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Analysis of the effects of temperature and light after planting on bud blasting in *Iris hollandica* [1]

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Summary

Bud blasting in Dutch irises is primarily caused by too high temperatures and insufficient light or moisture after planting. Quantitative aspects of temperature and light influences have been studied under controlled conditions. The optimum temperature for the earliest flowering and minimum daily light energy required to prevent bud blasting as much as possible, cannot be given. They depend on too many other factors such as cultivar, bulb size, storage and even on pre-harvest conditions. However, the following trends were observed.

Increased temperatures accelerate flowering and augment minimum daily light requirement. Only a specific combination of temperature and light intensity gives the smallest total light energy requirement from sprouting till flowering, which eventually determines the necessity of additional light. The optimum levels of temperature and light change during plant growth and depend on the acceptable percentage of flowering.

Sensitivity to high temperature and insufficient light increases with plant development until an optimum is reached which coincides with the stage of largest stem elongation. Comparing similar daily light energies or temperatures, intensity and duration of light as well as day and night temperature are within certain limits of a comparable importance regarding either time of flowering or percentage of bud blasting.

Photoperiod has no clear effect on both phenomena, while these are more affected by air temperature than by soil temperature. Sum of temperature till flowering is only constant for each planting and is not correlated with bud blasting. An increase of air temperature during the day as compared with one during the night only occasionally produced more bud blasting. A possible explanation is sought in the occurrence of an unfavourable positive difference between air and soil temperature during the light period.

Introduction

In bulbous iris the development of a bud into a flower may fail either partially or completely. This failure, abortion or blasting, may occur in all developmental stages from the completion of bud initiation until flowering (Elliot, 1943; Kamerbeek, 1965, p. 340; Rees, 1972, p. 247). An incomplete initiation, an imperfect opening or an

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insufficient protrusion of the flower from the two spatha, which is often accompanied by discolouring, are considered as marginal cases of bud blasting. Excluded are cases in which an expected initiation did not take place. For these the term 'blindness' should be reserved (Kamerbeek, pers.comm.).

Blasting of the bud may be induced either before or after its initation, which mostly occurs shortly after planting. Cultivar, bulb size, conditions before and during bulb storage, and growth conditions after planting, are important (Beyer, 1952; Blaauw, 1934, 1935, 1941; Halevy et al., 1964; Hartsema & Luyten, 1962; Kamerbeek & Beyer, 1964; Walla & Kristoffersen, 1969). Blasting is very common during early and late flowering. 'Wedgwood' and its mutants 'Dominator' and 'Ideal' are considered as by far the least susceptible cultivars. Compared with these 'Prof. Blaauw' and 'Imperator' flower with more difficulty under poor light conditions (Fortanier, unpublished; Hartsema & Luyten, 1955a, b, 1961; van de Nes, 1962).

Most of the literature on bud blasting deals with the causes of it before bud initiation and emphasizes the effects of bulb size and storage temperature (Blaauw et al., 1936b; Hartsema & Luyten, 1962; Kamerbeek, 1963b; Stuart et al., 1955). Flower initiation is ensured when harvested bulbs of a sufficient size are first stored at higher temperatures (35–17 °C) until more than 3 leaves have been initiated (to prevent the initiation of a terminal daughter bulb) and then at lower temperatures (17–9 °C) (Halevy et al., 1963; Kamerbeek, 1963b, 1965; Kamerbeek & Beyer, 1964; Kimura & Stuart, 1972). These treatments may also lower the change of bud blast after planting. Research in this field, started in 1928 by Blaauw and his co-workers, is being continued and leads to an almost continuous alteration of the advised standard treatments considered better for a more rapid flowering with less failures (Durieux, 1972b; Kamerbeek & Beyer, 1964; Stuart & Gould, 1967). In general, storage temperatures leading to a suppressed leaf growth after planting may limit bud blasting when plants are forced under poor light conditions. Retardation of the bulbs by high storage temperatures (25–30 °C) increases the risk of bud blasting (Durieux, 1972a; Hartsema & Luyten, 1961). However, when forced to flower from December till November under similar conditions, the chance of bud blasting at first decreases and increases only after a certain period of retardation (Fortanier, unpublished).

Climatic conditions after planting are variable and more difficult to control than storage conditions. This may explain why research into the causes of bud blasting that operate after planting, is rathed limited. The pioneers in this field were again Blaauw, Hartsema and Luyten. Shortage of water, insuffient light and high temperatures are the best known causes of bud blasting (Hartsema & Luyten, 1953, 1955a, b, 1961, 1962; Kamerbeek, 1966, 1969; Kamerbeek & Beyer, 1964; Mayak & Halevy, 1971). Light requirement increases at high temperatures and both factors are of a comparable importance. Only in a few cases attention has been paid to the importance of day and night temperature, air and soil temperature, and photoperiod (Cathey, 1954; Kamerbeek, 1963a, 1969; Kamerbeek & Beyer, 1964; van de Nes, 1962).

Research on the physiological background of bud blasting in iris is of a more recent date. Bud blasting seems to be correlated with the accumulation and distribution of assimilates. A shortage of transportable sugars is the most plausible cause (Kamerbeek, 1965, p. 341). The amount required for flowering depends on factors such as storage conditions and time of forcing. These assimilates are drawn in different proportions from the reserves in the mother bulb and from the leaves, which for their formation already utilized part of the reserves (Kamerbeek, 1966, 1969; Wassink, 1961, 1969; Wassink & Wassink-van Lummel, 1952). When flowering is required under poor winter light conditions, forcing conditions have to be chosen in such a way that a maximum part of total available assimilates is diverted to stem and flower development, while other morphogenetic processes including the growth of leaves and daughter bulbs receive the minimum (see below). Very little is known about the fundamentals of mobilization, distribution and utilization (Kamerbeek, 1962; Rodrigues Pereira, 1970; Wassink, 1961). It is supposed that hormones play a role. Of these growth regulators, ethylene seems to be particularly important in bud blasting (Stuart et al., 1966).

