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Onions and Garlic

17

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Both onions and garlic are grown mainly for their bulbs, although the green shoots of salad onions are also an important crop. The onion bulb consists of the swollen bases (sheaths) of bladed leaves surrounding swollen bladeless leaves. The garlic bulb consists of numerous cloves, consisting largely of swollen, bladeless storage leaves. Cloves form in the axils of the leaf blades, the sheaths of which remain as the dry papery tunics which enclose the cloves in the mature bulb (Brewster, 1994). Onions are usually grown from seed, and flowering and seed production are important for crop production. Garlic is vegetatively propagated by planting cloves and, although bolting sometimes occurs, seeds do not form. The crop production cycle in onions is quite complex, involving vegetative growth, bulb formation, bulb dormancy and sprouting, flowering and seed production (Fig. 17.1). Garlic production involves a subset of these phases which excludes those concerned with seeds (Fig. 17.1). Switches from one phase of development to another, and rates of development and growth within each stage, are controlled by environmental conditions. This review is concerned primarily with these aspects of environmental physiology, since they are fundamental to crop production. Probably because it is a convenient experimental subject, onion has been used to study many other aspects of plant physiology, notably ion uptake by roots (Clarkson and Hanson, 1986) and the cell division cycle (Gonzales-Fernandez *et al.*, 1968). Stomatal physiology is also interesting and unusual (Schnabl and Raschke, 1980). These aspects of physiology are not considered here.

GERMINATION AND EMERGENCE

The storage potential of the seeds varies with seedlot, but tends to be lower than for other crops (Ellis and Roberts, 1977). Compared to other crops, and

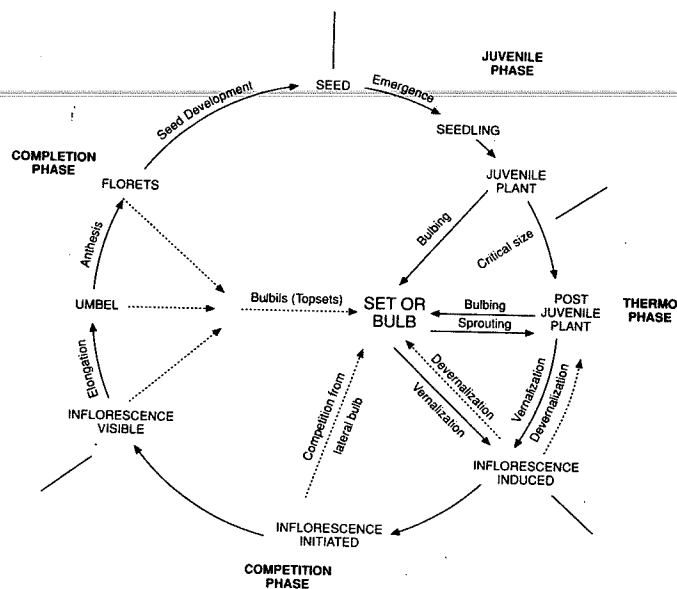


Fig. 17.1. The life cycle of onions: unusual or reversionary development is shown by dotted lines.

relative to their short average longevity, onions have very variable seed longevity with seed death widely distributed over time. The higher the moisture content and the warmer the temperature of storage the more rapidly the seed deteriorates. Constants quantifying these effects of moisture and temperature are similar to those for other crops, but because onion seed is innately short lived the accelerated deterioration at high moisture content and temperature is more practically significant (Ellis and Roberts, 1977; see also Chapter 1). An equation by Ellis and Roberts (1980) predicts percentage viability after a given period of storage at known temperature and moisture content from the initial viability of the seedlot.

The rate of germination can be quantified as the reciprocal of the time for a certain percentage of the final total (usually 50%) to germinate. Over the temperature range 5–25°C this rate increases linearly with temperature (Fig. 17.2a). The intercept of this relation with the temperature axis at zero rate is the base temperature (T_{min}), and the reciprocal of the slope is the heat sum (S) (day-degrees) above T_{min} required for 50% germination. The value of S increases as seed deteriorates and loses viability (Dearman *et al.*, 1986; Ellis and Butcher, 1988). Base temperatures for onion germination ranging

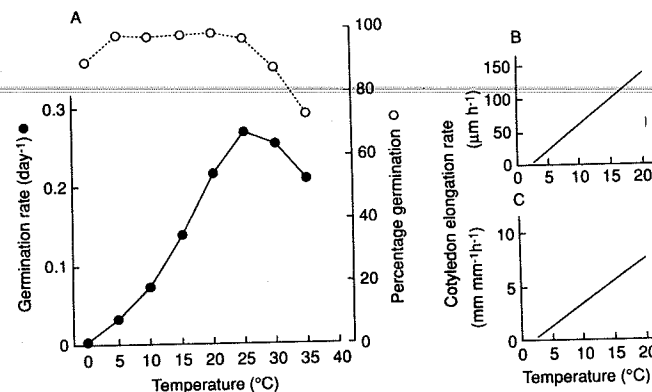


Fig. 17.2. (a) The relationship between temperature and the rate and percentage of germination of onion seeds on moist paper. Rates are reciprocals of the number of days for 50% of viable seeds to germinate (data of Harrington, 1962). (b) The relationship between temperature and the rate of cotyledon elongation before hook formation for newly germinated onion seedlings cv. White Lisbon (Wheeler and Ellis, 1991). (c) The relationship between temperature and the relative rate of cotyledon elongation after hook formation for the same seedlings as in (b).

from 1.4 to 3.5°C have been derived. The base temperature was the same for seedlots differing in viability (Ellis and Butcher, 1988). Deteriorating seed quality reduces viability, lowers the mean rate of germination but does not change the base temperature.

Bierhuizen and Wagenvoort (1974) showed that a similar relationship predicted the emergence of onion seedlings from seed sown in moist soil. More than 70% of seeds emerged between 13 and 28°C, the minimum temperature for good emergence being higher than for most temperate vegetables. Their equation was:

$$\text{Time (d) to 50\% emergence} = S / (T - T_{min}) \quad (1)$$

where S (in day-degrees) was 219 and T_{min} (°C) was 1.4. Equation 1 applied over the temperature range 3–17°C. The base temperature was similar to that of many other temperate zone vegetables, but the heat sum (S), ranked fourth out of a list of 31 common vegetable species. Only celery, parsley and leek had higher values of S , and the former two species are notoriously slow to emerge due to the presence of inhibitors in the seed coat. The implication of a high value of S is that emergence will be slow; for example, the results indicate that onions take 2.25 times as long as turnips to reach an equivalent stage of emergence after sowing.

Further studies showed that this relationship also applied to fluctuating

as well as constant temperatures within the range 3–21°C (Wagenvoort and Bierhuizen, 1977). This model can therefore be used to predict time to emergence from moist soil in cool conditions (mean temperature less than about 20°C), such as typically occur from spring sowings at high latitudes (Finch-Savage, 1987; Wheeler and Ellis, 1992).

Emergence involves two processes, germination and then elongation of the radicle and cotyledon until the seedling is visible above soil. The rate of elongation before the formation of the cotyledon hook is linearly related to temperature above a base temperature of 1.4°C and below 20°C (Fig. 17.2b). After hook formation elongation is exponential and the relative rate of elongation shows a similar linear response to temperature until seed reserves are depleted (Fig. 17.2c) (Wheeler and Ellis, 1991). Differences in seed quality, as indicated by differences in percentage germination and mean rate of germination between seedlots, and by time-to-germination percentiles within seedlots, caused no differences in the elongation rates of normal seedlings. Furthermore, priming the seed, although it accelerated germination, did not change the subsequent elongation rate. It follows that differences in time to emergence from moist soil due to differences in seed quality or seed treatment are caused solely by differences in time to germination (Wheeler and Ellis, 1991).

The rate of emergence of seedlings is determined by temperature so long as soil moisture content is above some critical level (Wheeler and Ellis, 1992). Emergence from drier seedbeds cannot be predicted simply by thermal time but is influenced by rainfall or irrigation (Finch-Savage, 1986, 1987). Germination involves an initial rapid imbibition, a second phase when water content changes little and then an increase in water when the radicle bursts the seedcoat and grows. Germination processes before, and elongation after, radicle appearance can proceed at lower soil water potentials than those needed for the radicle to burst forth. This, then, is the most moisture sensitive step in germination that determines the lower limit of soil water potential needed for overall germination and emergence. Emergence from dry soils can be predicted by assuming that radicles burst the seed coat only if soil water potential is above -1.1 MPa (Finch-Savage and Phelps, 1993). If the soil is drier than this, germination is delayed until rainfall or irrigation raises soil water potential above this base level. If irrigation is limited, it is best applied when a thermal time of 50–130°Cd above a base of 1.4°C has elapsed since sowing, as seeds will then have reached the most water sensitive stage just before radicles burst out (Finch-Savage, 1990).

Decreases in both the percentage emergence and the rate of emergence occur as soil water potential decreases due to added nitrate fertilizer (Hegarty, 1976) (Fig. 17.3), and reductions in plant population and plant size early in the season occur at high rates of N (Greenwood *et al.*, 1992). Germination is much less sensitive than growth to increases in solute concentration, and salt damage to pre-emergence growth is probably the cause of reduced emergence (Wannamaker and Pike, 1987).

