

THE EFFECT OF AIR AND SOIL TEMPERATURE ON ASSIMILATE PARTITIONING AND FLOWER BUD INITIATION OF FREESIA.

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Abstract

Time of flower initiation of Freesia 'Blue Heaven' depends on the average temperature of soil and air. Flower initiation is delayed when that temperature is increased irrespective of the separate soil and air temperature. At 13°C soluble carbohydrate and in particular reducing carbohydrate level in the second leaf is higher than at 21°C. At a low level (21°C) the apex remains vegetative and continues to form leaves. Carbohydrate level in the stage considered is mainly regulated by sink-activity of the leaves. Both higher soil and air temperature enhanced leaf growth, thereby reducing carbohydrate level. Source strength of the mother corm is not a limiting factor. Other competing sinks: growth of contractile roots and new corm was little affected by the treatments (contractile roots) or started growth after flower initiation in most treatments (new corm). Further research is outlined to establish the role of assimilates in the process of flower initiation.

1. Introduction

Flower development of Freesia has been widely studied (e.g. Mansour 1968; de Lint, 1969; Gilbertson-Ferris et al., 1981). It is generally concluded that Freesia requires a temperature of about 15°C for earliest flower initiation. In greenhouse experiments soil temperature was found to be the main factor (Spithost, 1979; Berghoef et al. 1986). In these experiments, however, air temperature was only partly controlled, and was higher than soil temperature. To evaluate the importance of both temperatures on flower initiation divergent combinations of soil temperature and air temperature should be applied. At high temperature flower initiation is delayed, resulting in the initiation of more leaves by the apex (Mansour, 1968). This indicates that either a floral stimulus has not reached the apex, or that a limiting factor is involved. In the nutrient diversion hypothesis Sachs (1977) and Sachs and Hackett (1969) proposed that translocation of assimilates may have a role in flower initiation. Flower initiation will not occur if the target tissue (apex) receives less than a threshold level of substrates. It is the result of either activation of the target sink, inhibition of alternate sinks or increase of source strength (Sachs, 1987). By having different air and soil temperatures, sink-activity of organs below soil level (roots, leaf base, contractile roots and new corm) and above soil level (leaves) are affected in different ways. Similarly this holds for the source strength of mother corm (below soil level) and of leaves (above soil level).

2. Material and Methods.

In November 1985 and November 1987 corms of 'Blue Heaven', size 6/7 cm were planted after a dormancy-breaking storage period of 13-15 weeks at 30°C in 5 l pots at a depth of 8 cm, 5 corms per pot. Soil was covered with 2 cm of wood chips for insulation. Soil temperature (ST) was controlled by temperature controlled water tanks ('Wisconsin tanks'). Air temperature (AT) was controlled in the greenhouse chambers of the phytotron with natural light. In 1985 three AT (13, 17 and 21°C) and three ST (13, 17 and 21°C) were used in 9 combinations without replication. In 1987 the same combinations of AT and ST were used, ST was replicated by using

independently working 'Wisconsin tanks'. Both mean AT and ST were within 0.5°C of the set-point. Starting 20 days after planting developmental stage of the apex of plants from one pot of each replicate was recorded at weekly intervals for 90 days in 1985 and 78 days in 1987. In 1987 also dry weight of mother corm, leaves, contractile roots and new corm were determined at weekly intervals.

In a separate experiment starch, reducing and non-reducing carbohydrate content was determined in leaves of plants growing at 13 or 21°C and a daylength of 16 hrs (35 W.m⁻² PAR) by SON/T and HPI/T (Phillips) lamps. Two samples of the second leaf of two plants were taken at the start and end of a light-period 22, 30, 43 and 52 days after planting. Carbohydrates were extracted of freeze-dried leaf material for 2 times 30 minutes in ethanol 80% (v/v). After centrifugation for 15 minutes (3000 rpm), the pellet was used for starch determination and the supernatant for soluble carbohydrates. Starch was hydrolysed with 8N HCl at 100°C for 30 minutes. Reducing carbohydrates were determined by Nelson/Somogyi (Nelson, 1944) at an extinction of 520 nm. Total carbohydrates were determined by Anthrone (Morris, 1948) at an extinction of 625 nm.