Scope of research

When the bulbs are able to reach anthesis, prevention of bud blasting will mainly depend on the climatic conditions after planting. As outlined before, these have been the subject of research which, however, was mostly directed to the effect of individual factors and very little towards their mutual relationships. Therefore, quantitative information on the interaction between light and temperature is very scarce. Because of the dependence on other conditions, experimental results are difficult to reproduce quantitatively and many replications are required to form a better notion.

We tried to acquire more information by forcing bulbs of different cultivars prepared for early or late flowering, under controlled conditions of temperature and light in different combinations. In particular, the influence of duration and intensity of light and of air and soil temperature during the day and the night were compared.

As this paper is intended as a general survey of our work in this field, some representative experiments will be discussed without a mathematical analysis or physiological explanation. The results provide information for an optimal forcing of Dutch irises and moreover may help to evaluate a model of the physiology of bud blasting.

Material and methods

Most of the experiments were done in a phytotron (Doorenbos, 1964) with a radiant flux density of 40 W m^{-2}* from fluorescent Philips TL 55. Available space limited the number of cultivars and plants per treatment. The latter exceeded 24 in most cases. Conditions during storage and forcing and number of plants are given at the legends of tables and figures.

The parameter for bud blasting depended on the results. Each trial is more or less a gamble, because an experiment with a result of either 100 % flowering or 100 % blasting prevents conclusions. Moreover the percentage of blasted buds is a poor quantitative measure because the individual bud can only open or blast, without intermediate values. These disadvantages have been overcome as much as possible in several ways:

1. Normally Dutch iris forms an inflorescence instead of a single flower (Luyten, 1942). Susceptibility for blasting increases from the first or terminal bud to the side buds of higher order, but their reactions to adverse conditions are similar (Blaauw, 1935, p. 52; Fortanier, unpublished; Hartsema & Luyten, 1961; Luyten, 1942, p. 16). If necessary,

* 1 W m^{-2} (= 1 J m^{-2} s^{-1}) = 1000 erg cm^{-2} s^{-1} $\approx$ 0.086 cal cm^{-2} h^{-1}. The radiant flux density has been expressed as erg cm^{-2} s^{-1} by Wassink, and as cal cm^{-2} h^{-1} by others. We conversed their figures to W m^{-2}, belonging to the SI units.

blasting percentages of the second and even the third bud have been used instead of those of the first one.
2. As growth conditions are less favourable, the bud aborts at an earlier stage or a smaller size, which is accompanied by an earlier termination of stem elongation and leaf growth (Kamerbeek, 1966; this paper). Similar effects were found after an artificial removal of the bud at progressively earlier stages of its development (Fortanier, unpublished). Length of bud or stem therefore reflects time of abortion and is considered to be a much better quantitative measure than the percentage of blasting.

The figures presented refer to plants which initiated at least one flower. Choice of bulb size and pre-treatment were such as to limit the number of vegetative plants to the utmost. To ensure equal sprouting, the bulbs have been graded according to weight, treated with fungicides and peeled before planting. In some cases the experiments started after the initiation of the flower bud, about three weeks after planting.

Results and discussions

Effect of temperature and light

Non retarded bulbs of 'Dominator', 'Prof. Blaauw' and 'Imperator', prepared for early flowering, were planted in the phytotron at 6 temperatures from 9 to 24 °C and 8, 12 and 16 h of fluorescent light per day. The daily energy corresponds with the average values in a greenhouse in the Netherlands at the end February, the beginning and the middle of March, respectively. Excepted some plants at 21 and 24 °C in 8 and 12 h

Table 1. Effect of temperature and light on percentage of blasting of 2nd bud and the number of days from planting till 50 % flowering of 1st bud. Storage 2 weeks at 35 °C + 2 weeks at 17 °C + 6 weeks at 9 °C; planted 63-12-17; 8 bulbs/treatment; light energy flux density 40 W m^{-2}.

Light (h)	Belasting (%) at							Days at						
	9 °C	12 °C	15 °C	18 °C	21 °C	24° C	mean	9 °C	12 °C	15 °C	18 °C	21 °C	24° C	mean
'Dominator'														
8	0	0	88	100	100	100	65	142	117	78	59	54	49	83
12	0	0	25	38	100	100	44	133	110	72	57	51	49	79
16	0	0	0	0	75	88	27	131	105	70	57	51	49	77
Mean	0	0	38	46	92	96	45	135	111	73	58	52	49	80
'Prof. Blaauw'														
8	13	25	75	63	100	100	63	152	128	85	65	58	50	90
12	0	0	0	38	75	88	34	148	119	82	64	56	51	87
16	0	0	0	0	38	38	13	147	113	73	62	54	51	83
Mean	4	8	25	34	71	75	37	149	120	80	64	56	51	87
'Imperator'														
8	50	50	25	88	88	100	67	160	141	111	86	84	73	109
12	0	0	0	13	88	100	34	158	135	103	84	84	72	106
16	0	0	0	0	75	100	29	155	132	96	84	83	68	103
Mean	17	17	8	34	84	100	43	158	136	103	85	84	71	106
Total mean	7	8	24	30	82	90	42	147	122	86	69	64	65	91

Table 2. Effect of light and temperature on percentage of blasting of 1st bud and stem length of plants with bud blasting. Storage at 30 °C + 6 weeks at 17 °C; planted 67-08-03; 54 'Wedgwood' bulbs per treatment; light energy flux density 40 W m^{-2}.