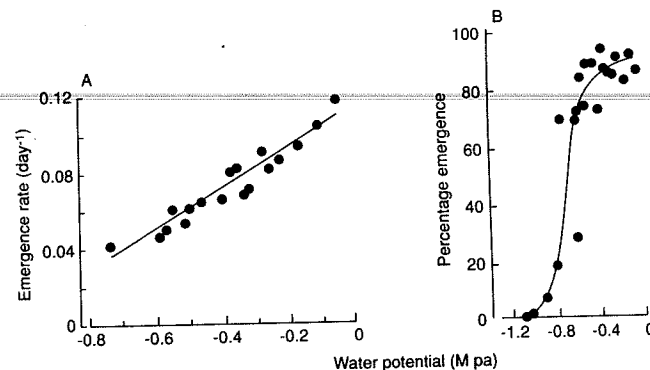


Fig. 17.3. The effect of soil water potential on the rate (a) and the percentage (b) of emergence of onion seeds incubated at 15°C. The rate was measured as the reciprocal of the time in days for 50% of the viable seedlings to emerge (redrawn from Hegarty, 1976).

The percentage emergence and the rate of seedling emergence can be affected by seed quality, seed treatments (e.g. priming), soil temperature, soil water potential and sowing depth. Seed quality and priming have been shown to affect germination rates rather than subsequent growth rates either before (Wheeler and Ellis, 1991) or after emergence (Ellis, 1989). Except in unusual circumstances, small advancements in emergence do not increase the marketable yield of bulbs, at most they result in a slight advancement of maturity (Brewster *et al.*, 1992) provided that plant populations are unaffected. However, yield and grade at harvest are highly sensitive to population (Frappell, 1973). Therefore, the most important effects of seed and seedbed are via their influence on the population established. Anything which promotes a stand of uniformly spaced seedlings emerging near synchronously is likely to facilitate subsequent husbandry. Some of the benefits of good emergence will be indirect and by nature sporadic in occurrence. For example, rapid emergence reduces the risk of population loss by entrapment of seedlings under a surface crust or cap which occurs as some soils dry after heavy rain. Rapid emergence maximizes the growing time during which pre-emergence herbicides remain effective, resulting in larger, more resilient seedlings by the time post emergence herbicides need to be applied.

GROWTH RATES

As with germination and emergence, the growth rate of seedling alliums after emergence is slow compared with most crop species. However, many

non-crop species are slower growing, particularly woody species and those adapted to non-productive environments (Brewster, 1979). The relative growth rate (RGR) of onion growing in near-optimal temperatures during the exponential, seedling phase of growth is only about half that of spring cabbage or lettuce. This means that, starting at the same weight and growing under the same conditions, onion will take nearly twice as long as spring cabbage or lettuce to reach a given weight.

Growth rates are strongly dependent on temperature. Figure 17.4 shows the relationships between RGR, relative leaf growth rate (RLGR) and leaf initiation rates and temperature. RGR and RLGR increase linearly over the range 6–20°C, whereas leaf initiation rates have a lower base temperature. This accords with field studies in which log seedling dry weight was a linear function of accumulated day degrees above 6°C whereas leaves initiated increased linearly with day-degrees above 2°C (Brewster *et al.*, 1977). A better model for growth in seedling shoot dry weight (W) in grams, which includes the effects of daily income of photosynthetically active radiation (PAR), as well as mean temperature (t), again in terms of accumulated day degrees above a base temperature (t_b) is from Scaife *et al.* (1987):

$$\log_e W = \log_e W_0 + \Sigma p / ((1/(t - t_b)) + f/R) \quad (2)$$

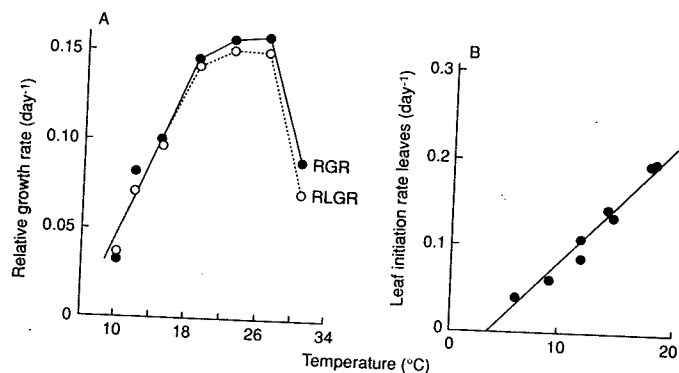


Fig. 17.4. (a) The effect of temperature on the relative growth rate of whole plant dry weight (solid symbols) and of leaf area (open symbols) of onion cv. Hygro (data of Brewster, 1979). relative growth rate (RGR) is the rate of increase in dry weight per unit of existing dry weight. $RGR = 1/W \cdot dW/dt$, where W = dry weight and t = time. Similarly, the relative growth rate of leaf area is the rate of increase of leaf area per unit of existing leaf area. (b) The effect of temperature on the rate of initiation of leaves by the main shoot apex (i.e. not counting leaves on side shoots) of cvs Hygro, Hyton and Rijnsburger, all 'Rijnsburger types', growing in controlled environments (unpublished data).

The summated term is accumulated using daily values of t and PAR (R) from emergence onwards. For onions t_b was found to be 5.9°C. The parameters p and f had values of 0.0160 and 0.136, respectively (Brewster and Sutherland, 1993). R is in units of $\text{MJ m}^{-2} \text{day}^{-1}$. An appropriate value for $\log_e W_0$, the log of the shoot dry weight (g) at emergence is -6.086 . The value of f was larger than for other species indicating greater sensitivity to light income probably because the leaves are narrow and erect. The difficulty of growing onions satisfactorily in conditions of low light is a familiar problem to experimenters who have to raise them in glasshouses during the winter.

Relative leaf growth rate and stomatal conductance decrease as leaf water potential and the associated turgor pressure decline (Millar *et al.*, 1971), the growth rates being affected first (Fig. 17.5). These authors measured a maximum turgor pressure of 0.4 MPa in onion leaves, less than half the value found in some other crop species. Moreover, increases in the osmotic pressure of the leaf sap can only compensate for about half such an increase at the roots when exposed to saline solutions. In contrast, leaf sap concentrations of bean and cotton plants fully compensate for such changes in the root medium (Gale *et al.*, 1967). These findings are reinforced by studies of overall growth which show that onions are more severely affected by salinity than most crops. Growth was reduced by 50% by sodium chloride solutions of 0.125 MPa osmotic pressure, whereas for cabbage, lettuce and beans an equivalent growth reduction required an osmotic pressure of 0.4 MPa (Bernstein and Hayward, 1958). Yield reductions due to salinity are more severe in hot dry climates than in more humid conditions (Magistad *et al.*, 1943).

The root system of onions is rather shallow, sparse and lacking root hairs (Greenwood *et al.*, 1982; Bhat and Nye, 1974). Consequently, water extraction is confined mainly to the top 25 cm of soil (Goltz *et al.*, 1971). They require higher levels of soil P and K for maximum yields than most crops (Greenwood *et al.*, 1980a,b), and their recovery of N fertilizer is poor (Greenwood *et al.*, 1992). These factors, coupled with the fact that, as with most vegetable crops, the nutrient requirement per unit root length is at its peak just after seedling emergence (Brewster *et al.*, 1975) have prompted experimentation with starter fertilizer solutions placed just below the seed at sowing. Even in fertile soils such ammonium phosphate 'starter' solutions accelerate early growth (Brewster *et al.*, 1992) and dramatically increase the efficiency with which N fertilizer is recovered in the crop (Stone and Rowse, 1992). Both morphological and physiological traits make onions more sensitive to water and nutrient deficiencies than the majority of crops, but on the other hand, they can survive long periods of water stress, making no growth, but ultimately recovering when water becomes available (Levy *et al.*, 1981). In these and other traits, like the inherently low relative growth rates, they exhibit features typical of species with a stress tolerant ecological strategy (Grime, 1979).

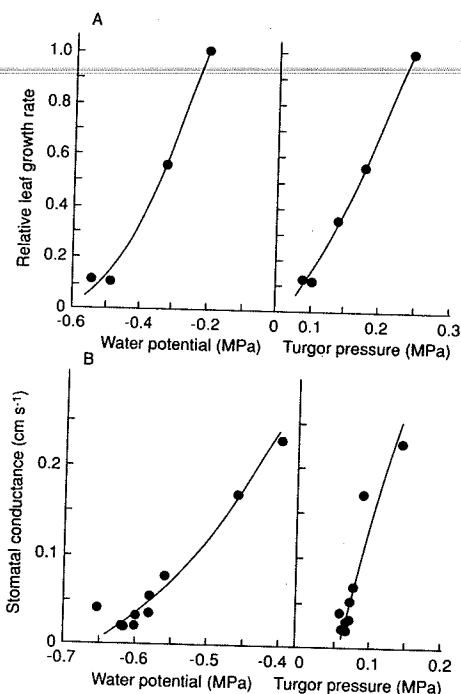


Fig. 17.5. (a) Relative growth rate of onion leaf length at 25°C as a function of leaf water potential and of turgor pressure (redrawn from Fig. 17.9 of Millar *et al.*, 1971). (b) Stomatal conductance of onion leaves at 25°C as a function of leaf water potential and of turgor pressure (redrawn from Fig. 17.7 of above source).