Statistical analysis was done by ANOVA at P=0.05. Mean separation was done by Tukey's Honestly Significance Difference test (HSD) at P=0.05. The best fitting polynome (up to the sixth degree) for the relation of leaf dry weight, mother corm dry weight and total plant dry weight against time was calculated. The degree of the polynomials was chosen by using the ordinary 'least squares estimate' (Draper and Smith, 1966). In more than 80% of the relationships polynomials of degrees 2 were necessary and sufficient. Therefore, in the present study, a quadratic relationship was fitted to all the plots of weight of above mentioned parameters against time. Thus for total plant dry weight as a function of time the following relation was assumed: $DW = a + b*t + c*t^2$ ($c \neq 0$). Curves of leaf weight were judged significantly different when estimates of a, b and c differed significantly by Student's t-test at P=0.05. Mother corm weight and total plant weight were judged significantly different when estimates of b and c differed significantly. Parameter a was ignored as mean starting weight of the mother corm, and thereby of total plant weight were equal (2850 mg).

3. Results.

3.1. Days till flower initiation

According to Hartsema (1962) flower initiation with Freesia starts with a rise of the apex (stage II) and shortly thereafter initiation of the first bract (stage Br). As it is sometimes difficult to observe whether stage II is reached we considered flower initiation as started when stage Br was reached. At a ST of 13°C flower initiation started after 36 days irrespective of AT (figure 1) but at 17 or 21°C increasing AT delayed flower initiation. At ST and AT of 21°C the apex was still vegetative at the end of the experiments. Time till flower initiation at ST/AT 13/17 did not differ significantly from ST/AT 17/13. The same is true for combinations of 17 and 21°C. At ST/AT 21/13 flower initiation is slightly, but not significantly delayed by 7.3 days when compared to 13/21. An average temperature (\bar{T}) of ST and AT can be calculated. Using the ordinary 'least squares estimate' for polynomial curve fitting a polynome of degrees 2 was necessary and sufficient for the relationship of the number of days till flower initiation N and \bar{T} , giving the quadratic function: $N = a + b*\bar{T} + c*\bar{T}^2$. Adding either ST or AT as a regressor to this function does not give a significantly better prediction of N, indicating that N only depends on \bar{T} .

3.2 Number of leaves and leaf area

At increasing temperature, either by higher ST or AT, the total number of leaves at the end of the experiment increased. At the combination 21/21 4.0 more leaves were initiated than at 13/13 (Table 1). Leaf area increased significantly with an increase of ST and AT from 13 to 17 and 21°C (Table 1).

3.3. Assimilate partitioning

Dry weight of all plant parts was determined, except of the normal roots. Weight of contractile roots and new corms are not included in the figures. Contractile root weight was 150 - 200 mg at the end of the experiment, without being significantly affected by treatment. New corm weight in all treatments was less than 20 mg until day 63. At day 78 weight was about 50 mg without significant differences between treatments.

At the combination ST/AT of 21/21 leaf growth was much faster than at 13/13 (figure 2A). Decrease of mother corm weight was also faster at the high temperature combination. Total weight at 21/21 decreased until day 41, thereafter it increased rapidly. At 13/13 total weight decreased less, but till the end of the experiment. Increase of AT at a fixed ST of 17°C (figure 2B) or increase of ST at a fixed AT of 17°C (figure 2C) gave significantly faster leaf growth and a significant decrease of mother corm weight. Total weight during the first 45 days of growth was not affected by AT, but was less at an increased ST. Combination 17/17 occupied an intermediate position and was omitted in both figures. As figures with a fixed ST or AT of 13 or 21°C showed comparable effects on leaf, mother corm and total dry weight they are omitted. At a calculated average temperature of 15°C (figure 3A), 17°C (figure 3B) or 19°C (figure 3C) AT nor ST had a significant effect on leaf growth, decrease of mother corm weight and total weight. The same effect was reached with either low ST and high AT or the inverse.

3.4. Starch and soluble carbohydrate content

In this experiment plants grown at 13°C started flower initiation at day 30, plants grown at 21°C were still vegetative after 52 days.

According to ANOVA starch content differed significantly between samples taken at the beginning and the end of the light-period. Mean comparison by Tukey's HSD-test at $P=0.05$, however, did not show significant differences. There were also no significant differences between starch content of the second leaf of plants grown at 13 or 21°C.

As there was no significant difference in soluble carbohydrate level at the beginning or end of a light-period, these values were combined. At 13°C soluble carbohydrate content was high at day 22 and then decreased (Table 2). At 21°C total soluble carbohydrate content was significantly lower at day 22 and 30 compared to 13°C. At day 43 and 50 it was significantly higher compared to 13°C. Reducing carbohydrate content on day 22 and day 30 was much higher at 13°C than at 21°C. At 13°C content of reducing carbohydrates decreased after day 30, whereas it increased in plants grown at 21°C.

