FLOWER DEVELOPMENT AND FLOWERING DISORDERS IN BULBOUS IRIS

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Abstract

Flowering failure in bulbous iris 'Wedgwood' was examined in plants given several pre-planting temperatures and transfers between temperatures to produce a range of morphologically different plants. Correlations were determined between growth of flower plus stem and several measures of vegetative growth. Successful flowering was associated with extensive vegetative development and rapid vegetative growth. A similar effect was also obtained with post-planting interactions of temperature and light treatments. Bulbing was promoted by high temperature and by long photoperiods, to the detriment of flowering. These results are explained in terms of internal competition for mother-bulb reserves and photosynthates from the leaves which lead to flower failure if assimilation is low and if competition from daughter bulbs is intensified by temperature or photoperiod.

1. Introduction

Attractive flowers of bulbous iris can be produced all-year-round by using appropriate storage temperature treatments (Durieux and de Pagter, 1967). The bulb during storage contains no initiated flower - unlike some other bulbous plants - and post-storage treatments must be given to ensure flower initiation. When buds are initiated they can subsequently fail to develop to anthesis and are said to 'blast' if conditions are unfavourable.

Thus there are two times in the plant's life cycle when flowering is at risk: at floral initiation, and during the development of a flower bud to a flower. Flower initiation is affected by bulb size (small bulbs do not initiate a flower, Doss, 1979; Doss and Christian, 1979), by cultivar, and by temperature treatment (high-temperature treatment can induce flowering in bulbs at or near the critical size for flowering (Tsukamoto, 1973; Le Nard, 1973; Schipper, 1980)). Treatment with smoke, or ethylene, can also stimulate flower initiation (Kamerbeek et al., 1980). Failure later in flower development is also affected by bulb size and storage conditions and also by growing conditions, especially temperature (Fortanier and Zevenbergen, 1973; Le Nard, 1980), light (Mae and Vonk, 1974), and soil moisture. Flowers are particularly likely to fail to develop to anthesis under low light conditions in winter, and growers use wider plant spacings to increase light interception by individual plants.

In the glasshouse the failure of flowering at the two stages are readily distinguishable, as illustrated by Durieux and de Pagter (1967). Failure of initiation produces "three-leaf" plants with no inflorescence stem, the apex instead produces a new central bulb after 3 or occasionally 4 leaves. Later failures have 6-8 leaves and an inflorescence stem.

2. Materials and Methods

Bulbs of several grades of 'Wedgwood', 'Ideal' and 'Prof. Blaauw', taken from our own stocks, were stored at different temperatures to encourage different rates and extents of subsequent growth of leaves, flowers and daughter bulbs by modifying the pattern of partition of reserves. Subsequently, the amount of current photosynthesis is also affected by the amount of leaf growth. The lower the storage temperature, the earlier flower initiation occurs in the plant's development, i.e. after fewer leaves. Low pre-planting temperatures induce daughter bulbs, and their subsequent growth is favoured by warmer temperatures. Final leaf length is greater as storage temperatures are increased from 8-20°C. After planting, plants were grown in four glasshouses at different temperatures, with mimima of 12,16,18 and 20°C, and subjected to treatments of 0, 64 and 90% shading, either to blocks of plants using plastic greenhouse shade material, or to individual flower buds or leaves using aluminium foil. Some plants were also grown in controlled environment cabinets to separate light intensity and light integral effects from those caused by photoperiod.

A range of plants of different morphologies were thereby produced whose flowering behaviour was examined to assess the relative importance of several contributory environmental factors on flower development (using flower plus shoot dry weight at anthesis as an index of flower quality) and on flowering failures, and to seek some rationalisation of earlier, somewhat conflicting reports on causes of flowering problems, with a final objective of determining practical measures to ensure high flowering percentages with high flower quality.

The results presented in this brief account can only represent a small selection of the complex interactions between light and temperature, time of year, daylength, cultivar and bulb size on flowering and flower blasting. All the data refer to 'Wedgwood'. A fuller account will be published elsewhere (Elphinstone et al., in press).