Temp. (°C)	Blasting % at ... h light							Stem length at ... h light						
	2	4	8	12	16	24	mean	2	4	8	12	16	24	mean
15	100	95	68	4	2	0	45	8	15	38	34	54	(60)	35
18	100	100	100	80	6	0	64	2	13	20	19	27	(51)	22
21	100	100	100	90	56	17	77	2	2	9	12	26	29	13
24	100	100	100	100	100	100	100	1	1	3	6	7	24	7
Mean	100	99	92	68	41	29	72	3	8	18	18	28	41	19

light (TL), all plants produced a first flower. Differences regarding the second bud were greater. Table 1 gives the percentages of blasted second buds and number of days from planting to 50 % open flowers of the main buds, for each of the cultivars.

Blasting of the second bud was promoted by high temperatures and short irradiations. Within certain limits the unfavourable effect of high temperatures can be diminished or even nullified by more light, and the effect of low light energies by lower temperatures. In the case of 'Dominator' 1.17 MJ m^{-2} day $^{-1}$* was sufficient for almost 100 % flowering of the main buds within 7 weeks from planting at 24 °C. Regarding blasting percentage, differences with the two other cultivars were small. In most other experiments, however, 'Dominator' was the least susceptible cultivar with the lowest light requirement.

Flowering was accelerated by high temperatures, especially in the range of 9 to 18 °C. The somewhat earlier flowering in longer light periods could also be a result of a small increase in air and soil temperature by the light. In this and most other experiments 'Dominator' flowered earlier than the other cultivars. It differs from the others in a smaller number of leaves which grow more rapidly, especially at a low temperature. Therefore 'Dominator' seems to have a lower minimum temperature for growth.

In a similar experiment with retarded bulbs of 'Wedgwood' we also measured stem length of the non-flowering plants as a parameter for the stage of development at which the bud blasted. Percentage of blasting of the first bud and stem length are presented in Table 2. Blasting was much more severe than in the preceding experiment: temperature had to be lowered to 15 °C while daylength had to be extended to 12 h (1.76 MJ m^{-2} day^{-1}) to reach also 100 % flowering within 11 weeks from planting. As 'Wedgwood' and 'Dominator' are almost identical, these differences indicate an increased light requirement of retarded bulbs. Apart from this, the effects of temperature and light were similar: more buds blasted in an earlier stage of development at higher temperatures and lower energies of light. In 24 h light at 15 and 18 °C all the buds opened but some could not be regarded as full-grown. Stem length of these plants is presented between brackets. The figures indicate that similar blasting percentages coincide with different stem length. The latter therefore represent a better measure. The more unfavourable the conditions, the earlier the bud will blast and the shorter the stem will remain.

Discussion. These results are in general accordance with those of other publications, discussed in the introduction. Light requirement per day increases at high temperatures

* 1 MJ (megajoule) = 10^6 J; 1 MJ m^{-2} = 10^9 erg cm^{-2} $\approx$ 23.9 cal cm^{-2}.

and depends on cultivar and duration of storage. Hartsema & Luyten (1961) mentioned a light requirement for 100 % flowering of the first bud of 'Imperator', ranging from 0.34 to 1.97 MJ m^{-2} day^{-1} at a forcing temperature from 15 to 17 °C. The variability depends on conditions before and after planting, while daylength was also a very important factor. We will discuss this aspect later. However, light was measured with a spherical light meter and the values found by Hartsema & Luyten are therefore expressed per sphere of 1 cm^2 cross-section. They would have been lower if measured in a plane. A value of 0.34 MJ m^{-2} day^{-1} must therefore be considered exceptionally low. The fact that bulbs were planted at 9 °C and transferred to 15 °C after the sprout had reached a certain length, could have lowered the light requirement. Kamerbeek (1969) who did his experiments in the same phytotron, mentioned a minimum light requirement of 1.26 MJ m^{-2} day^{-1} for non-retarded bulbs of 'Wedgwood' planted at 15 °C, and this is very close to our value of 1.17 MJ m^{-2} day^{-1}, but at 24 °C. We consider 0.84 MJ m^{-2} day^{-1} as a minimum value at 15 °C.

Effect of photoperiod

In the preceding experiments daily light energy was regulated by varying the length of the daily irradiation. This introduces the photoperiod as a factor that could have influenced the results. To investigate this, retarded bulbs of six cultivars were forced in summer at 8 h of sunlight, extended daily with 0, 4, 8 or 12 h of weak incandescent light. During the 8 h of sunlight the plants were in the open. Temperature was not regulated but similar for all groups. Because all combinations produced less than 10 % blasting of the first bud, the percentages are presented for the second bud in Table 3, together with the number of days from planting to 50 % open flowers from the first bud. The figures show that 'Dominator' produced the lowest percentage of blasting together with 'Prof. Blaauw' and flowered much earlier than the other cultivars. In general, photoperiods of 16 and 20 h produced a little more blasting, especially in 'Dominator'. These small differences could have been caused by a small increase in air temperature during the additional irradiation, but this is only partially supported by the differences in flowering time. Therefore, the experiment was repeated several times.

Table 4 presents the results with retarded bulbs of 'Dominator' forced in 6 and 9 h of summer light, both extended with weak incandescent light to photoperiods of 10, 13, 16 and 19 h. The figures clearly demonstrate that light requirement for flowering

Table 3. Effect of photoperiod on percentage of blasting of 2nd bud and number of days from planting to 50 % open flowers from the 1st bud. Storage at 30 °C + 9 weeks at 17 °C; planted 65-06-22; 40 bulbs per treatment; 8 h daylight extended with 0, 4, 8 and 12 h of weak incandescent light.