BULBING

ESTIMATION OF BULB INITIATION

A feature that unequivocally indicates that bulbing has started is the development of leaf initials into bladeless 'bulb scales'. This can be diagnosed as the first occurrence of a 'leaf ratio' (leaf blade length : sheath length) of less than unity (Heath and Hollies, 1965) (Fig. 17.6). Where many plants are available for sampling, scale initiation can be quite quickly estimated from examining plants sliced longitudinally upwards through the centre of the

sheath. Mean dates of bulb initiation can be estimated from a series of such samples (Visser, 1994a). Normally a leaf ratio below unity is coincident with marked swelling of the outer leaf sheaths and a consequent rapid increase in 'bulbing ratio' (maximum bulb diameter : minimum sheath diameter). This latter ratio has been more commonly used in bulbing studies, since it can easily be measured non-destructively, whereas the assessment of minimum leaf ratio involves the dissection of plants and is more laborious. However, the occurrence of the first leaf ratio less than unity is not invariably linked with the attainment of a particular bulbing ratio. Bulbing ratios greater than 2, commonly used to define bulb initiation, can occur in the absence of bulb scale development in N-deficient plants (Brewster and Butler, 1989a). In field-grown plants grown at densities of 25 and 400 m⁻², bulbing started on almost the same date when measured by bulbing ratio, whereas bulb scales were initiated about 2 weeks earlier in the plants at high density (Brewster, 1997). Conditions which favour carbohydrate accumulation within the plant can lead to thickening leaf sheaths and increased bulbing ratios without formation of bulb scales. In addition, leaf initials differentiate into bulb scales on lateral shoots before this occurs on the main shoot axis. As a result, in cultivars and conditions which produce many side shoots, a high bulbing ratio can occur long before the main axis stops producing green leaves (Wiles, 1994). Because of this variability in the linkage between increases in bulbing ratio and decreases in leaf ratio on the main shoot, and because a decrease in leaf ratio is the first indication of the initiation of the storage scales which ultimately results in the cessation of leaf blade growth and the ripening of bulbs, a decrease in minimum leaf ratio below unity on the main shoot axis is the preferable method of defining

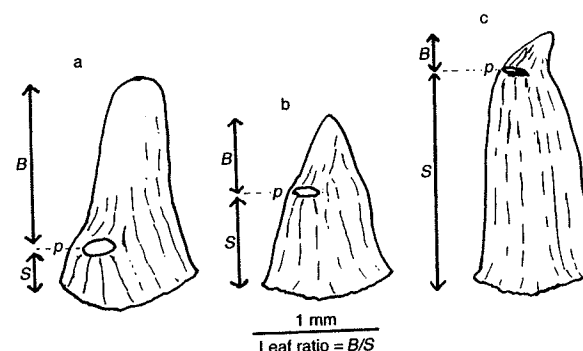


Fig. 17.6. The appearance of developing leaf initials during leaf growth (a), early stage bulbing (b) and established bulbing (c). *p* is the pore through which the blade of the next leaf emerges from its encasing sheath during leaf growth. Bulbing is characterized by a decrease in the ratio of blade length (*B*) to sheath length (*S*) termed the 'leaf ratio'. Initials with *B/S* below unity are termed 'bulb scales' (Heath and Hollies, 1965).

bulb initiation. Since leaf initiation rates are temperature-dependent (see Fig. 17.4b), it is possible to use thermal time to estimate leaf initiation date from leaf number, and hence estimate the date of initiation of the first bulb scale from a sample taken after the event (Brewster, 1996).

ENVIRONMENTAL CONTROL OF BULBING

Garner and Allard (1920) first showed that onions develop bulbs in response to long photoperiods, and later it was shown that onion varieties grown at different latitudes could be distinguished by the minimum daylength needed to induce them to bulb. Further research showed that, in a given daylength, bulbing was faster the higher the temperature (Thompson and Smith, 1938). These effects of photoperiod and temperature have since been confirmed by many studies (Brewster, 1990a). There is evidence that very warm temperatures (38–49°C) slow down bulbing compared to 27–30°C (Abdalla, 1967).

Onion leaves must be exposed continuously to bulb inductive photoperiods in order to start and complete bulbing. Several authors have shown that bulbing can be reversed and green leaves will resume growth if plants are transferred to short, non-inductive photoperiods (e.g. Kedar *et al.*, 1975). This can occur even in plants at an advanced stage of bulb development (Fig. 17.7).

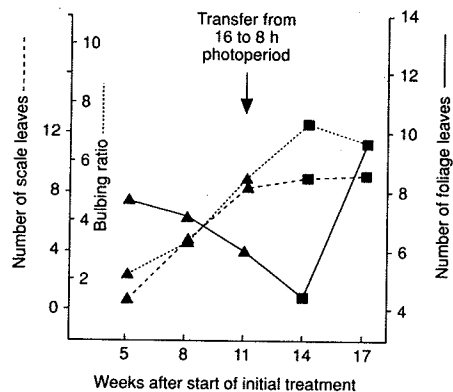


Fig. 17.7. The reversal of bulbing in onion cv. Rocket at an advanced stage of bulbing, following transfer from 16 to 8 h photoperiods at $135 \text{ E m}^{-2} \text{ s}^{-1}$ PAR. Note the resumption of foliage leaf production even though many bulb scales had formed (redrawn from Sobeih and Wright, 1986).

The rate of bulbing in a particular photoperiod depends strongly on the red : far-red (R : FR) ratio of the light, and a non-inductive photoperiod at high R : FR can be inductive at lower R : FR (Austin, 1972; Mondal *et al.*, 1986b). Because leaves absorb red wavelengths much more than far-red, R : FR decreases under a leaf canopy. As a consequence, the rate of onion bulbing increases as leaf area index (LAI) increases (Mondal *et al.*, 1986c). The action spectrum for 3 h continuous irradiation in the middle of a bulb inductive (18 h) light period has a maximum at 714 nm (Lercari, 1983). In these experiments the bulbing response was fluence-rate dependent and nullified by simultaneous irradiation with red light, features typical of a 'high irradiance' phytochrome response. Some rhythmicity in the response of onion bulbing to R : FR is indicated by the promotive effect of FR exposure being greatest when applied during the middle of a long photoperiod, and the optimum R : FR changing at different times in the inductive photoperiod (Lercari, 1982).

Exposure of onion seedlings that had just emerged from soil to 8 days at 24 h photoperiods followed by 10 days at 8 h photoperiods, resulted in small bulbs in which bulb scales had formed (Terabun, 1971). On these plants the cotyledon and the first true foliage leaf developed. The latter is already initiated within the embryo and differentiates during germination (Hoffman, 1933), so its development is unlikely to be affected by photoperiod. Terabun (1971) also exposed single leaves of four-leaved plants to 24 h photoperiods for 14 days having removed the other leaves. Bulbing was similar whichever leaf remained for photoperiodic treatment. These experiments show no evidence for juvenility and prove that even emerging seedlings can be induced to bulb by a strong long day stimulus. However, Sobeih and Wright (1986) observed that rate of bulbing upon transfer from 8 to 16 h photoperiods increased as plants grew older. Also, in defoliation experiments, they found that 4.5-month-old plants defoliated to the two youngest leaves bulbed more rapidly than younger plants of greater leaf area at the start of long day treatment. Therefore, there is no evidence for an absolute juvenile phase in which bulbing cannot occur given a strong photoperiodic induction, but sensitivity to long days may increase with age.

Onions grown from bulbs or sets will bulb and ripen more quickly than onions grown from seed, unless the sets are 'heat treated' by storage at about 30°C for several months before planting (Aura, 1963). This indicates that the photoperiodic induction required for plants grown from sets is less than for seedlings. Some bulbing stimulus seems to be stored in the set which can be destroyed by prolonged warm storage (Heath and Holdsworth, 1948).

PHOTOTHERMAL RESPONSE MODELS FOR RATE OF BULBING

The bulbing response to temperature and photoperiod can be quantified (Brewster, 1997):

$$1/\text{time to bulb} = \text{rate of bulbing} = C + A \cdot \text{photoperiod} + B \cdot \text{temperature} \quad (3)$$

Here, A , B and C are constants. Equations like this describe the flowering responses of a number of both long- and short-day crop species (Summerfield *et al.*, 1991). An implication of this equation is that photoperiodic induction is a quantitative process, during which the bulbing stimulus may accumulate gradually, rather than a sudden switching to the induced from the non-induced state by brief exposure to inductive conditions. The rate of bulbing was defined as the reciprocal of the interval from the start of inductive photoperiods until the formation of the first leaf scale. The values of the constants of equation 3 (A , B and C), were, respectively, 0.0043, 0.0027 and -0.079 for cv. Keepwell, which is autumn-sown in England, and 0.0032, 0.0018 and -0.066 for cv. Hyton, which is spring-sown (Fig. 17.8). These give the time in days from transfer to inductive photoperiods until bulb initiation, as defined above, when the photoperiod is in hours and the temperature in $^{\circ}\text{C}$. The equations show that there is not a sudden transition from non-inductive to inductive as daylengths increase, rather an increasing rate of induction as daylengths exceed a certain minimum. This minimum, and the rate of increase with photoperiod depends on cultivar. The response surfaces and the corresponding equations characterize cultivars Keepwell and Hyton better than the terms like 'intermediate' and 'long' day type, or '14 h' or '16 h' type. Both these cultivars can bulb in 14 h photoperiods, but at different rates and also at a rate which varies with temperature.

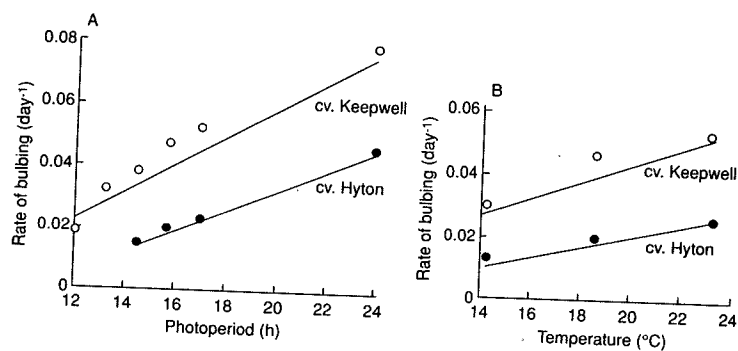


Fig. 17.8. (a) The effect of photoperiod on the rate of bulbing of two onion cvs growing at a mean temperature of 18.6°C . The rate of bulbing was derived as the reciprocal of the time in days for 50% of the plants to initiate bulb scales (Brewster, in preparation). (b) The effect of temperature on the rate of bulbing under a constant photoperiod of 15.75 h. The lines are from equation 3 and the points are some of the experimental data used in deriving equation 3 (Brewster, in preparation).

