Acta Bot. Neerl. 21(3), June 1972, p 285–291

EFFECTS OF LONG DAY, HIGH TEMPERATURE AND GA_3 ON FLORAL INDUCTION AND STEM ELONGATION OF SAMOLUS PARVIFLORUS

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SUMMARY

In *Samolus parviflorus* Raf. long day induces flowerbud formation and increases stem length directly. Suboptimal induction by long day is completely desinduced by subsequent short day.

High temperature, 40°–45°C, when applied during 6 hours in the middle of the light phase of short day, has no flower inducing effect, but when applied in the middle of the dark phase it leads to complete induction. This similarity to *Silene armeria* L. suggests that also in *Samolus parviflorus* flower formation depends on two processes: light removes a blocking, darkness has a reblocking effect, but high temperature prevents this reblocking.

The inductive effect of GA_3 on flower formation was confirmed. Although high temperature in the light does not induce flowerbud formation, while in the dark it induces completely, both applications in combination with GA_3 have a pronounced stem elongating effect. Hence *S. parviflorus* offers another case of separating flowerbud formation and stem elongation.

1. INTRODUCTION

The remarkable phenomenon that the long-day ('LD') plant *Silene armeria* L. can be induced to flower formation in short day ('SD') by very high temperature has been studied in detail by VAN DE VOOREN (1969–1971, 1971). The temperature must be higher than 30°C, while the response increases from 35° to 50°C. It is active only when applied during the dark phase of SD, more specifically with an optimum after 6 to 7 hours from the beginning of the dark phase and a duration of action of 4 hours. These results led to a hypothesis on the mechanism of flowerbud formation which will be mentioned in the discussion. Other cases of flower induction by high temperature in LDP under SD conditions, as cited by VAN DE VOOREN, are *Hyoscyamus niger* (Schwemmle), *Scrophularia alata*, and *Stenactis annua* (Chouard).

The question arose whether more LD plants react like *Silene armeria*. As an experimental plant the american *Samolus parviflorus* Raf. was chosen, according to some taxonomists differing from the european *S. valerandi* L. In SD it remains in a vegetative rosette stage indefinitely. In LD its stem elongates and flowerbuds are visible after about four weeks. According to LANG (1957) and LANG *et al.* (1957) *S. parviflorus* belongs to the first plants which react to GA_3 (gibberellic acid) by flower formation in SD.

In the present study some details about the LD-induction, the effect of high temperatures, and the effect of the latter combined with GA_3 are discussed.

2. MATERIALS AND METHODS

Seeds of *S. parviflorus* were kindly put at my disposal by Anton Lang, so that the same material was used in his and my experiments. Seeds were sown in an ordinary greenhouse in flats with soil, pricked out after germination, and then grown in 9 cm pots with garden soil.

SD consisted of 8 hours natural light, in the poor-light season supplemented with HPL lamps, alternating with 16 hours of darkness. LD consisted of natural light, according to season supplemented with HPL lamps to 16 hours, alternating with 8 hours of darkness. High temperature was applied in two growth cabinets (VAN DE VOOREN 1971-IV), in which, in combination with each desired daylength, alternating temperatures could be given with two changes a day. Details about the programming and about the GA_3 treatments will be mentioned later.

3. EXPERIMENTAL RESULTS

3.1. LD-induction

Out of a group of vegetative plants grown in SD, 10 plants were put in LD and this was repeated daily, until finally a series was obtained which had been exposed from 1 up to 20 cycles of LD. Then all plants were put back in SD simultaneously. One set with 0 LD-cycles and one set in permanent LD were added. The essential observations are compiled in *table 1.*

Table 1. Effects on *Samolus parviflorus* of increasing numbers of LD-cyles, followed by SD, on numbers of plants out of 10 with flowerbuds and with open flowers, on days from beginning of SD to visible flowerbud formation, on effect of last LD-cycle, and on stem length in cm at flower bud stage.

LD-cycles	Plants with		Days	Effect last LD	Stem length
	buds	flowers			
0–5	0	0	–	–	–
6	1	0	56.0	–	0.5
7	2	0	38.0	18.0	0.5
8	5	2	34.8	3.2	0.8
9	7	7	27.7	7.1	0.8
10	10	9	25.2	2.5	1.1
11	10	9	24.7	0.5	1.2
12	10	9	20.7	4.0	2.0
13	10	10	19.5	1.2	2.0
14	10	10	16.3	3.2	3.6
15	10	10	15.3	1.0	4.3
16	10	10	14.4	0.9	5.3
17	10	10	12.8	1.6	6.9
18	10	10	11.6	1.2	7.1
19	10	10	9.7	1.9	8.7
20	10	10	8.6	1.1	10.8
∞	10	10	29.2*	–	38.0

* in LD!