Cultivar	Blasting (%) at photoperiod					Days at photoperiod				
	8+0	8+4	8+8	8+12	mean	8+0	8+4	8+8	8+12	mean
'Dominator'	50	75	94	92	78	50	49	49	47	49
'White Superior'	80	82	95	88	86	73	71	71	70	71
'La Marquette'	100	100	97	100	99	84	81	82	80	82
'Imperator'	77	69	84	91	80	84	83	79	78	81
'Van Vliet'	95	95	87	94	93	85	82	84	81	83
'Prof. Blaauw'	72	55	82	85	74	88	85	86	83	86
Mean	79	79	89	92	85	77	75	75	73	75

Table 4. Effect of light energy and photoperiod on percentage of blasting of 1st, 2nd and 3rd bud and days from planting to opening of 50 % of 1st and 2nd flower. Storage at 30 °C + 9 weeks at 17 °C; planted at 66-06-29; 50 bulbs of 'Dominator' per treatment; 6 or 9 h of daylight extended with weak incandescent light.

Sunlight + incandescent light (h)	Blasting (%)				Days to opening		
	1rd bud	2nd bud	3rd bud	mean	1st bud	2nd bud	difference days
6+4	0	60	100	53	47	51	4
6+7	6	62	100	54	46	49	3
6+10	0	75	100	58	46	52	6
6+13	0	77	100	59	46	50	4
Mean	2	69	100	57	47	51	4
9+1	0	7	86	31	47	52	5
9+4	0	0	96	32	47	52	5
9+7	0	7	100	37	46	51	5
9+10	0	14	100	38	46	50	4
Mean	0	7	95	34	47	51	5
Control outside	0	0	93	31	53	60	7

increases from the first to the third bud. They show no clear effects of photoperiod, neither on percentages of blasted buds, nor on time of flowering. The repeated tendency of a small increase in blasting percentage at a longer photoperiod, is probably due to the small increase in temperature mentioned earlier, which could also explain the small acceleration of flowering. Blasting, particularly of the second bud, was much less in 9 h than in 6 h of daylight, due to the difference in light energy only. The control group remained outside all the time and flowered 6 to 9 days later because of the lower night temperatures, but with about the same percentage of bud blasting as the 9-h group.

Discussion. The fact that light energy had a distinct effect on bud blasting, but not on flowering time, confirms the results discussed earlier. No indication has been found of an influence of the photoperiod. The latter term is used instead of 'daylength' if we refer to the duration of light independent of light energy. The absence of an effect confirms the conclusion of Kamerbeek (1969) that 'a photoperiodic long day effect does not seem to be involved'.

Effect of daylength and light intensity

If the daily light energy is kept similar, it is to be expected that a long illumination with weak light will be more effective than a shorter illumination with stronger light. This aspect could be investigated more easily after we found that photoperiod has no significant influence. Bulbs of 3 cultivars were planted on 3 dates at the 12 combinations of 4 daylengths and 3 light intensities. As the 9 groups (3 cultivars × 3 dates) of plants reacted in a similar way, the results are presented for all the plants as one group. Table 5 presents the blasting percentages of the first bud and the measured

Table 5. Effect of daylength and light intensity on percentage of blasting of 1st bud and daily light energy (MJ m^{-2}) actually measured. Several cultivars and storages; 120 bulbs per treatment; planted 65-12-30, 66-02-22 and 66-03-17; temperature 22 °C and light energy flux density 45 W m^{-2}.

Light intensity (%)	Blasting (%) at ... h light					Energy (MJ m^{-2}) at ... h light				
	4	8	12	16	mean	4	8	12	16	mean
50	94	94	86	85	90	0.33	0.67	1.00	1.34	0.83
75	94	92	76	55	79	0.50	1.00	1.46	1.97	1.23
100	88	79	67	27	55	0.67	1.34	1.92	2.59	1.63
Mean	92	88	76	56	78	0.50	1.00	1.46	1.97	1.23

daily energies. Within the range investigated there were no specific differences in the effects of duration and intensity of light.

Discussion. Comparing the results of many experiments, either with 16 h light of different intensities or with different daylengths of the same intensity, Hartsema & Luyten (1955b, p. 374) concluded: 'It is of great importance, whether the total amount of light is given in a short or long day: the light requirement is significantly higher in longer days.' Their results relate to 'Imperator' at 0.34 to 1.97 MJ m^{-2} day^{-1} measured spherically. A conversion to horizontally measured values is practically impossible. It can only be stated that the converted figures will be lower when more reflected light was measured with the pherical sensor (Wassink & van der Scheer, 1953). Therefore, the conclusion of Hartsema & Luyten is probably valid only under marginal light intensities. In our opinion the general rule is that an extension of daylength is at least equally effective in lowering the blasting percentage as an increase of light intensity, provided that the intensity is not much below 30 W m^{-2}. Within certain limits, energetically as well as photoperiodically, the distribution of a specific light energy over the 24-h period has no influence on the percentage and time of flowering.

The sum of light until flowering

The preceding experiments indicate that when the temperature is raised, higher daily light energies are required to reach the same percentage of flowering. Because the higher temperature leads to an earlier flowering, the increased energy is given for a smaller number of days, so that the sum of light energy from sprouting till flowering may be higher than, similar to, or lower than the required light-sum at a low temperature. The second possibility of a similar value could indicate that total light requirement is constant at all temperatures. However, this is not the case as can be illustrated with the figures of Table 1. 'Dominator' produced 12 % second flowers after 78 days at 15 °C and 8 h of light. A similar percentage was reached after 49 days at 24 °C and 16 h of light. The required total energy sum can be calculated as 91 and 115 MJ m^{-2}, respectively. With regard to light energy the first condition was therefore the more economical, but as will be demonstrated, an increase of temperature may also diminish the light-sum required until flowering.