Since bulbing has been shown to require continued inductive photoperiods to complete, it seems reasonable to make the assumption that rate of bulbing depends on current photoperiods and temperatures alone. If this is the case, development in changing photoperiods and temperatures can be modelled as a sum of rates of development at a given temperature and photoperiod multiplied by the duration of time during which these conditions prevail (McNaughton *et al.*, 1985). By substituting daily values of photoperiod and mean temperature into equations 2 and 3 daily rates of bulbing were calculated. Negative values of rate were assumed to be zero, and progress towards bulbing was calculated as the cumulative sum of the positive values of daily rates. The date when this cumulative sum exceeded unity was the predicted date of first bulb scale initiation. Using weather data for 1983 from Wellesbourne, bulb initiation of Keepwell was predicted on 2 June and Hyton on 9 July. Field-grown, widely spaced (25 plants m^{-2}) plants of Keepwell and Robusta, a cultivar closely similar to Hyton in maturity date (NIAB, 1982), reached 50% bulb scale initiation on 7 June and 19 July, respectively, in fair agreement with predictions.

AGRONOMIC IMPLICATIONS

Equation 3 and Fig. 17.8 show that bulbing is definitely not an 'all or nothing' inductive response with sharp switching close to one photoperiod. So long as photoperiod remains longer than some minimum, then bulbing will continue, albeit slowly, when close to the minimum photoperiod. In such conditions there is much time for leaf growth before bulb initiation. This may be why in some low latitude areas with little seasonal fluctuation in photoperiod or temperature, suitably adapted cultivars can produce large bulb yields at any time of year (Jones and Mann, 1963). In many regions bulbing continues in declining photoperiods and temperatures, e.g. with spring-sown crops in northern Europe or summer-planted crops in Israel (Kedar *et al.*, 1975). Again, so long as the photothermal conditions exceed some threshold, bulbing will proceed albeit at a diminishing rate as this threshold is approached.

The increase in rate of bulbing under a given photoperiod as $R : FR$ decreases, and the decrease in $R : FR$ within the onion leaf canopy as LAI increases, permits the modulation of the basic photothermal response of a cultivar by the many factors which influence leaf growth. In the situation just considered, of bulbing in decreasing photoperiod, a crop with a high LAI can continue to differentiate bladeless bulb scales, resulting in hollow pseudostems which ultimately soften and collapse to give ripe bulbs. Whereas, at a lower LAI, the same cultivar may revert to differentiating leaf blades which fill the pseudostem and prevent the softening and collapse associated with normal ripening (see Fig. 17.7). Large differences in the date of bulb initiation in crops of the same cultivar at different LAI will be reflected by parallel differences in maturity date (foliar fall-down) (Fig.

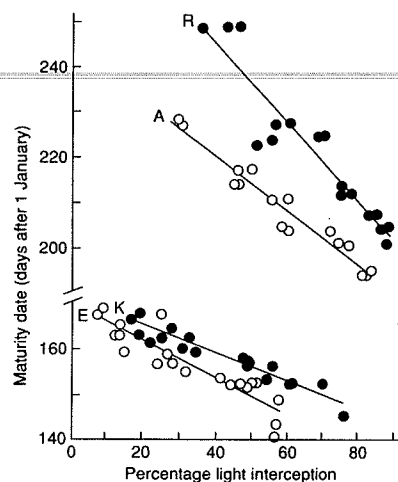


Fig. 17.9. Relationships between mean percentage light interception by the crop leaf canopy during bulbing and the maturity (80% foliage fall-down) day of the year for early maturing and late maturing spring-sown onion cvs (upper two graphs) and autumn-sown cvs (lower two graphs) at Wellesbourne. Cultivars are Robusta (R), Augusta (A), Keepwell (K), and Express Yellow OX (E) (Mondal *et al.*, 1986a).

17.9). Among the agronomic factors which determine LAI are:

1. Those that affect plant population, like seed rate, seedbed soil conditions, salinity in the seedbed, herbicide damage, temperature, and diseases and pests during germination and emergence.
2. Conditions affecting leaf growth rate, e.g. temperature, water stress, nutrient availability, salinity, and root damage by pests or disease.
3. Factors directly damaging the leaves like pests, disease, hail, herbicides or damage during cultivations.

Therefore, virtually every agronomic operation can ultimately influence bulbing rate and maturity date via its influence on LAI. This effect is most prominent in conditions where bulbing would otherwise be slow, e.g. in the declining photoperiods described above. When bulbing occurs in increasing photoperiods and temperatures, as normally occurs with autumn-sown crops, the influence of LAI is less important, since the climatic factors are then accelerating the rate of bulbing (Mondal *et al.*, 1986a, c). In conditions where the LAI effect is important, early and uniform bulbing is promoted by cultural practices which ensure the establishment of a uniform plant population which then grows as rapidly as the climate allows, and is therefore not afflicted by stress, damage or disease. The uniform bulbing and

maturity of such a crop ensures that all bulbs can be harvested at the optimum stage for quality and long storage. So, in addition to the innate qualities bred into an onion cultivar, the growing conditions the farmer creates can profoundly influence bulbing and the quality of the bulbs harvested.

FACTORS INFLUENCING BULB YIELDS

In a study comparing well-irrigated autumn- and spring-sown bulb onion crops, yields varied by a factor of more than five depending on cultivar, sowing date and plant density (Mondal, 1985). These large differences in yield can be explained mainly by differences in the percentage light interception by the leaf canopy during bulbing I% (Fig. 17.10). Light interception increases with LAI according to equation 4 (Mondal *et al.*, 1986c):

$$I\% = 85.4 (1 - \exp(-0.377 \cdot \text{LAI})) \quad (4)$$

Several cultural practices can influence the LAI attained by bulbing time. Late maturing cultivars have longer than early types to develop a high LAI before the switch to bulb growth (Brewster, 1982c). Late-sown plants often switch from leaf blade to bulb production when LAI is lower than for earlier sowings. LAI increases with plant density, but although yields increase, individual bulb size is reduced, and this is not normally acceptable. To achieve a high yield of medium to large bulbs, a cultivar must be capable of producing sufficient leaf area to intercept a high proportion

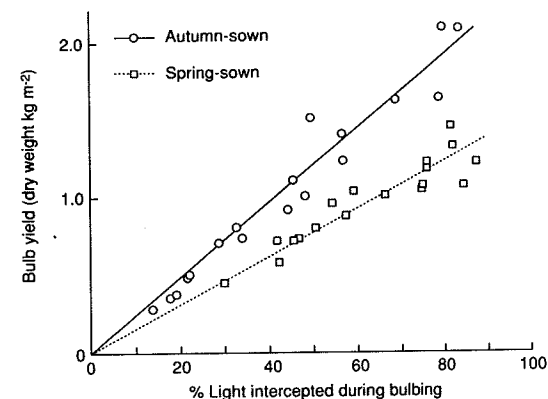


Fig. 17.10. The relationship between bulb dry-matter yields and percentage radiation interception by the leaf canopies during bulbing of irrigated, well-fertilized small plots of onions at Wellesbourne (data from Mondal, 1985).

(> 60%) of the incident light when grown at 50–100 plants m^{-2} . This requires sufficient time in conditions conducive to leaf blade growth before bulbing starts.

Although dominant, percentage light interception is not the only factor involved. In Fig. 17.10 autumn-sown onions produced a higher yield than spring-sown at a given percentage interception. For crops with 60% light interception the duration of bulbing was 55 days when autumn-sown and 43 days when spring-sown, consequently the former intercepted more light in total during bulbing. Longer duration of bulbing may be caused by cooler temperatures giving slower bulb ripening and leaf senescence. Mean temperatures during bulbing were 13°C for the autumn-sown crops and 17.5°C for the spring-sown.

Well-irrigated onion crops produce, during bulbing, an average of about 1.6 g of shoot dry matter per MJ of solar radiation intercepted by the leaf canopy (Brewster *et al.*, 1986). Similar conversion efficiencies have been reported for potatoes, sugarbeet and in cereals before anthesis. However, values of mean conversion efficiency vary, and range from 1.2 g MJ^{-1} in conditions of high irradiance and high temperature to 2.0 g MJ^{-1} in lower irradiance, lower temperature conditions. As might be expected, lack of irrigation in dry weather decreases conversion efficiency.

Bulb onions have a high 'harvest index' (the proportion of total yield in harvested material). At the optimum time for harvesting, when 80% of plants have 'soft necks', about 80% of the shoot weight is in the bulb. Bulb weight and the percentage of total weight in the bulbs continues to increase after this stage (Brewster *et al.*, 1977).

BULB DORMANCY AND SPROUTING

Upon ripening the onion bulb enters a phase of true dormancy during which growth ceases. As bulbs approach maturity new leaves and roots cease to be initiated, and after harvest and curing a dramatic decrease in mitosis at the shoot apex has been observed (Abdalla and Mann, 1963). From then on there is a gradual loss of dormancy as shown by slow increases in respiration rate (Ward and Tucker, 1976; Tanaka *et al.*, 1985), increases in the weight of the growing sprout within the bulb (Brewster, 1987a), and progressively decreasing times to produce roots and visibly sprout after planting on a moist substrate (Abdalla and Mann, 1963). Cultivars differ widely in their duration of dormancy. In a study comparing ten varieties stored at 10°C Miedema (1994a) found the time to 50% sprouting in dry storage ranged from 149 to 310 days, and times for 50% rooting and sprouting after planting on moist vermiculate were 8–63 days and 49–156 days, respectively. Within cultivars the time to visible sprouting of individual bulbs was spread over about 20 weeks in dry storage.