4. Discussion

Time from planting till flower initiation primarily depends on calculated average temperature of soil and air. Increasing temperature delays flower initiation, independently whether a higher temperature is obtained by a higher soil or air temperature. In earlier experiments great effects of soil temperature were observed (Dijkhuizen and van Holstein, 1975). Air temperature, however, was not controlled in their experiments. A lower soil temperature means a lower average temperature, and as a consequence leads to earlier flower initiation as is confirmed by our results. When flower initiation is delayed, the apex continues to produce leaves. More leaves at higher growth temperatures were also found by Mansour (1968). Continuation of leaf initiation and delay of flower initiation by higher temperatures has been found with other species with storage organs like *Nerine* (Berghoef and van Brenk, 1983), *Allium porrum* (Dragland, 1972) and *Allium sphaerocephalon* (Berghoef, unpublished). We have found a considerable higher level of soluble carbohydrates in the second leaf at 13°C compared to 21°C. Assuming that this level is correlated with the carbohydrate level in the tissue surrounding the apex, assimilate level may be a limiting factor in flower initiation at high temperature. In the nutrient diversion hypothesis of Sachs (1977) this indicates that either the apex as target sink is activated insufficiently or that there are competing sinks involved. Alternatively source strength may be limited.

With *Freesia* there are four sinks in addition to the apex i.e. roots, contractile roots, the new corm and the leaves. Growing the plants in soil made it difficult to determine root dry weight.

Visual observations, however, at each sampling date showed no obvious differences between treatments. Contractile roots constitute about 7% of total dry weight 60 days after planting. Neither ST nor AT affected weight significantly, so although they are an important sink, they cannot be responsible for differences in flower initiation. The same conclusion can be drawn for the new corm. Increase of weight in all conditions started after 60 days i.e. after flowers were initiated in most of the treatments.

Leaf weight is affected by both AT and ST. Freesia being a monocot, leaf meristem is situated basically and thereby below soil level. As further development and leaf growth occurs above soil level, it can be expected that these processes are positively affected by both ST and AT as was found in combinations with the same average temperature. A high ST and low AT resulted in the same growth as the inverse. This indicates in other words that sink-activity of the leaves is equally determined by AT and ST. Sources available are photosynthesis and reserves in the mother corm. Photosynthesis will not be important as a source during the first part of the growing period, as can be concluded from the decrease of total plant weight. Moreover, in another experiment we have observed that at 13°C increase of leaf weight in the first 50 days of growth was the same at high (35 W.m⁻²) or low irradiance (5 W.m⁻²) (unpublished results). The mother corm constitutes the main source for assimilates during the first phase of growth. Source capacity of the mother corm, as a storage organ, is potentially not limited by carbohydrate content, but only by the possibility of mobilization and translocation. Mobilization should be affected by ST, being an enzymatic process, but also by rate of translocation. Translocation will be mainly regulated by sink-activity. As can be concluded from figure 3 both ST and AT affect decrease of mother corm weight in a similar way. Sink-activity of the leaves is regulated by both ST and AT, which leads us to the conclusion that decrease of mother corm weight mainly depends on sink-activity of the leaves either of the leaf base (ST) or the foliage (AT). At both high ST or AT translocation rate to the leaves will be high, resulting in a high mobilization rate, and thereby decrease of mother corm weight and a low soluble carbohydrate level due to increased sink-activity of the leaves. At low AT, translocation to the leaves will be less but potential source activity the same, resulting in a higher soluble carbohydrate level. At low ST, mobilization in mother corm will be less, but also translocation to the leaves. At low AT sink-activity of leaves is low, resulting in a high soluble carbohydrate level. Increase of AT will increase sink-activity and translocation, thereby reducing soluble carbohydrates and weight of the mother corm.

So far we have only data of carbohydrate levels of plants grown at equal ST and AT of 13 and 21°C and in artificial light. Verification has to be done with the diverged combinations of ST and AT. This will also include the use of small cormlets to reduce source capacity of the mother corm.

Assimilate level might also be hormonally controlled, as it was observed that gibberellin treatment enhanced flowering of Freesia (Cocozza Talia, 1983 and 1985). As in particular the level of reducing carbohydrates is higher at low temperature, temperature regulated invertase-activity may also be of importance.

Furthermore assimilate level might be regulated by dissimilation as loss of total weight depends on average temperature and is quite substantial during the first growth phase. Research on these topics should elucidate how assimilate level in the apex is regulated and whether it is important in controlling flower initiation.

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Table 1 - Effect of AT and ST on leaf number and leaf area, 78 days after planting.