From a large number of experiments the overall relation between temperature and days to flowering is represented by Curve A in Fig. 1. The overall relation between temperature and the daily light requirement for 50 % flowering of the first bud is

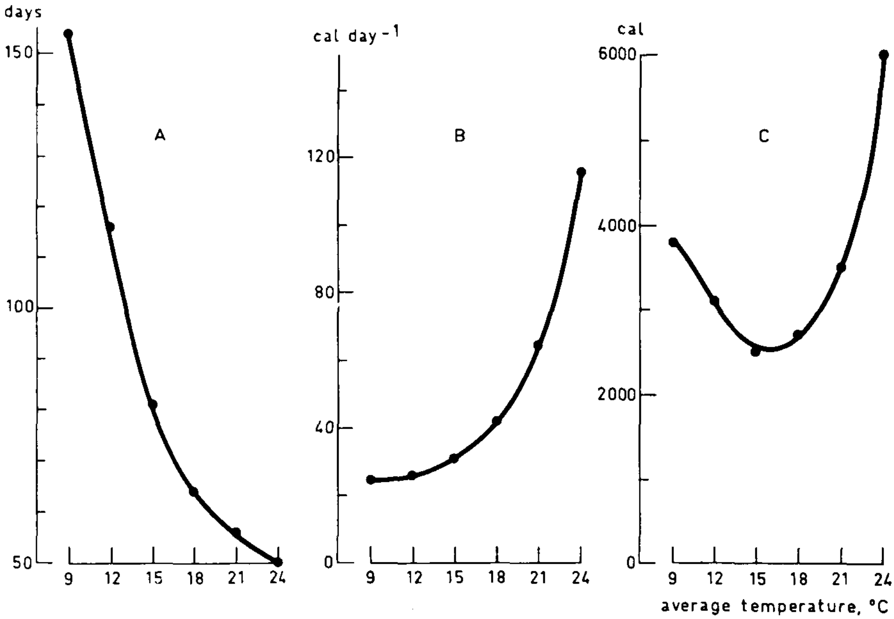

Fig. 1. Averaged for a number of experiments in different years with retarded and non retarded bulbs of different cultivars, the relation between the daily temperature and: A. days from sprouting to flowering; B. daily light requirement for 50 % flowering of the 1st bud; C. total light-sum (A $\times$ B) from sprouting to flowering. 1 cal $\approx$ 4.2 J.

represented by Curve B. From A and B the overall relation between temperature and the light-sum until flowering has been calculated. This is represented by Curve C, which has its lowest value at 15 °C.

Discussion. Curve C in Fig. 1 clearly demonstrates that a specific combination of temperature and light energy has to be chosen to arrive at the lowest total light requirement from sprouting till flowering. In practice the choice is almost impossible, because too many factors are involved. It depends amongst others on the acceptable percentage of flowering and on the levels of temperature and light at which this percentage will be reached. For 50 % flowering and low levels of both factors an increase of temperature and light will be at first more economic than a maintenance of the conditions and less if increased too much. At high levels an increase of temperature and light will directly lead to a larger total sum of light, because the daily light requirement increases more rapidly than the acceleration of flowering. It seems worth-while to compile more information for computing the relations more thoroughly for specific cultivars, forcing conditions, stages of growth and time of flowering.

Comparison of day and night temperature effects

To investigate whether a temperature increase during the day was more detrimental to flowering than one at night, plants were forced at 6 day and night temperatures (DT and NT) ranging from 9 to 24 °C, in all possible combinations. DT and NT each

Table 6. Effect of day and night temperature (DT, NT) on percentage of blasting of 2nd bud and days from planting to flowering of 1st bud. Storage 2 weeks at 35 °C + 3 days at 40 °C + 2 weeks at 17 °C + 6 weeks at 9 °C; planted 68-11-17; 54 'Wedgwood' bulbs per treatment; in phytotron on 68-11-18; 12 h light per day of 40 W m–2.

DT (°C)	Blasting (%) at ... °C NT							Days to flowering at ... °C NT						
	9	12	15	18	21	24	mean	9	12	15	18	21	24	mean
9	0	10	13	46	90	92	42	116	101	83	69	63	53	81
12	15	19	19	63	88	79	47	100	92	76	65	57	50	73
15	33	48	63	81	71	100	66	79	73	64	58	51	45	62
18	81	75	84	90	100	100	88	72	65	57	52	47	43	56
21	94	92	86	100	100	100	95	62	58	52	47	43	39	50
24	94	90	100	100	100	100	97	56	54	49	44	40	37	47
Mean	53	56	61	80	91	95	73	81	74	64	56	50	45	62

lasted for 12 h daily. Non-retarded bulbs of 'Wedgwood' produced 100 % flowering of the first bud in all 36 temperature combinations. Differences in blasting percentages of the second bud, however, were great. These are presented in Table 6, together with the number of days from planting till flowering. The figures demonstrate that the differences in the effects of a comparable change in DT and NT are small on percentage of bud blasting and on time of flowering. On an average an increase during the day stimulated bud blasting a little more than an increase during the night. In preceding experiments with retarded and non retarded bulbs (not presented), no difference was found and in one case even a greater effect of a temperature increase during the night. However, in all experiments time of flowering was mainly determined by the average daily temperature.

Table 7 presents the blasting percentages of the first and second bud in a similar experiment with retarded bulbs of 'Wedgwood'. In this case the effects of DT and NT on time of flowering were similar but on bud blasting they were much different. An increase of temperature during the day was definitely more harmful than an increase during the night. Of the first buds a smaller number blasted than of the second buds, but in both cases the relation between temperature and blasting percentage was similar.

The difference in both experiments regarding the effects of DT and NT becomes

Table 7. Effect of day and night temperature (DT, NT) on percentage of blasting of 1st and 2nd bud. Storage at 30 °C + 7 weeks at 17 °C; planted 69-06-23; 54 'Wedgwood' bulbs per treatment; 12 h light per day of 40 W m-2.