From the numbers of plants with flowerbuds we see that 0–5 LD cycles had no effect, that 6–9 were transitory, while 10 or more resulted in 100% flowerbud formation. However, from the numbers of plants with open flowers it follows that 13 LD-cycles or more were needed to reach 100% and that open flowers have a slightly higher daylength requirement than flowerbuds. Not to be seen in the table is that, once open flowers were formed, flowering continued in SD, so that the LD-action is clearly inductive. The numbers of days in *table 1* decreased regularly as more LD-cycles had been given. This is self-evident, but by subtraction of a certain value from the one above it, the effect of the last LD-cycle can be found and apart from the marginal values up to 9 LD-cycles without 100% induction it appears that most values were higher than 1.0. This means that most LD-cycles had a somewhat greater effect than an increase of 1 day in the rate of flowerbud formation.

The numbers of days from flowerbud to open flower, not mentioned in the table, averaged 14 days with only slight variations. The stem length at the flowerbud stage (*table 1*) increased rather regularly as more LD-cycles had been given. Since the plants in ∞ LD produced very much higher stems than those after a limited number of LD-cycles, LD appears to influence stem elongation directly.

After 136 days from the beginning of the experiment all 94 non-flowering plants were put into LD. They flowered simultaneously, no matter how many LD-cycles they had received previously. The suboptimal LD-effect was completely lost, hence a complete 'desinduction' had taken place in SD.

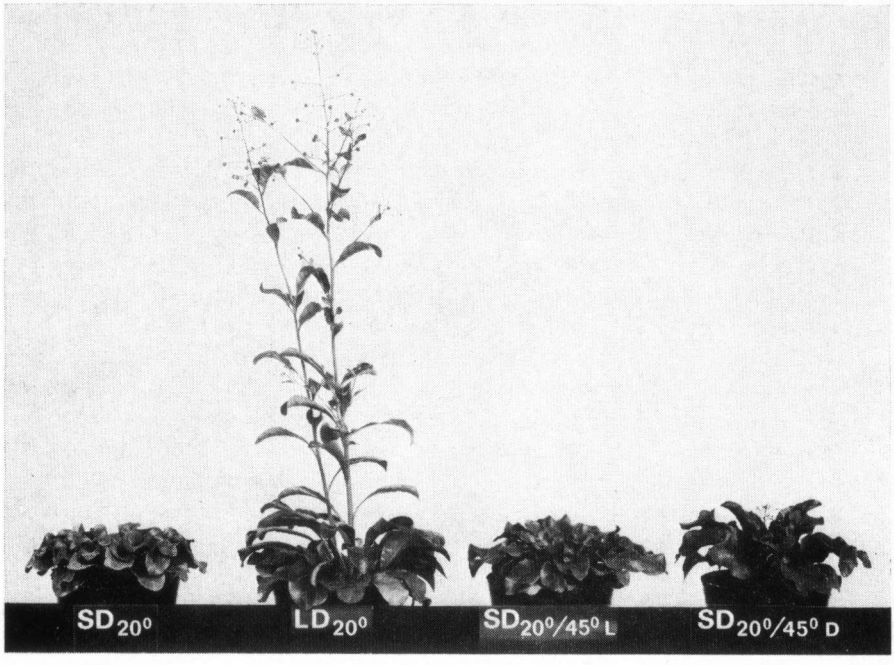
3.2. High temperature induction

Vegetative plants were exposed to SD at 20°C, beside that one group received 45°C during 6 hours in the middle of the light phase, another group 45°C during 6 hours in the middle of the dark phase. These treatments are coded as '45°L' and '45°D', respectively, and lasted 3, 4, or 5 weeks, each with 16 plants. Control plants were kept in SD or LD with uninterrupted temperature. The colour of the 45°L plants gradually turned into dark green, of the 45°D-plants into light green with necrotic margins. The former stood the treatment much better than the latter. Similar observations were made with several other species.

None of the SD-controls and 100% of the LD-controls flowered, as expected. None of the 45°L-plants flowered. However, from the 45°D-plants treated during 3, 4, or 5 weeks, 50%, 100%, and 81%, respectively, flowered. Evidently 3 weeks was too short, 4 weeks was optimal, 5 weeks was too long, which was also apparent from the habit of the plants at the end of the treatment. The stems of the flowering plants were remarkably short, as seen in *figs. 1* and *2*. No further data of this experiment are mentioned, because the next one with more treatments yielded a complete confirmation.