Soil temperature	Air temperature					
	13°C		17°C		21°C	
	number of leaves	leaf area	number of leaves	leaf area	number of leaves	leaf area
13°C	8.1	175	8.6	271	9.6	312
17°C	9.0	288	9.2	343	10.6	352
21°C	10.2	283	10.8	354	12.1	382

Leaf number: Tukey's HSD= .6 (P=0.05)

Leaf area: Tukey's HSD= 157 (P=0.05)

Table 2 - Effect of temperature on reducing and soluble carbohydrates in second leaf (mg/g dry matter)

Days after planting	13°C		21°C	
	reducing carbohydr.	soluble carbohydr.	reducing carbohydr.	soluble carbohydr.
22	102.5	137.6	35.8	78.2
30	91.2	118.7	38.4	89.6
43	44.2	92.3	77.1	132.4
50	58.4	97.3	59.5	130.9

Reducing carbohydrates: Tukey's HSD= 30.0 (P=0.05)

Soluble carbohydrates: Tukey's HSD= 24.4 (P=0.05)

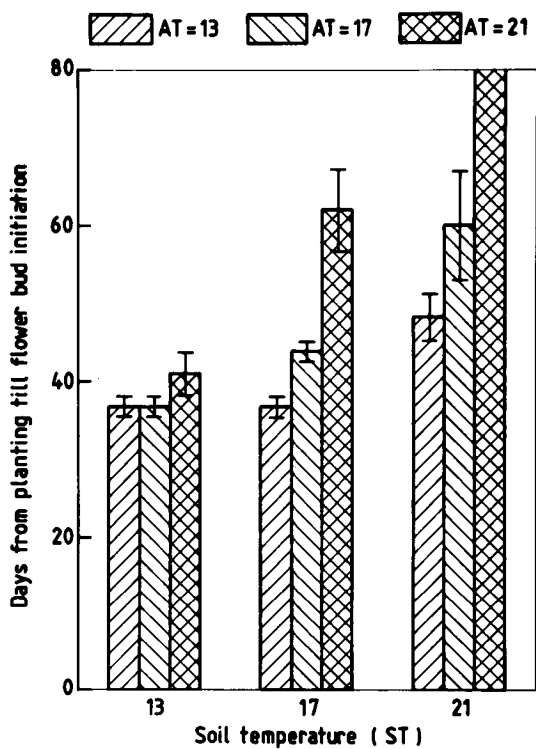


Figure 1 - Effect of soil temperature (ST) and air temperature (AT) on the number of days from planting till flower bud initiation.

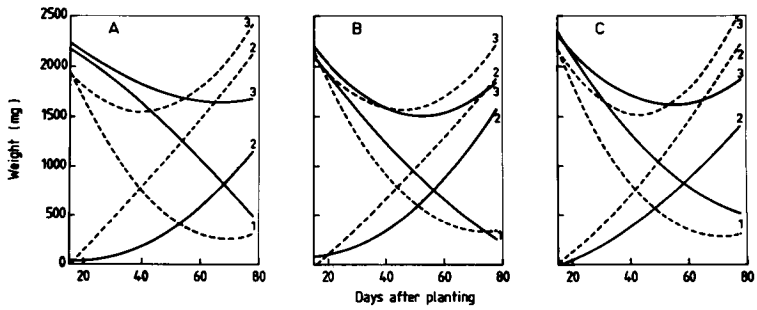


Figure 2 - Effect of soil temperature (ST) and air temperature (AT) on dry weight of mother corm (1), leaves (2) and total plant (3). Fig. 2A: ST/AT: 13/13 (—) and 21/21 (---); Fig. 2B: ST/AT: 17/13 (—) and 17/21 (---); Fig. 2C: ST/AT: 13/17 (—) and 21/17 (---). All curves in each figure showed significant differences for temperature, except total plant weight in fig. 2B.

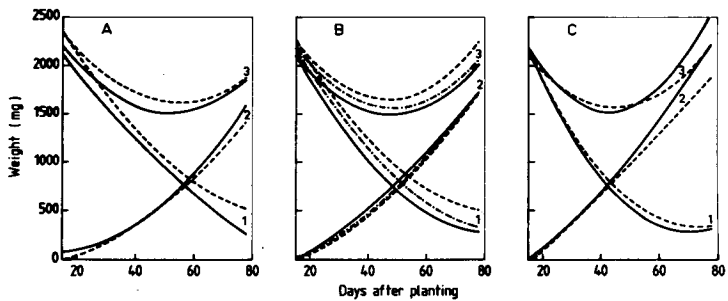


Figure 3 - Effect of soil temperature (ST) and air temperature (AT) on dry weight of mother corm (1), leaves (2) and total plant (3). Fig. 3A: ST/AT: 17/13 (—) and 13/17 (---); Fig. 3B: ST/AT: 21/13 (—), 17/17 (-.-) and 13/21 (---); Fig. 3C: ST/AT: 21/17 (—) and 17/21 (---). All curves in each figure showed no significant differences for temperature.