DT (°C)	Blasting (%) 1st bud at ... °C NT						Blasting (%) 2nd bud at ... °C NT					
	12	15	18	21	24	mean	12	15	18	21	24	mean
12	0	0	0	2	7	2	6	33	30	69	98	47
15	0	0	21	20	48	18	26	52	88	98	100	73
18	10	37	28	67	97	44	79	100	94	100	100	95
21	50	74	83	83	100	78	100	100	100	100	100	100
24	75	93	98	100	100	93	100	100	100	100	100	100
mean	27	41	46	54	66	47	62	77	82	93	100	83

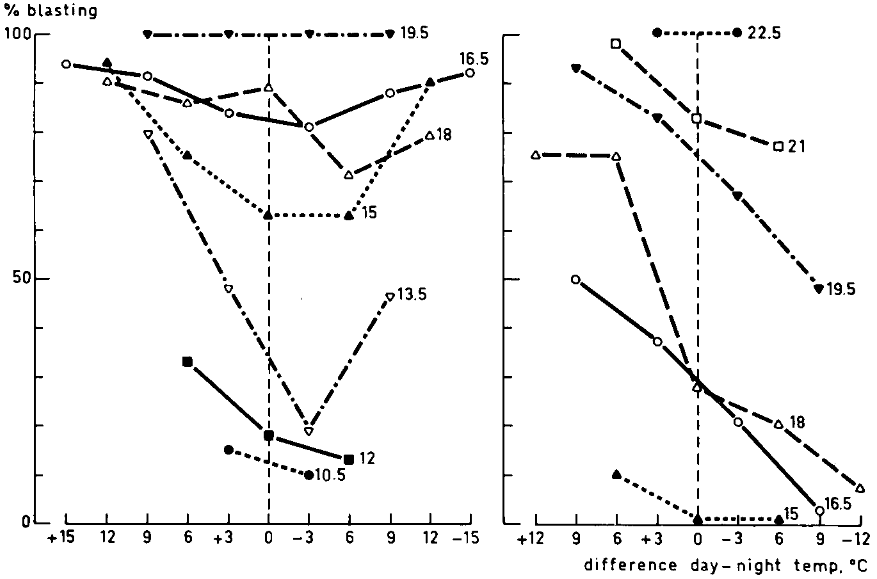

Fig. 2. Relation between a decreasing positive and increasing negative difference between a 12-h day and night temperature on percentage of blasted flower buds, for different averages of both temperatures indicated at the curves. Curves at the left side refer to percentage of blasting of the 2nd bud from Table 6, those at the right side refer to percentage of blasting of the 1st bud from Table 7.

clear in Fig. 2. It shows the relation between blasting percentage and a positive or negative difference between DT and NT for treatments with equal average daily temperatures, indicated on each curve. The left group of curves represents the results of the first experiment, the group on the right those of the second one. Both groups demonstrate that bud blasting increases with: 1) a higher daily temperature, given similar differences between DT and NT; 2) a larger positive difference between DT and NT, given similar daily averages. However, at a larger negative difference, the first experiment demonstrates also an increase of bud blasting whereas the second experiment shows a decrease. The latter indicates that in some cases an equal decrease of DT and increase of NT may diminish bud blasting, even in spite of the development of a negative difference between DT and NT. Both experiments clearly show that in general an increase of DT as well as of NT is detrimental, but an increased NT is sometimes less harmful than an increased DT.

Discussion. The incidental greater influence on bud blasting of an increase in DT compared with an increase in NT is quite unexpected, but in accordance with results of Kamerbeek & Beyer (1964) and Kamerbeek (1966). They reported that an increase of DT from 15 to 23 °C augmented bud blasting from 10 to 75 %, while a similar increase of NT diminished bud blasting from 10 to 0 %. This is the more remarkable because the day period was only 8 h (Kamerbeek, pers. commun.). On the basis of these results they considered an increase of NT as a more promising method to accelerate flowering than an increase of DT. Taking the difference in duration of DT and NT into account, one can calculate from their data that the effect of an increase of either DT or NT on the flowering date is about the same, which supports our results.

Wassink & Wassink-van Lummel (1952) investigated the effects of lowering NT, expecting that this would have a favourable influence on the energy balance by reducing the rate of dissimilation. This could lead to a lower total light requirement and thus to a decreased blasting at a given light intensity. However, the results failed to show any appreciable effect. This probably supports the above-mentioned results of Kamerbeek & Beyer. Nevertheless, van de Nes (1962) recommended a lowering of NT rather than DT to prevent bud blasting.

In a discussion of these contradicting results, J. F. Bierhuizen suggested that differences in the plant water status caused by differences in air and soil temperature, could be involved. A change in air temperature may cause a difference in air humidity and soil temperature. These secondary changes could induce differences in the requirement for and availability of water. Hartsema & Luyten (1961) found that a water shortage could induce bud blasting. Therefore, we had to consider the fact that during the research we gradually changed from dune sand as a medium for rooting to an organic pot soil, which adapts itself more slowly to air temperature. With this in mind we started to investigate the effect of soil temperature. It did not seem very likely that the increased bud blasting at high temperature was caused by a water stress due to a decreased humidity of the air. In that case more light would not have had a beneficial effect.

Comparison of air and soil temperature effects

Soil temperature (ST) lags increasingly behind a change in air temperature (AT) as pot size increases and as pot soil contains less sand or moisture. A positive difference between day and night temperature may therefore result in a positive difference between AT and ST during part of the daytime and a negative difference during part of the night. The reverse is true when the day temperature is lower than the night temperature. A positive difference between AT and ST during daytime is the particular condition for the occurrence of a water stress in the plant. This will be more likely to occur when the day is short and the difference between day and night temperature is large, because of the greater fall in ST during the long and cool night.

To verify this hypothesis, plants of 'Wedgwood' and 'Ideal' were grown in the open under a plastic cover. Only the temperature of the pot soil was regulated and changed every 12 h between 8 and 18 °C with an adaptation period of about 2 h. Four groups were distinguished with a change to the higher temperature at 0600, 1000, 1400 and 1800, respectively. Evapotranspiration was measured. Since no space was available in the phytotron, the experimental approach was not as ideal as could be. Besides, the third group did not flower at all due to a short period of overheating. Percentage of blasted second buds and days to flowering are presented in Table 8. The results support our expectation; bud blasting increased as the change in soil temperature was less synchronized with the change in air temperature. Time of flowering was not affected and the expected differences in transpiration were not found.

