthate allocated to storage tissue) and 0 (all photosynthate allocated to storage tissue). The shape of  $A$  is genetically determined, and will vary between cultivars with different photoperiod responses. The history of the plant, and the birth and death of its leaves, enter

through the  $S$  term, which must be the result of previous leaf growth.

A conceptual model for growth in dry matter of the simplified bulb illustrated in Figure 3 is provided by considering Equations (1) and (2) together. As in Figure 3, the bulb is considered as the sum of its component leaf sheaths (Equation (1)). Bulb growth depends on four terms. Import of photosynthate from the laminae ( $I'$ ) depends on net photosynthesis, which in turn depends on available leaf area (resulting from growth and death of leaves) and the radiation this area intercepts. Export of photosynthates,  $E'$ , from bases of mature and senescing leaves contributes to growth of new leaf primordia and roots. Loss of dry matter as new leaf tissue,  $L'$ , is controlled by daylength and light quality (equation (2)). Respiration ( $R'$ ) is a loss from all tissue. Thus, young plants grown in short days partition all photosynthate to formation of structural carbohydrates for the elongation of leaf tissue. Older plants in lengthening days partition some photosynthate to storage carbohydrates in the leaf sheaths, resulting in 'swelling' of the bulbs. Maturing plants partition all photosynthate to storage carbohydrates as long as the remaining leaves stay green, and for a while during senescence.

In principle it would be possible to carry out an experiment that would provide data for fitting the functions in equation (2). However, the relationships are clearly complex, and such an undertaking would be costly in time and resources. It is more efficient to consider the implications of the form of the model.

The model expressed in equation (2) summarises the results described earlier and involves certain assumptions. The first of these is that partitioning is independent of the state of the plant. This may not hold for very young plants; there is some evidence that young leaves may be less sensitive to photoperiod (Sobeih and Wright, 1966). However, given that leaf growth will resume if bulbing plants are transferred from long days to short days, producing atypical leaves, it seems a reasonable assumption.

A second assumption is that partitioning is independent of the radiation intercepted. Again, none of the published evidence contradicts the assumption. Wright and Sobeih (1986) collected dry weights of leaves and bulbs, but did not present the results. Analysis of their data should be of interest.

The dependence of bulbing on current light quality as well as daylength means that diurnal fluctuations in carbohydrate metabolism and leaf extension would be expected, as photosynthates are partitioned to storage carbohydrates by day and to structural carbohydrates by night. However, under long-day conditions, these fluctuations should be superimposed on the accumulation of storage carbohydrates in the bulb observed by Lercari (1973). Diurnal variations in levels of non-structural carbohydrates were measured by Darbyshire *et al* (1979) for non-bulbing onions in 12h photoperiods, but the light quality and lamp combinations used in these experiments are not mentioned. The changes in carbohydrate metabolism observed by Lercari (1973) raise the possibility

of screening cultivars from a breeding programme in the laboratory. It might not be necessary to raise plants in a given environment, or to sacrifice whole plants; instead, plants could be shifted between environments over a period of days or weeks, and a series of tests done on tissue samples cut from the bulb. However, the consequences of wounding on carbohydrate metabolism need to be investigated.

Leaf extension would be expected to be slower during the day and faster, at least for a time, during the night. Darbyshire *et al.* (1979) measured a transient increase in leaf extension rate at 'lights off', which they attributed to stomatal closure in darkness resulting in an increase in turgor. This hypothesis could be tested using a low vapour pressure deficit, changes in light quality or changes in daylength.

The model is also consistent with the observation that in very long days very small onion bulbs are formed. The observation that onions mature early in long days would result from partitioning of a large proportion of photosynthate to the bulb at an early stage, leading to early formation of scale leaves, early top down, and smaller bulbs. This is supported by the observation of de Ruiter (1986) that rate of growth in diameter of onion bulbs is related to time of maturity. It may also be the reason for the noticeably smaller leaves of the early-maturing cultivar Yozui Yellow, compared to many later maturing cultivars (de Ruiter, pers. comm.). Thus, variations in the partitioning function A would explain differences between cultivars.

The model suggests that summer 'dormancy' might be a response to long days, and that bulbs might not have a true dormant period. If this is the case, it should be possible to control sprouting of bulbs by the appropriate daylength regime. Bulbs would be expected to sprout in short days, and to keep best in continuous light. Sprouting of bulbs in short days has been observed for bulbs just after top-down, but does not appear to have been tried for freshly cured bulbs in maximum 'rest'. If such control of sprouting were possible, it would be of use to breeders trying to synchronise flowering between different strains of onion.

Onion seedlings, with narrow, upright leaves, intercept very little light and are slow to form a closed canopy. Any variability in this habit might be of use in breeding programmes, to maximise leaf area index during early bulbing.

## CONCLUSION

The available evidence suggests that the development of onion leaves as either storage organs or photosynthetic organs depends on partitioning of photosynthate, which responds to current conditions of light quality, daylength and temperature. Thus, in short days, all photosynthate is partitioned to structural carbohydrate, and bulbs do not form. In very long days, all photosynthate is partitioned to storage carbohydrate, resulting in low leaf area, and small bulbs that mature early as growth of foliage ceases. The size of the foliage or scale leaves produced depends on the rate

of accumulation of dry matter, which is a function of temperature, intercepted radiation and time. A model describing onion leaf growth in terms of a partitioning function A and a growth function G is proposed. This model constitutes a testable hypothesis which explains the observed behaviour of onion plants in the field and suggests further physiological responses to daylength and light quality. Some of these responses could be of interest to breeders for screening plants, synchronising flowering or increasing the rate of generation turnover.