3. Effects of temperature and light

3.1. Pre-planting

To test earlier reports (eg. Fortanier and Zevenbergen, 1973) that leaf growth should be kept to a minimum in order to favour flower growth and development, a range of preplanting cold treatments was given to produce different amounts of vegetative growth which would be in competition with the flower. Table 1 shows data for bulbs kept at constant temperatures: it shows how flower quality increases with temperature, as does leaf number and dry weight. In contrast there is no close relation with mother bulb dry weight nor daughter bulb dry weight. Over a 9 week pre-planting storage period when plants were kept initially at 5°C and moved at weekly intervals to 9, 13, 17 or 20°C, earlier transfer from 5°C resulted in more plants with two flowers initiated, but a move to higher temperatures within the range increased the extent of flower failure. Correlations between the growth of the various vegetative sinks and that of the flower and stem, for 17 temperature combinations, were determined to establish where competition between parts was important. Flower plus stem dry weights were highly correlated with the following: leaf dry weight ($r = 0.89$), days to anthesis ($r = 0.83$), rate of vegetative growth ($r =$

0.97) and stem length (r = 0.96). Correlations between daughter bulb dry weight and flower plus stem dry weight were not significant, an indication of the low level of within-plant competition between these two sinks. With mother bulb weight the correlation was negative and low.

When the dry weights of leaves plus daughter bulbs (as a measure of vegetative growth) were plotted against the dry weights of flower plus stem, 88% of variance was accounted for by the regression. When the rate of vegetative growth was used, 94% of the variance was accounted for. This somewhat unexpected result means that, far from vegetative growth being in competition with flower growth and development, successful flowering is associated with rapid rates of vegetative growth.

3.2. After planting

Our plants were grown in four glasshouses, using three planting dates, three levels of shading, and three bulb grades. Data were examined relative to mean measured glasshouse temperatures for the 14 days prior to anthesis. Each 1°C rise in mean daily temperature decreased the time to anthesis by c. 5d. A mean daily temperature of 18°C halved the number of flowers reaching anthesis compared with 16°C, although higher light intensity could counteract some of the adverse effect of high temperature. Shading had only a small effect on anthesis date, with a maximum effect of c. 4d, but increased the number of blasted flowers - eg from 30 to 69% in 10cm and from 36 to 96% in 6-7 cm bulbs.

To examine the relationship between vegetative growth and floral development in the plants given post-planting treatments, data for 10+ and 8-9cm bulbs of three planting dates were used. The relationship between flower plus stem dry weight and leaf dry weight was linear, the regression accounting for 82% of the variance with no differences between planting dates or bulb size (Fig. 1). There was an increase in leaf number with later planting dates, and flower weight responded positively to increased leaf weight irrespective of whether this was achieved by more leaves or by larger leaf area.

The proportion of flowers developing successfully to anthesis showed interaction between time of planting (Jan, Feb or March), bulb size and glasshouse temperature. A single curve could represent all the data for 10cm bulbs linking the amount of blasting and total short-wave radiation at 14-17°C, with a minimum integrated value for 14 days of about 130 MJ m^{-2} being required for maximum numbers of flowers developing successfully. At 17-18°C, January-planted 10cm bulbs could develop successfully at lower light integrals than those planted later. For smaller bulbs temperature was more important than planting date. The data suggested the operation of a photoperiodic effect.

An experiment to test this hypothesis in controlled environment cabinets showed that at 16°C more flowers blasted than at 14°C. For large bulbs (10-11cm) there was no effect of photoperiod on blasting at 14°C, but at 16°C there was more blasting in 24h days than in 8h days. For 8-9cm bulbs long photoperiods increased blasting at both 14 and 16°C, but more blasting occurred at the higher temperature.

At the most susceptible developmental stage for blasting, when the flower stem is elongating most rapidly and the bud is just visible, there are two main competing sinks: the flower and the daughter bulbs.

In short photoperiods the daughter bulb weights at 14°C did not differ from those at 16°C. But in long days, bulbs produced at 16°C were heavier, even before the normal time of bud blasting. A similar effect was also observed in plants which had not initiated a flower, which indicates that increase in daughter bulb weight is a cause rather than a consequence of flower bud blasting.

Localised shading of leaves increased the extent of blasting whilst shading buds had no effect. This, and data on dry-weight changes induced by shading treatments, suggest that the major cause of blasting is a reduction in plant carbohydrate status because of reduced photosynthesis, which reduced dry weights of all plant parts.

4. Discussion

These results confirm other workers' findings that both pre- and post-planting temperature treatments affect flowering in iris, and that light interacts with temperature in the post-planting phase (Fortanier and Zevenbergen, 1973). Our results indicate that flower development is more closely related to rates of vegetative growth than to the time taken to reach anthesis. The more rapid the vegetative growth, the better the flower development, whether the rate of vegetative growth is determined by pre-planting (storage) temperature or a post-planting (glasshouse) temperature.