Table 9 presents the results with retarded 'Wedgwood' grown at combinations of three constant air and soil temperatures. Because of its possible relation to bud blast, the new bulb weight at time of flowering has been included. Bud blasting and speed of flowering increased with an increase of each of the temperatures, but the effect of AT was much greater. The deviating high value of 76 % at 21 °C AT and 15 °C ST could have been caused by the large positive difference between AT and ST. The

Table 8. Effect of an 8 °C and 18 °C soil temperature, changing every 12 h at different times of the day, on blasting % and days to flowering of 'Wedgwood' and 'Ideal'. Storage at 30 °C + 1 week at 17 °C + 7 weeks at 9 °C; planted 71-03-29 in a 15 °C greenhouse; 24 bulbs per treatment and cultivar; 71-04-13 placed outside at controlled soil temperatures.

Time of change from 8 to 18 °C	Blasting (%) of 2nd bud		Days to flowering of 1st bud	
	'Wedgwood'	'Ideal'	'Wedgwood'	'Ideal'
0600	42	61	48	49
1000	42	67	48	49
1400	†	†	†	†
1800	61	92	47	48

Table 9. Effect of constant air and soil temperatures (AT, ST) on percentage of blasting of 1st bud, days to flowering and on new bulb weight at flowering time of plants with (+) and without (–) flowers. Storage at 30 °C + 6 weeks at 17 °C; planted 67-05-25; 54 bulbs of 'Wedgwood' per treatment; 8 h light per day of 40 W m^{-2}.

AT (°C)	Blasting (%) at ... °C ST				Days to flowering at ... °C ST			
	15	18	21	mean	15	18	21	mean
15	10	17	23	17	55	49	46	50
18	26	36	69	44	46	45	44	45
21	76	46	72	65	38	35	32	35
Mean	37	33	55	42	46	43	41	43
AT (°C)	Weight (+) (mg) at ... °C ST				Weight (–) (mg) at ... °C ST			
	15	18	21	mean	15	18	21	mean
15	164	226	278	223	392	401	706	500
18	125	185	136	149	215	315	404	311
21	75	149	278	180	50	252	391	231
Mean	121	187	231	167	219	323	500	347

daughter bulb weight of flowering plants (+) was smaller than of those which did not flower (–). In both groups there was a positive correlation of bulb weight with ST and a negative correlation with AT.

Discussion. Wassink & Wassink-van Lummel (1952) already stated that the possible effects of soil temperatures differing from air temperatures should not be overlooked. Kamerbeek (1963a) found that an increase in root temperature from 13 to 18 °C increased bud blasting from 10 to 73 %. Cathey (1954), however, mentioned 18 °C as the best soil temperature. Durieux (1972a) stated that 'Wedgwood' and 'Ideal' are less susceptible to high soil temperatures than 'Prof. Blaauw'. He recommended special storage temperatures to decrease this susceptibility. Our conclusion is that lowering the soil temperature may decrease bud blasting, provided the difference with air temperature is not too large. Our supposition that a positive difference between AT and ST is particularly detrimental during daytime, has to be investigated. This may well be the reason of the observed greater susceptibility to an increase in temperature during the daytime as compared with an increase during the night.

The observed differences in bulb weight at flowering time indicate that bud blast may also be caused by early growth of the bulb, which competes with the flower for the available assimilates. The possibility that an advanced development of the daughter bulb is a cause rather than a result of bud blast, deserves more attention. The negative effect of an excessive leaf growth is no longer overlooked.

The total sum of temperature until flowering

It was shown earlier that time of flowering is almost independent of light and mainly determined by the average daily temperature *Ta*. This suggests that time of flowering could be expressed as the number of days *D* at which a specific temperature sum *Ts* is reached, taking into account the ineffective temperatures below a specific minimum temperature *Tm*. As *D* is known for a large number of *Ta*, *Ts* and *Tm* can be calculated with the formula $Ts = (Ta - Tm)\ D$. After conversion, the formula becomes $Ta = Ts \times 1/D + Tm$, a straight line representing a linear relation between *Ta* and the reciprocal of *D*. The line crosses the ordinate *Ta* at *Tm*, and makes an angle with the abscissa $1/D$ of which the tangent is *Ts*.

Fig. 3 presents the relation between $1/D$ and *Ta* for four of our temperature experiments with 'Wedgwood'. The relation is clearly linear, proving that date of flowering of each group is indeed determined by the temperature sum. However, this heat-sum is different for each group and diverges from about 400 to 900 degree days, while the minimum temperature ranges from 3 to 6 °C.

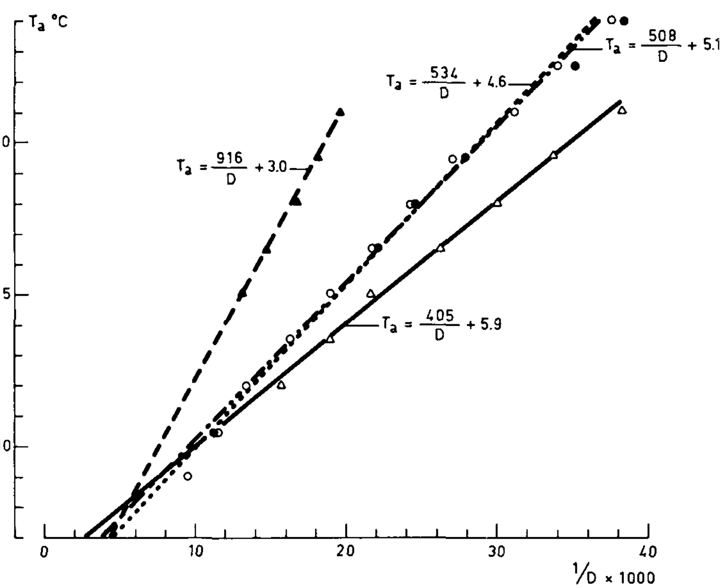

Fig. 3. Relation between the average daily forcing temperature *(Ta)* and the inverse of number of days to flowering *(D)*, for four experiments with 'Wedgwood' in different years. The formulas are explained in the text.