The onset of dormancy is thought to be caused by the translocation of growth inhibitory substances from the leaves to the bulbs as the crop

matures (Komochi, 1990). Stow (1976) found inhibitors in the leaves of onions approaching maturity and showed that defoliation at this stage shortened dormancy. Abscisic acid was identified but it accounted for only 10–20% of the growth inhibitory activity. During subsequent storage there is a progressive decline in inhibitor activity extractable from bulbs, followed by increases first in cytokinin activity and then by gibberellin and auxin activity (Isenberg *et al.*, 1974).

The time until sprouting is affected by the temperature of storage and the gas composition of the store atmosphere and is drastically foreshortened by moisture on the baseplate of the bulbs and by wounding bulbs. The response of sprouting rate to temperature is in remarkable contrast to that of other physiological processes (Fig. 17.11a). Rate of sprouting increases from a minimum around 0°C to a maximum in the range 10–20°C, depending on cultivar (Miedema, 1994a), but then decreases again as temperatures increase to 25–30°C (Abdalla and Mann, 1963; Miedema, 1994a). This response applies to dormant bulbs, but the rate of sprout growth in long-stored, non-dormant bulbs peaks around 25°C; typical of most growth processes. In addition, temperatures in the range 25–35°C applied for 1–3 weeks straight after harvest can reduce the time to sprouting, with 35°C giving up to 30% decrease in storage life (Miedema, 1994a). The response of sprouting to temperatures around 30°C therefore passes through three phases as the bulb ripens, becomes dormant and finally loses dormancy and begins to sprout. Only in the middle dormant phase, which can, however, last many weeks, are such temperatures suppressive of sprouting. A rise in endogenous cytokinins that preceded sprout growth in bulbs stored at 5 or 15°C was prevented by storage at 30°C (Miedema, 1994b). Furthermore, injection of bulbs with benzyladenine, but not with GA_3 or ethephon, accelerated the sprouting of such warm stored bulbs. It seems then that sprouting is initiated by increases in cytokinins and that production of these is suppressed by warm storage of dormant bulbs.

Further evidence for cytokinins initiating sprouting comes from studies on the effects of roots. If the baseplate of the bulb is maintained wet, root growth begins and sprouting occurs much sooner than in dry stored bulbs (Miedema, 1994a). The inclusion of mineral nutrients in the solution, which enhances root growth, can further accelerate sprouting. If roots are repeatedly removed as they develop, sprouting is delayed, but if benzyladenine (BA) is included in the solution then, in some cultivars, rapid sprouting still occurs (Miedema, 1994c). In these cultivars cytokinin appears to be the main factor limiting sprout growth and the root system probably supplies cytokinin to the bulb. Some cultivars only responded to cytokinin in this way if they were wounded by slicing away some corky baseplate tissue, so additional factors were limiting sprouting for these. Wounding can stimulate the production of growth substances and it may increase gas permeability.

Atmospheres containing elevated CO_2 and reduced O_2 prolong the storage life of onion bulbs. Smittle (1988) found 5% CO_2 and 3% O_2 prolonged

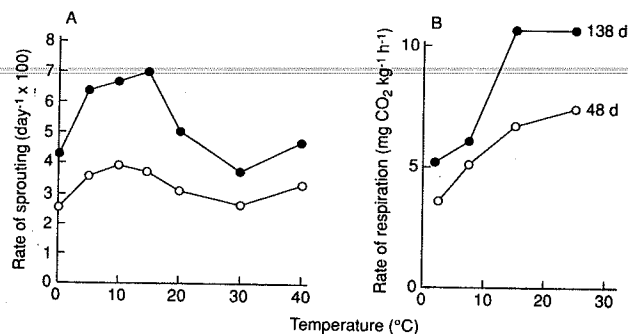


Fig 17.11. (a) Effects of temperature on the rate of sprouting after planting on moist peat at 15°C of two onion cultivars previously stored for 4 weeks at the temperatures shown. Solid symbols (top graph) the long-storing cv. Australian Brown, open symbols the short storing cv. Excel (data from Abdalla and Mann, 1963). Rates of sprouting were calculated as the reciprocals of the number of days for 50% of the bulbs to sprout. (b) Effects of temperature of storage on the respiration rate per kilogram of fresh weight of onion cv. Rijnsburger stored at different constant temperatures. Open symbols after 48-day storage, solid symbols after 138-day storage (data of Ward, 1976).

dormancy in cv. Granex. The internal atmosphere of bulbs shows similar increases in CO₂ : O₂ (Ladeinde and Hicks, 1988) and the intact onion skin and baseplate may act as a barrier to gas exchange. Removal of the dry outer skin increases respiration rate nearly twofold (Apeland, 1971) and accelerates sprouting (Tanaka *et al.*, 1985). Bulb wounding may accelerate sprouting by allowing increased respiration rates, especially since the acceleration of sprouting can be prevented by sealing the wound with paraffin wax (Boswell, 1924). Bulb respiration rates are low compared with other vegetables after harvest (Robinson *et al.*, 1975). Respiration increases with temperature but the Q_{10} of dormant bulbs is remarkably low at about 1.3 (Ward, 1976) rather than about 2 which is typical of most other vegetables (Fig. 17.11b).

Storage temperatures have a major influence on growth and development when bulbs or sets are subsequently planted out. Provided the bulbs are larger than the juvenile size, inflorescence initiation and development will proceed during bulb storage at a rate that depends on temperature (see below). There are numerous reports that storage of sets for periods of months at temperatures around 25–30°C, not only prevents or reverses inflorescence development, but increases the vigour of plants after sprouting and delays subsequent bulbing so that a bigger leaf area and higher bulb yield results compared to sets stored at lower temperatures (Heath *et al.*, 1947; Aura, 1963). Similar after effects of storage temperature on vigour of growth and date of bulbing occur with garlic (see below).

FLOWERING

RESPONSES TO TEMPERATURE AND PHOTOPERIOD

Onion seedlings have a sharply delineated juvenile phase for flowering which ends when they reach a certain critical shoot dry weight, or number of leaves initiated. This critical size can vary with cultivar, and an eight-fold larger critical size is the most striking difference between bolting-resistant cultivars suitable for autumn sowing and more bolting-susceptible varieties suitable only for spring sowing (Shishido and Saito, 1975; Brewster, 1985). In onion bulbs or sets, the critical size is not so sharply defined. The duration of cool treatment needed to induce flowering tends to decrease with size over a ten or 20-fold range of bulb weight (Shishido and Saito, 1977; Brewster, 1987b).

Once larger than the critical size, the plants need an extended period of cool temperatures to vernalize and induce flowers to initiate. Some Japanese spring-sown cultivars can be vernalized by as little as 20 days at 9°C, whereas autumn-sown types require a minimum of 30–40 days (Shishido and Saito, 1976). For Japanese and north European cultivars, rate of vernalization shows an inverted U-shaped response to temperature with an optimum around 9–12°C (Fig. 17.12a). West African cultivars can be vernalized satisfactorily under minimum night temperatures of 15–20°C (Rabinowitch, 1990a). So the temperature response for vernalization, as well as the critical size and the duration of vernalization treatment required, depend on cultivar, and tropical cultivars can be induced to flower in warmer conditions than temperate types.

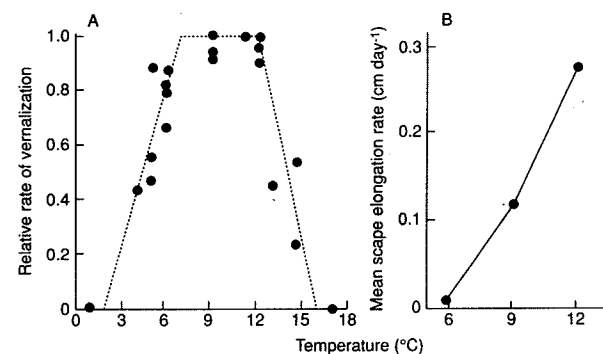


Fig. 17.12. (a) The effect of temperature on the relative rate of vernalization of European and Japanese onion cultivars (Brewster, 1987b). (b) The effect of temperature on the mean rate of elongation of onion scapes in a 16 h photoperiod following spathe formation. Data is meaned over cvs Senshyu semi-globe yellow and Rijnsburger growing with plentiful nitrate (Brewster, 1983).

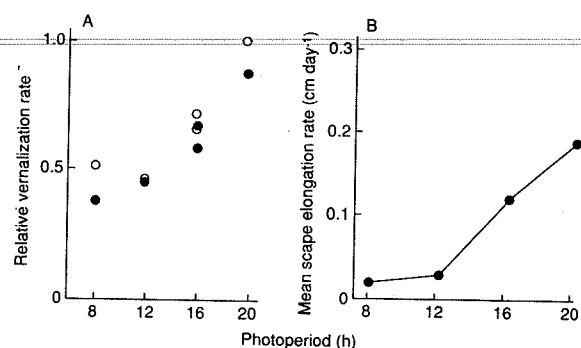


Fig. 17.13. (a) The effect of photoperiod on the rate of vernalization, measured as the reciprocal of the time for 50% of plants to initiate inflorescences for cv. Senshyu semi-globe yellow (open symbols) and cv. Rijnsburger (closed symbols) growing at 9°C. The results are scaled relative to the fastest rate found in the series of experiments (Brewster, 1987b). (b) The effect of photoperiod on the mean elongation rate of scapes following inflorescence initiation. The data are means of the same two cultivars as in (a) and are averages over plants growing in 6, 9 and 12°C (Brewster, 1983).