This is at variance with common belief that leaf growth competes with flower development and that suppression of the former encourages the latter. In indeterminate dicotyledonous plants, such as the tomato, such competition is well known, particularly when environmental conditions are unfavourable. The explanation of the difference lies in the morphology of the iris. All organs are initiated and start their development in darkness. After planting, further growth occurs in these existing organs, utilizing food reserves in the mother bulb. The leaves elongate first, and amount of the reserves consumed depends on the extent of leaf growth as influenced by earlier storage treatment and the environmental conditions after planting. The final developmental stage of the flower occurs subsequently using more and more of the assimilates produced by the leaves, as the storage reserves in the mother bulb become depleted. The maximum demand from the flower occurs as the requirement by the growing leaves is becoming very low. Further, longer leaves provide a greater area and as longer leaves become more divergent, their light-interception also increases.

At high temperatures, long photoperiods increase daugher bulb sink strength (bulbing) so that high light integrals are required to allow high numbers of flowers to reach anthesis - as occurs in short photoperiods or at lower temperatures with less competition from the daughter bulbs. The higher light integrals compensate for adverse effects of high temperature by either increasing the sink strength of the flowers or by increasing the assimilates available because of higher rates of photosynthesis.

These results are not in conflict with the known effects of smoke or ethylene on iris bulbs. Although such treatment reduces leaf growth and promotes flower development (Duineveld and de Munk, 1983), sprouting is earlier, leaf growth is faster and it is completed earlier than in untreated bulbs. There is less drain on mother-bulb reserves and the demand for substrates occurs before that of flower development, so that there is less blasting.

The flower competes for current assimilates with other parts of the plant during its development to anthesis, and the critical stage occurs late in the growth of the stem, because the exponential nature of the growth curve increases the absolute demand for assimilate with time. In contrast with tulip (Ho and Rees, 1977), where flower growth normally precedes that of daughter bulbs, and daughter-bulb weight increases as a consequence of blasting, the iris mother-bulb reserves become exhausted earlier in development leaving a delicate balance between the competing demands of the flower and of other sinks. Several factors can affect this balance. In general terms there is a close relation between the dry weight of flower plus stem and that of the leaves produced, with little relation to depletion of mother-bulb reserves. This indicates an allometric relation between plant parts, with flower failure occurring when conditions prevent or restrict increases in total plant weight.

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Table 1 - Effect of different temperatures for 9 weeks before planting on the growth and flowering of 'Wedgwood' iris.

	9	13	17	20°C	SED
DW flower + stem (g)	2.4	2.6	3.2	4.5	0.38
Leaf no $plant^{-1}$	5.9	6.0	7.0	8.2	0.33
Leaf DW $plant^{-1}$	1.7	2.4	2.8	4.3	0.33
Mother bulb DW at anthesis (g)	1.4	1.7	1.5	1.7	0.38
Daughter bulb DW (g)	0.99	0.85	0.74	1.20	0.26

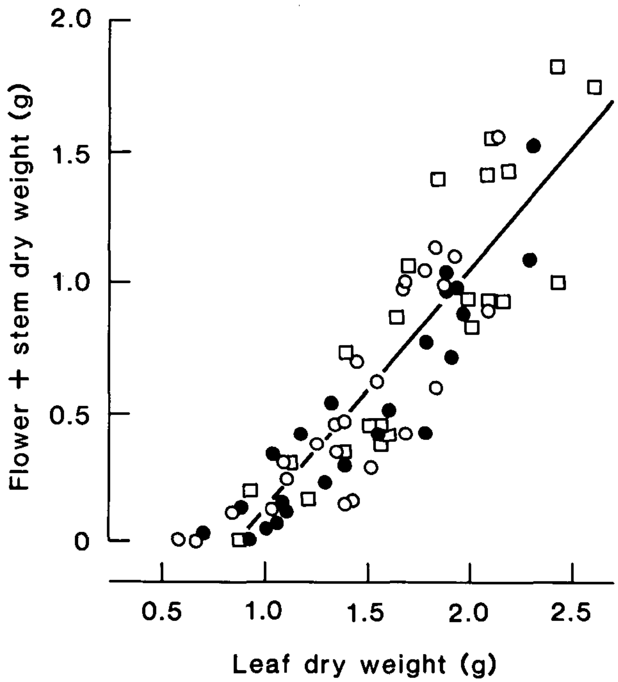

Fig. 1.

Relationship between the dry weight of the flower and stem and the dry weight of leaves $r^2 = 0.82$ ($p < 0.001$)

(o) = Jan planting
(●) = Feb planting
(□) = Mar planting