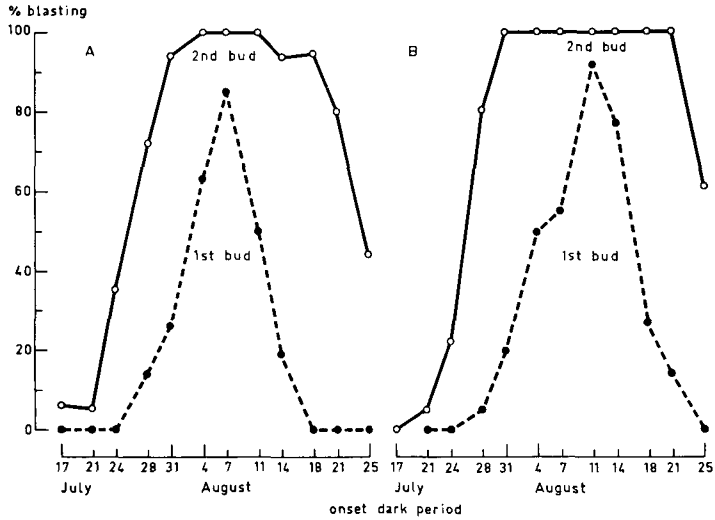

Fig. 4. Effect of a successive intercalation during growth of a four day period in darkness at 24 °C, on the blasting percentage of 1st and 2nd bud in two groups of 'Wedgwood' plants, planted 70-06-23 (A) and 70-06-27 (B) and grown in daylight at 15 °C. Storage at 30 °C + 6 weeks at 17 °C; 24 bulbs per treatment.

Discussion. The preceding results indicate that the heat-sum until flowering differs for each planting. Therefore, it is not useful under all circumstances to program flower production, even for one cultivar. Fig. 3 shows that the heat-sum decreases with an increase of minimum temperature, which indicates that differences in growth vigour existed, possibly because of differences in preparation of the bulbs. It is likely that blasting itself is not related to the heat-sum, but to daily temperature only.

The critical period for bud blasting

In the preceding discussions of the importance of different environmental factors, the period from sprouting till flowering was without an exception treated as a whole. To gain a deeper insight, similar studies have to be undertaken for successive short periods in the development of the plant. This would inform us whether and how temperature and light requirement for flowering change with time. To find the developmental stage most susceptible for blasting, two lots (A and B) of retarded 'Wedgwood' bulbs were planted 4 days after each other in daylight at 15 °C. After sprouting, groups of 24 plants of each lot were transferred successively to darkness at 24 °C and returned to the original conditions after 4 days. From an untreated group 10 plants were harvested weekly for various measurements of the stage of development reached. Percentages of blasted first and second buds for each of the successive treatments are presented in Fig. 4, for both lots.

The curves show that the effect of 4 days darkness at 24 °C on blasting increased with time, and then decreased. The susceptibility of the second bud follows a similar curve but is greater than that of the first bud. The curve representing the first bud reaches an optimum in the seventh period (7 August) of Lot A and 4 days later in the eighth period (11 August) of Lot B, thus indicating the same stage of development during which the plant is particularly sensitive. The curves representing the first and second bud in particular, demonstrate that susceptibility to bud blasting exists over a much longer period, i.e. at all stages of development. From the other observations it could be concluded that most blasting occurred in the group treated at the moment of optimum stem elongation when the bud just became visible. This was $3^1/_2$ weeks before flowering. In this group the first and second bud had reached a length of about 40 and 15 mm, respectively.

Discussion. Hartsema & Luyten (1953, p. 103) already stated that supplementary light should be given at least 40 days before flowering. They worked with 'Imperator' which requires more time to flower than 'Wedgwood'. The existence of a period during which iris is most susceptible for bud blasting could mean that a loss of flowers under marginal forcing conditions can be prevented by a slight lowering of temperature or a moderate increase of light intensity during a short period, if applied at the right time.

Main conclusions

1. Bud blasting after planting of bulbs potentially able to flower is mainly caused by too high temperatures and too low light energies.
2. Temperatures and light requirements change with the stage of plant development and are difficult to predict, because many other factors are involved, such as forcing time, storage and pre-harvest conditions, bulb size and cultivar.
3. The developmental stage during which the plant is most susceptible for the occurrence of bud blast, coincides with the period of the most rapid elongation, i.e. at the moment when the bud just becomes visible.
4. In the range of 9 to 24 °C a higher temperature accelerates flowering and increases the daily amount of light required to prevent bud blasting.
5. Within certain limits the distribution of the required daily light energy brought about by intensity and duration is of no importance for percentage and time of flowering.
6. The effect of day and night temperature on percentage as well as on time of flowering is about the same. Cases where the influence of the day temperature was greater than that of the night temperature could be explained by other factors, such as an insufficient adaptation of soil temperature to air temperature.
7. Bud blasting increases at high soil temperatures. Air temperature has a greater influence than soil temperature. In addition, bud blasting is promoted by a large positive difference between air and soil temperature, perhaps during daytime in particular.
8. Total light requirement till flowering is lowest at a specific combination of temperature and light intensity, depending on the acceptable percentage of flowering.
9. Time of flowering is determined by a specific heat-sum for each planting. Heat-sum and minimum temperature differ with each group and have no effect on bud blasting.
10. The physiological background of blasting is largely unknown. Internal competition for the assimilates plays an important role. The hypothesis that early development of the daughter bulbs is a cause rather than a result of bud blasting deserves more attention.

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