Long photoperiods shorten the duration required to vernalize growing plants (Fig. 17.13a), in some cases more than halving the time requirement. This photoperiod requirement can be lessened by N deficiency in the plants (Shishido and Saito, 1976; Brewster, 1983).

Temperatures of 28–31°C applied to bulbs previously induced by low temperatures can reverse inflorescence induction; this is termed 'devernalization'. The duration of 28–31°C storage needed to prevent flowering increases the more advanced the stage inflorescence initiation. This is illustrated by the results of Aura (1963) on Finnish cultivars. In accord with the results discussed above, he found that inflorescence initiation was more rapid in bulbs stored at 9–13°C than at 3–5°C and that it was more rapid in large bulbs than in small ones. Reflecting these differences, in a total storage period of 8 months a terminating duration of 5 months at 28°C was needed to suppress flowering in bulbs stored at 9–13°C but only 2 months in those stored at 3–5°C. Also the duration of 28°C treatment needed to suppress flowering in 15 g bulbs was less than needed for 108 g bulbs, since inflorescence development was more advanced in the larger bulbs.

After vernalization, the rate of development of inflorescences increases with photoperiod and with temperature in the range 6–12°C (Brewster, 1983). After spathe formation, the inflorescence begins to elongate at a rate which increases with temperature and with photoperiod (see Figs 17.12B and 17.13B), provided bulbs do not develop too rapidly (see below).

COMPLETION PHASE, FLOWER OPENING AND POLLINATION

Once a spathe is visible the plant enters the 'completion phase' of flowering (see Fig. 17.1) and higher temperatures become optimal. Experiments in glasshouses showed that inflorescence development from appearance to spathe opening required a mean of 310 day-degrees above 10°C base temperature (Brewster, 1982b). Scapes normally elongate to a length of 1–2 m. Individual bulbs may produce between 1 and 20 inflorescences depending on genotype, bulb size and environmental conditions; 3–6 inflorescences is common (Rabinowitch, 1990a). The spathe opens to produce a roughly spherical umbel containing between 50 and 2000 individual flowers, although 200–600 is the normal range. There is no very regular sequence of flower opening on an umbel. The most strongly insolated parts of the umbel tend to produce open florets first and there is a general tendency for upper florets on the umbel to precede the lower ones in opening. The pedicels of later-opening florets elongate to carry them clear of earlier-opening, maturing florets (Currah, 1990).

The sequence of individual flower development consists of petal opening (anthesis) coinciding with the start of nectar secretion, the dehiscence of the inner whorl of anthers, and then the outer whorl. Meanwhile the style elongates from 1–2 to 5–6 mm and develops a sticky stigma knob after the anthers have dehisced. Then nectar secretion ceases and petals, stamens and style start to wither (Currah and Ockenden, 1978). The whole process takes 10 days at 18°C and 5 days at 30°C (Currah, 1986). Air relative humidity below 70% accelerates pollen shedding by anthers (Ogawa, 1961). The ovary in each flower contains six ovules and about half the pollen tubes at the top of a stigma grow as far as the ovary, therefore 12 or more initial pollen tubes are needed to achieve maximum seed set. In fact, the production of 3–4 ripe seeds per ovary is common in good seed crops (Currah, 1990).

FERTILIZATION AND SEED DEVELOPMENT

Following pollination, fertilization of ovules starts within 12 h and is complete in 3–4 days (Rabinowitch, 1990b). The greatest seed set and best embryo development and most rapid pollen tube growth occurred at 35/18 (day/night °C), rather than 24/18 or 43/18 (Chang and Struckmeyer, 1976). Pollination itself stimulates the initial development of ovules and ovaries. The shrinkage and loss of green colour in unfertilized ovaries does not occur until about three weeks after flowering, making the early assessment of seed set difficult (Currah, 1990). Temperatures in the range 40–60°C have been recorded in the ovaries of the insolated side of umbels (Tanner and Goltz, 1972) causing high levels of embryo abortion and low seed set (Peterson and Trammell, 1976).

In fertilized ovules the endosperm nuclei start to divide first, and cell division and expansion by the embryo occurs 5–6 days later. The embryo

develops from a globular, few-celled pro-embryo, which is first visible in microscope sections about 6 days after pollination. It then develops through an oval to tubular, and finally to a coiled tubular structure embedded within the endosperm (Rabinowitch, 1990b). Initially the endosperm is liquid; this is termed the 'milk stage'. At about 330 degree-days above 0°C after pollination, cell walls develop within the endosperm and it progresses to the pasty 'dough stage' at about 450 degree-days above 0°C after flowering. At this point the seed coat starts to turn black. The seed attains its maximum fresh weight at about 570 degree-days above 0°C after flowering. Up to this point seed dry weight growth is near exponential and seed dry weight is then about half its maximum. The endosperm then becomes solid and the seed reaches its maximum dry weight, typically 3–3.5 mg, at 810 degree-days above 0°C after flowering, normally about 45 days after flowering but depending on temperatures (Gray and Ward, 1987). At this stage capsules begin to shatter and to shed seed, and the food-reserve oil globules and protein bodies can first be seen within seeds. Seed water content declines after the attainment of maximum fresh weight. Germinability commences just before the maximum fresh weight is attained (570 degree-days above 0°C after flowering) and is near maximum at seed shatter (Steiner and Akintobi, 1986).

INTERACTIONS BETWEEN FLOWERING AND BULBING

Since both bulbing and flowering are controlled by temperature and photoperiod it is not surprising that the two processes can interact. A vegetative shoot apex normally develops axillary to the inflorescence (Rabinowitch, 1990a), and this can develop more rapidly than the inflorescence under a combination of warm temperatures (20°C or higher) and long photoperiods. This results in the swelling of the axillary bud to form bulb scales and the shrivelling and degeneration of the young scape, hence the term 'competition phase' was coined by Kampen (1970) to describe this apparent competition between axillary bud and inflorescence. When onions are planted out in bulb-inducing conditions, for example, in a warm spring, or in a glasshouse in spring, such inflorescence abortion can be common, even from bulbs with advanced inflorescence initials (Brewster, 1982a).

As discussed under bulbing, bulb or set storage at 28–30°C also delays bulb initiation. Because bulb development suppresses inflorescence elongation during the competition phase, a short period (1–2 months) of storage at such a high temperature at the end of a long period of cool storage can, by delaying bulbing, counteract this 'competition' and result in increased bolting (Aura, 1963).

Quite frequently small bulbs, known as 'bulbils' or 'topsets' may form in the inflorescence rather than normal flowers and seed capsules. When this occurs the scape is shorter than normal. Various degrees of this condition have been observed, ranging from the production of a single large 'bul-

bil' on an extremely short scape through to near normal inflorescences with a mixture of normal seed capsules and bulbils. This late reversion from flowering to bulbing was favoured by 6 weeks at 28–31°C applied pre-planting to bulbs after a cool treatment of sufficient duration to produce advanced inflorescence initials (Aura, 1963). Applied at an earlier stage of inflorescence differentiation such high temperatures can totally suppress floral development (see above). Bulbils can be induced to form in normal inflorescences by clipping off the developing florets. Such bulbil production can be increased by spraying the clipped heads with water, or better, benzyl adenine solution (Thomas, 1972).

Temperatures of 12–16°C in combination with photoperiods of 16–17 h have been found satisfactory for inflorescence emergence from induced bulbs and plants of intermediate-day cultivars (Brewster and Butler, 1989b). Since the photoperiods and temperatures needed for bulbing vary with cultivar, it is almost certain that the photoperiods and temperatures needed to avoid suppression of developing inflorescences by competition from bulbing will depend on the cultivar. The inflorescence of a short-day cultivar will be suppressed by a shorter daylength than a long-day cultivar. Since plants raised from bulbs or sets bulb more rapidly than those raised from seeds competition from bulbing probably suppresses inflorescences in bulb-raised plants at shorter photoperiods and lower temperatures than in seed-raised plants. In view of cultivar differences in bulbing response to photoperiod and temperature, and the fact that in order for flowering to proceed the young inflorescence must avoid suppression by bulbing, it seems a foregone conclusion that cultivar differences in the response of flower elongation to photoperiod and temperature must be parallel to the cultivar differences in bulbing response. Experiments are needed to confirm this, however.