## ACKNOWLEDGEMENT

My thanks to Dr K. G. McNaughton, for helpful discussions while formulating the model.

## REFERENCES

- Abdalla, A.A. and Mann, L.K. 1963. Bulb formation in the onion (*Allium cepa* L.) and the effect of storage temperature on bulb rest. *Hilgardia* 35: 85-112.
- Austin, R.B. 1972. Bulb formation in onions as affected by photoperiod and spectral quality of light. *Journal of Horticultural Science* 47: 493-504.
- Brewster, J.L. 1977. The physiology of the onion. I. *Horticultural Abstracts* 47: 17-23.
- Brewster, J.L. 1982. Growth, dry matter partition and radiation interception in an overwintered bulb onion (*Allium cepa* L.) crop. *Annals of Botany* 49: 609-617.
- Brewster, J.L. Mondal, M.F., and Morris, G.E.L. 1986. Bulb development in onion (*Allium cepa* L.) IV. Influence on yield of radiation interception, its efficiency of conversion, the duration of growth and dry-matter partitioning. *Annals of Botany* 58: 221-233.
- Darbyshire, B., Henry, R.J., Melhuish, F.M. and Hewett, R.K. 1979. Diurnal variations in non-structural carbohydrates, leaf extension, and leaf cavity carbon dioxide concentrations in *Allium cepa* L.. *Journal of Experimental Botany* 30: 109-118.
- de Ruiter, J.M. 1986. The effects of temperature and photoperiod on onion growth development. *Proceedings of the Agronomy Society of New Zealand* 16:.
- Denne, M.P. 1960. Leaf development in *Narcissus pseudonarcissus* L. II The comparative development of scale and foliage leaves. *Annals of Botany* 24: 32-47.
- Garner, W.W. and Allard, H.A. 1920. Effect of the relative length of the day and night and other factors of the environment on growth and reproduction in plants. *Journal of Agricultural Research* 18: 553-606.
- Kedar, N., Levy, D. and Goldschmidt, E.E. 1975. Photoperiodic regulation of bulbing and maturation of Bet Alpha onions (*Allium cepa* L.) under decreasing daylength conditions. *Journal of Horticultural Science* 50: 373-380.
- Lercari, B. 1982a. The promoting effect of far-red light on bulb formation in the long day plant *Allium cepa* L. *Plant Science Letters* 27: 243-254.
- Lercari, B. 1982b. The effect of far-red light on the photoperiodic regulation of carbohydrate

- accumulation in *Allium cepa* L. *Physiologia Plantarum* 54: 475-479.
- Lercari, B. 1983. Action spectrum for the photoperiodic induction of bulb formation in *Allium cepa* L. *Photochemistry and Photobiology* 38: 219-222.
- Magruder, R. and Allard, H.A. 1937. Bulb formation in some American and European varieties of onions as affected by length of day. *Journal of Agricultural Research* 54: 719-752.
- Mann, J.D. 1983. Translocation of photosynthate in bulbing onions. *Australian Journal of Plant Physiology* 10: 515-521.
- Mondal, M.F., Brewster, J.L., Morris, G.E.L. and Butler, H.A. 1986a. Bulb development in onion (*Allium cepa* L.) I. Effects of plant density and sowing date in field conditions. *Annals of Botany* 58: 187-195.
- Mondal, M.F., Brewster, J.L., Morris, G.E.L. and Butler, H.A. 1986b. Bulb development in onion (*Allium cepa* L.) II. The influence of red:far-red spectral ratio and of photon flux density. *Annals of Botany* 58: 197-206.
- Mondal, M.F., Brewster, J.L., Morris, G.E.L. and Butler, H.A. 1986c. Bulb development in onion (*Allium cepa* L.) III. Effects of size of adjacent plants, shading by neutral and leaf filters, irrigation and nitrogen regime and the relationship between the red:far-red spectral ratio in the canopy and leaf area index. *Annals of Botany* 58: 207-219.
- Rabinowitch, H.D. 1985. Onions and other edible *Alliums*. p. 398-405 in A. H. Halevy [ed], CRC Handbook of flowering, Vol. I. 568p.
- Salisbury, F.B. 1982. Photoperiodism. *Horticultural Reviews* 4: 66-105.
- Sobeih, W.Y. and Wright, C.J. 1986. The photoperiodic regulation of bulbing in onions (*Allium cepa* L.). II. Effects of plant age and size. *Journal of Horticultural Science* 61: 337-341.
- Willis, J.C. 1966. A dictionary of the flowering plants and ferns. 7th edition. Cambridge University Press, Cambridge.
- Wright, C.J. and Sobeih, W.Y. 1986. The photoperiodic regulation of bulbing in onions (*Allium cepa* L.). I. Effects of irradiance. *Journal of Horticultural Science* 61: 331-335.