3.3. High-temperature and GA_3 induction

As controls ordinary LD and SD served. Similar high-temperature treatments as in the experiment sub 3.2 were applied, except that at 45° soon some damage


SD 20°
LD 20°
SD 20°/45° L
SD 20°/45° D

became visible and therefore after 1 week 45° was replaced by 40°, to be coded as '45°/40°'. All treatments were or were not combined with GA_3. The GA_3 was administered by applying on the growing-tip 0.3 ml GA_3 100 ppm twice a week, total amount during the 31 days of the treatment 300 μg per plant. A few drops of Tween as spreader were added to the solution. The aftertreatment, excepted the LD-controls, was ordinary SD. The essential results are summarized in *table 2.*

Table 2. Effects on *Samolus parviflorus* of LD or SD ∓ GA_3 (controls), of SD interrupted by 45°/40° in light ('L') phase, of SD interrupted by 45°/40° in dark ('D') phase, both ∓ GA_3 during 31 days, on numbers of plants out of 10 with flowerbuds, on numbers of days for visible flowerbud formation, and on stem length in cm at flowerbud stage.

Treatment	Flowerbuds		Stem length
	number	days	
1. LD − GA_3	10	24.5	12.3
2. LD + GA_3	10	22.4	17.7
3. SD − GA_3	0*	–	–
4. SD + GA_3	10	23.2	6.1
5. SD 45°/40°L − GA_3	0	–	–
6. SD 45°/40°L + GA_3	10	27.7	19.2
7. SD 45°/40°D − GA_3	10	41.2	4.8
8. SD 45°/40°D + GA_3	10	30.4	18.7

* 1 plant with a few flowerbuds more than 2 months after the others.

The numbers of plants with flowerbuds – which all turned into open flowers – were according to expectation: LD alone, 45°/40°D alone and all treatments with GA_3 induced, SD alone and 45°/40°L did not. The one flowering plant from treatment 3 is clearly an exception and may be illustrative of the identity of Anton Lang's material and mine: 'one plant flowered spontaneously for unknown reasons' (LANG 1957, p. 712).

The numbers of days, indicating the rate of flowerbud formation, show that the plants of treatment 7 are the only ones which did not flower during the 31 days' duration of the treatments and needed 10 more days in ordinary SD. The much lower value of treatment 8 shows that GA_3 enhanced the rate of flowerbud formation considerably.

Fig. 1. Representative plants of treatments, from left to right:
SD 20° = in permanent SD from sowing.
LD 20° = in permanent LD from 133 days after sowing.
SD 20°/45°L = From 105 days after sowing in SD at 20°, interrupted by 45° in the middle of the light phase during 4 weeks.
SD 20°/45°D = same, but interrupted in dark phase; detailed in Figure 2.
Photo taken 47 days after end of high-temperature treatments.
Fig. 2. Flowering in the rosette with very little stem elongation in SD 20°/45°D of Figure 1.

Also in treatment 7 the stem length at the flowerbud stage was exceptionally low, slightly less than in treatment 4. It was increased very considerably by GA_3. The most striking result follows from a comparison of treatments 4, 6 and 8, which shows that 45°/40°L, although in itself not inducing flowerbud formation, in combination with GA_3 had a pronounced effect on stem length, so that SD 45°/40° both in L and in D (treatments 6 and 8) reached practically the same stem length, even slightly higher than after treatment 2. This indicates that in combination with GA_3 both 45°/40°L and 45°/40°D in SD have a similar promoting effect on stem elongation.

4. DISCUSSION

The typically inductive action of LD on flower formation and the desinduction in SD after suboptimal induction are similar to those in *Silene armeria* (WELLENSIEK 1966). The higher LD-requirement of flower opening in comparison with flowerbuds is similar to e.g. peas (WELLENSIEK 1969, p. 392) and regarding SD-requirement to *Kalanchoë blossfeldiana* (VAN DE POL 1972, p. 30). The results on the inductive action of GA_3 confirm those of LANG (1957) and LANG *et al.* (1957).

High temperature, acting on floral induction only when applied in the middle of the dark phase of SD, acts essentially as in *Silene armeria.* VAN DE VOOREN (1971, p. 25) presented very good arguments for the hypothesis that flowerbud formation in originally vegetative *S. armeria* depends on two processes: (*a*) a deblocking in light and (*b*) a reblocking in darkness. Which of these processes dominates depends on the ratio of light and darkness: in LD (*a*) and in SD (*b*) will dominate. Furthermore, the reblocking in darkness is slowed down or completely nullified by high temperature, so that in this case also in SD flowerbud formation takes place. The analogy between *Silene armeria* and *Samolus parviflorus* suggests that in the latter species a similar mechanism acts. This might generally hold true for long-day plants. The stem elongating effect of high temperature, no matter whether applied in the light or in the dark phase of SD, if in combination with GA_3, has not been described before. No hypothesis on the mechanism of its action can be offered at present. The absence of floral inductive effect of high temperature in the light phase, in contrast to its positive action on stem elongation, offers another instance that floral induction and stem elongation can be separated.

BALDEV *et al.* (1965) reached the same conclusion for *Samolus parviflorus.* They found that growth retardants, AMO-1618 and CCC, inhibit flower formation and stem elongation, but that these actions are counteracted bij GA_3. It would be worth-while to study the combined effects of growth retardants and high temperature.

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