MODELLING OF GROWTH, BULBING AND FLOWERING

In view of the interrelations between growth, bulbing and flowering, and the control of all three by temperature and light conditions (Fig. 17.14), advances in understanding of crop behaviour are possible by combining models for these processes. Predictions of how bolting, bulb yields and maturity date are affected by sowing date, locality and season can be compared with field experiments, to see if the models are satisfactory. For example, the photothermal bulbing model (see above) predicts that widely-spaced cv. Keepwell will initiate bulb scales on 31 May, with the mean daily temperatures at Wellesbourne, UK. Cultivar Keepwell is very similar to cv. Senshyu in its date of bulbing and maturity (NIAB, 1982) and similar in bolting response. A model for inflorescence formation, based on the vernalization responses described above, with inputs of daily temperature and photoperiod, predicted that in some seasons early-sown, overwintered Senshyu crops would reach the stage of spathe initiation well before 31 May (Brewster, 1997). Such

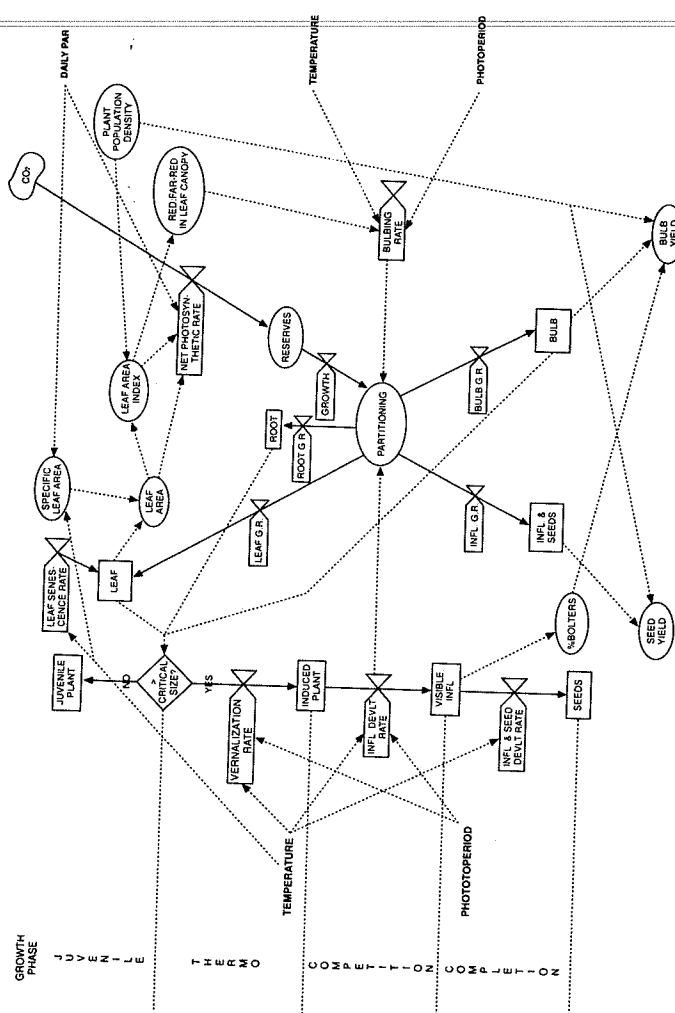


Fig. 17.14. A relational diagram indicating the main environmental controls of growth and development in onions, showing how growth, bulbing and flowering interrelate to determine bulb or seed yield. Progress through the growth phases of Fig. 17.1 is indicated on the left. Devit, development; Infl, inflorescence; GR, growth rate (dry matter growth); PAR, photosynthetically active radiation.

crops are likely to bolt because scape elongation will occur before competition from bulbing begins to suppress developing inflorescences.

As a simple illustration of how growth rate and bulbing rates interrelate to determine yield, with a plant population of 60 plants m^{-2} , a crop emerging on 1 May at Wellesbourne will, in an average year, achieve an LAI of 3.2 and a light interception of 60% (equation 4), if leaf growth continues until 6 July. This is assuming leaf area per plant (cm^2) is given by:

$$\log_e(\text{leaf area}) = \log_e(0.5) + 0.0108 \text{ DD} \quad (5)$$

DD is the summation of day-degrees above base $6^\circ C$ and below $20^\circ C$ accumulated since emergence (Brewster, 1994). 1 May is a typical emergence date from late March sowing. Sixty per cent interception gives bulb yields of about $0.9 \text{ kg } m^{-2}$ dry weight (about $75 \text{ t } ha^{-1}$ bulb fresh weight) (see Fig. 17.10). The photothermal model for bulbing (see above), predicts that cv. Hyton initiates bulb scales on 7 July using mean temperatures for Wellesbourne. Hyton is therefore well adapted, and will have a higher potential yield than cv. Keepwell, which the model predicts will initiate bulb scales on 7 June from 1 May emergence.

In a trial comparing cvs Keepwell and Rijnsburger-bola (a cultivar very similar to Hyton in season of bulbing), both sown on 28 February, the latter yielded $41 \text{ t } ha^{-1}$ with $25 \text{ t } ha^{-1}$ of bulbs greater than 45 mm diameter and was mature on 20 August, whereas the former yielded only $24 \text{ t } ha^{-1}$ with none bigger than 45 mm and was fully mature on 9 July (Salter, 1976). This illustrates in practice the critical importance of the response of bulbing to photoperiod and temperature in determining the yield potential of a cultivar at a given location and season of sowing. The response must allow sufficient leaf growth to occur before bulbing starts.

In fact, cv. Keepwell is grown as an overwintered crop and will typically produce a leaf area of about 25 cm^2 per plant in early March from a sowing made in mid to late August at Wellesbourne. Equation 5 predicts that the leaf area per plant will reach 442 cm^2 by 31 May in an average year at Wellesbourne, when equation 3 indicates that bulbs will be initiated. If the plant population is 60 plants m^{-2} this implies a leaf area index of 2.65 which, would intercept 54% of the incoming PAR, giving a potential experimental plot yield of about $1.2 \text{ kg } m^{-2}$ dry weight (about $100 \text{ t } ha^{-1}$ bulb fresh weight) (see Fig. 17.10).

Visser (1994a,b), has developed a model for bulb development which includes much of the information reviewed above, and has combined this with the universal crop growth simulator sucros '87 (Spitters, 1989) to produce a simulation model for bulb onion growth, development and yield. In validation trials, agreement between predicted and recorded maturity dates were satisfactory. Yield predictions were satisfactory under optimal soil conditions, but recorded yields were much lower than predicted at some sites, indicating some limitations, possibly by drought stress. This illustrates the usefulness of models in highlighting unexplained differences which need further investigation.

PHYSIOLOGICAL DISORDERS

THICK-NECKS

Sometimes a proportion of an onion crop will fail to complete bulbing. Green leaves continue to appear from the top of the partially formed bulb, the neck does not soften and the bulb does not become dormant. This problem is most severe in seasons, sites and cultivars where crop maturity, as shown by foliage fall-down, is already late (Brewster *et al.*, 1987). As might be expected from the effects of temperature on the rate of bulbing, late maturity occurs in cool summers (Brewster, 1990b). Late maturity is also a feature of sites where low soil temperatures result in slow emergence and seedling growth and the late development of a high LAI (Brewster *et al.*, 1987). With spring-sown crops such delays can result in bulbs still developing in the late summer and autumn as photoperiods and temperatures decline below those needed for bulbing. Controlled experiments show that plants will revert to leaf blade growth in these conditions (see Fig. 17.7). High-yielding, spring-sown cultivars adapted to cool regions are probably prone to this problem because, in order to make sufficient LAI for a high yield, they must continue leaf growth long after the summer solstice. The additional stimulus for bulbing associated with a high LAI may itself be important in pushing these crops to ripeness (see Fig. 17.9). Therefore, the crop can be predisposed to thick-necking by any factor which destroys leaves or slows leaf growth (Fig. 17.15).

PREMATURE BULBING

The opposite problem, bulbing very rapidly, soon after sowing, so that the plants remain dormant through much of the growing season, sometimes occurs with late summer sowings of overwintered crops (Robinson, 1971; Rabinowitch and Zig, 1989; Currah and Proctor, 1990). Here seedlings emerge while temperatures and photoperiods still favour bulbing. In tropical countries onions are normally raised at high plant densities in nursery beds prior to transplanting. High plant densities may contribute to premature bulbing via the red : far-red effect (Fig. 17.15).

SPLITTING

Bulb splitting as a result of multiple growing points is under strong genetic control with shallots being at the extreme in this respect. Growth in high temperatures and short days increases lateral shoot production in some cultivars (Robinson, 1971; Steer, 1980). Deep transplanting reduces bulb splitting (Chipman and Thorpe, 1977).

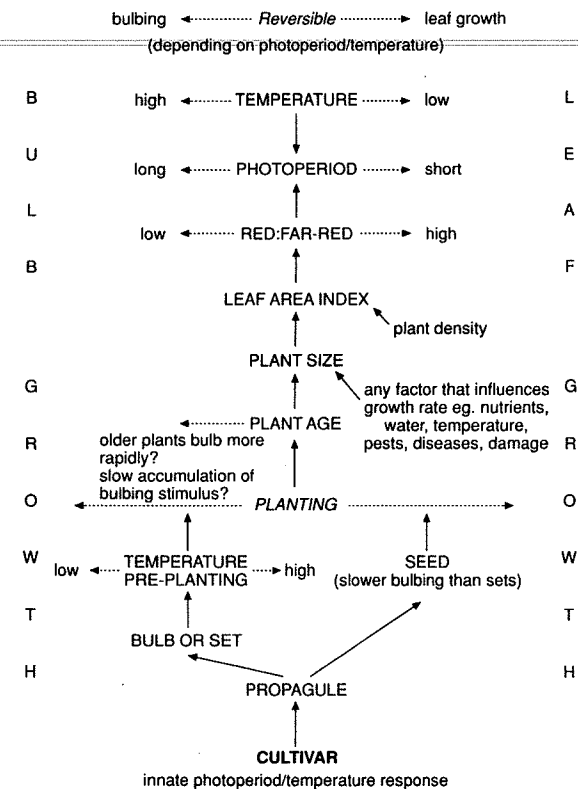


Fig. 17.15. The main factors that control onion bulbing, how they interrelate, and how numerous agronomic variables may exert an influence.

BOLTING

Unwanted bolting in bulb crops results from exposure to conditions which induce flowers to emerge before bulbs are sufficiently advanced to suppress them. Typically this would involve rapid seedling growth to the post-juvenile phase, weeks of exposure to cool temperatures optimal for inflorescence initiation (see Fig. 17.12a), followed by the lengthening photoperiods but rather cool temperatures which will favour inflorescence elongation rather than rapid bulbing. In many regions, over-early sowing of overwintered

crops results in a sequence of temperatures that favour this (Brewster, 1994). Furthermore, because temperatures vary from year to year, there can always be differences in bolting from crops sown on the same date in different years (Brewster *et al.*, 1977).

INFLORESCENCE SUPPRESSION

Failure of flower emergence is a familiar problem to breeders and often results from the suppression of fully developed inflorescences by bulbing during the 'competition' phase (Kampen, 1970). This is avoided using the sequence of growing conditions that favour bolting outlined above. In the case of bulbs, a long duration near optimum temperatures for vernalization will favour subsequent inflorescence emergence (Aura, 1963). Rapid increases in temperature and photoperiod can cause inflorescence suppression, and accelerating anthesis in this way almost inevitably reduces the number of flower stalks appearing (Brewster, 1982a).

WATERY SCALES

Watery scale is a disorder of stored bulbs the symptoms of which are a thick leathery outer skin which when peeled away reveals watery, glassy storage scales (Hoftun, 1993). The scales may be later infected by bacteria or fungi, but these are not the primary cause of the disorder. Up to 15% losses of stored bulbs have been reported, particularly in crops given high temperature drying treatments following harvest. Experiments in which the gas exchange of bulbs was restricted either by submerging them for several days or by injecting the necks with vegetable oil, showed that the internal concentration of CO₂ increased, and of O₂ decreased, as a result. Treatments in which the CO₂ concentration exceeded 13% resulted in some bulbs developing watery scales (Hoftun, 1993). The higher the postharvest drying temperature the higher the internal CO₂ concentration. In bulbs with oil-injected necks there was no pattern in the distribution of watery scales after a period of storage. Internal breakdown of bulbs stored in controlled atmospheres has been observed at CO₂ of 10% and this appears more harmful to onions than low O₂ atmospheres (Komochi, 1990).

LEAF BLAST

A catastrophic collapse of onion foliage in parts of the USA, associated with hot weather following cool wet weather, is caused by ozone damage (Eagle *et al.*, 1965). Some cultivars are resistant because their stomatal membranes are so sensitive to ozone that they rapidly become leaky, causing stomatal

closure. This prevents entry of ozone into the mesophyll and further leaf damage (Eagle and Gabelman, 1966).

GARLIC PHYSIOLOGY

SPROUTING AND EMERGENCE

Time from clove planting to sprout emergence decreases with increasing duration of bulb storage before planting (Mann and Lewis, 1956). Storage at about 7.5°C results in the fastest sprouting after planting (Mann and Lewis, 1956; Messiaen *et al.*, 1993). Storage at 0 or 20°C both give much slower emergence. Emergence rate also depends on field temperatures after planting, but by transforming emergence times to thermal times (accumulated day-degrees) with a base of 4.4°C, emergence rates became dependent just on pre-planting temperature and duration of storage (Mann and Lewis, 1956).

GROWTH

Pre-planting storage temperature also affects the vigour of growth and leaf morphology after sprouting. Storage at 5–10°C results in rapid growth with wide leaves and thick pseudostems, 20°C in slow growth and thin leaves and pseudostems, and 0°C thin shoots but the most vigorous growth in height (Mann and Minges, 1958). In the field, the rate of leaf appearance and the extension rate of leaves depends on thermal time. In a French study one leaf appeared per 100 day-degrees above a base of 0°C (Espagnacq *et al.*, 1987) and in New Zealand one leaf per 131 such day-degrees (Buwalda, 1986).

BULBING

EFFECTS OF PHOTOPERIOD AND TEMPERATURE

As with onion, bulbing requires long photoperiods and warm temperatures (Mann, 1952; Takagi, 1990). The lower the red : far-red ratio during inductive photoperiods the faster the bulbing (Terabun, 1978), and extensions of daylight photoperiods with far-red or blue light are more inductive than with red light (Takagi, 1990). These responses are similar to those for onion. However, the capability to bulb in response to these growing conditions is determined by storage temperatures before planting. Shading experiments show that a low light intensity reduces the number of cloves which initiate and develop in the leaf axils (Rahim and Fordham, 1990).

EFFECTS OF PRE-PLANTING BULB STORAGE TEMPERATURE

Mann and Minges (1958) showed that storage of the variety 'California Late' at 20°C before planting resulted in slow bulbing during subsequent growth under constant 16.5 h photoperiods, and completely prevented bulbing in several field trials at different locations. Storage temperatures of 0–5°C were best for inducing rapid bulbing after planting. In these experiments the optimum temperature for rapid bulb induction shifted from 5–10 to 0°C the longer the period of storage before planting. Trials in France with the similar cultivar 'Printanor' gave the same responses (Messiaen *et al.*, 1993). With Japanese cultivars storage temperatures of 15°C and lower are effective for bulb induction with an optimum of 2–4°C (Takagi, 1990). Low temperatures are necessary for the differentiation of axillary buds which form cloves (Rahim and Fordham, 1988). If low temperatures persist for too long before long photoperiods and warmth induce bulb enlargement, the axillary buds may develop into leafy side shoots. These side shoots then develop several cloves of their own, forming irregular bulges around the periphery of the main bulb. Such misshapen bulbs are termed 'rough' and are an unacceptable quality defect. Rough bulbs occur when planting stock is kept too long at optimal inductive temperatures (0–5°C) before planting, and occurs in practice after exceptionally cool winters (Mann and Minges, 1958; Messiaen *et al.*, 1993). In contrast, if some cultivars have insufficient exposure to low temperatures, for example following spring rather than autumn planting, they may fail to produce axillary buds and produce just one large terminal clove termed a 'round clove', rather than the usual multiclove bulb (Messiaen *et al.*, 1993). Such round cloves also occur when garlic is grown from very small cloves or from the small topsets formed in inflorescences (Takagi, 1990).

A minimum of 4 weeks storage at 5°C was required to have a measurable effect on subsequent bulbing (Mann and Minges, 1958). These authors also showed that 4 or more weeks storage at 20 or 25°C would measurably counteract the effect of many preceding weeks at 5°C and delay bulbing. So the cold induced acceleration of bulbing is reversed by subsequent warm storage, an effect also observed with onion sets.

DORMANCY

Storage conditions needed to prolong dormancy are essentially the reverse of those needed to promote sprouting discussed previously; therefore, storage at 7.5°C gives the most rapid loss of dormancy. The degree of dormancy of stored bulbs can be assessed by the ratio of the length of the internal sprout leaf to that of the storage leaf within a sample of cloves (Burba, 1993). For prolonged storage, temperatures of –1 to –3°C applied to well-ripened bulbs are optimal (Takagi, 1990). Dormancy is also prolonged at 20–30°C compared with intermediate temperatures. Respiration rates of dormant

garlic bulbs are lower at 20 than at 5, 10 or 15°C showing that the warmer temperature suppresses metabolic activity (Mann and Lewis, 1956). High temperatures (35°C) applied before the bulbs are completely ripened can reduce dormancy (Takagi, 1990; Messiaen *et al.*, 1993), as is the case with onions. Root emergence from dormant bulbs is promoted by moisture on the base plate and is most rapid at 15°C, 5–10° warmer than the optimum for sprouting (Takagi, 1990). As with onion, sprouting is promoted by exogenous cytokinin applications and associated with a rise in endogenous cytokinin activity (Takagi, 1990). Messiaen and his colleagues have experimented with a wide range of garlic clones from the western hemisphere and have outlined six groups based on particular combinations of the following elements:

- intensity of dormancy
- the ease of elimination of dormancy by low temperature
- the low temperature requirement for axillary bud formation
- the thermophotoperiodic requirement for bulb enlargement (Messiaen *et al.*, 1993).

Different combinations of these ecophysiological traits largely determine the adaptedness of a cultivar to the climate and agriculture of a region. These workers have also shown that infection with onion yellow dwarf virus increases dormancy and earliness of ripening compared to virus-free clones.

FLOWERING

Various degrees of flowering occur in garlic clones. Some never normally produce an inflorescence, whereas others produce an inflorescence but this is sterile and bears bulbils. True seed occurs in only a few clones collected from central Asia (Etoh *et al.*, 1991; Messiaen *et al.*, 1993). Various degrees of arrested inflorescence development are common ranging from a vestigial flower stalk within a normal bulb, through a short stalk with bulbils surrounded by the outer membrane of the bulb to a short stalk crowned by a few topsets (Burba, 1993; Messiaen *et al.*, 1993). Inflorescences are induced by low temperatures, –2 to 2°C being optimal for some Japanese varieties, a lower temperature than is optimal for induction of bulbing (Takagi, 1990). The differentiation of induced inflorescences occurs after planting and is favoured by growth at cool temperatures after planting. Long photoperiods stimulate inflorescence development, but as with onion, competition from bulbing can suppress inflorescences, therefore a combination of long photoperiods with temperatures sufficiently low to prevent bulbing favours bolting (Messiaen *et al.*, 1993). A large clove size at planting favours bolting (Takagi, 1990). Bolting reduces bulb yields and growers of bolting cvs in France remove the flower stalk thereby increasing bulb yields by about 15% (Messiaen *et al.*, 1993).

PHYSIOLOGICAL DISORDERS

The cause of irregular or 'rough' bulbs due to cloves formed on side shoots has been described under bulbing. In stored bulbs a 'waxy breakdown' can occur in which small, sunken, light-yellow areas of the clove flesh expand to give shrunken, somewhat translucent, amber cloves which are waxy to touch. Waxy breakdown is associated with inadequate ventilation and low oxygen during storage (Anon, 1976), suggesting it may be similar in cause to the 'watery scale' problem of onions discussed above and recently shown to be caused by CO₂ toxicity.

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