Neth. J. agric. Sci. 21 (1973) 245—255

Gibberellic acid, flower formation and stem elongation in *Silene armeria*[1]

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Accepted: 3 May 1973

Summary

Gibberellic acid (GA_3) induces complete flower formation in *Silene armeria* L. in short day (SD) only in certain genotypes, the GA^+ lines. In the GA^- lines GA_3 induces only partially. This partial induction disappears in SD, 'desinduction', while in GA^+ lines it remains and even procedes. The other flower-inducing factors, long day (LD), high temperature and vernalization, differ from GA_3 by always being able to induce completely, while after suboptimal induction always desinduction follows in SD.

The GA^+ characteristic is monogenically dominant over GA^-.

In GA^+ lines one single treatment with extremely high concentrations of GA_3, 0.3 ml 10 000 ppm per plant or more, induces flower formation in SD. For this shock treatment a juvenility exsists up to around 10 weeks.

Stem elongation after GA_3 treatment in SD increases with the concentration. No genetic difference regarding stem elongation occurs between GA^+ and GA^- lines. Stem elongation after GA_3 shock in SD does not take place in plants of clearly a much younger age than is required for flower formation. Stem elongation increases when the age of the treated plants increases.

After GA_3 treatment, flowering plants have much longer stems than comparable non-flowering ones. This GA_3-independent stem-elongation effect in flowering plants is greater when the GA_3 treatments take place at an older age of the plants. It probably does not directly arise from flower primordia, but from the prefloral stage.

Introduction

The vegetative growth habit of several horticultural crop plants consists of a rosette: a very short stem with many leaves close together. Arbitrary, but spectacular examples are cabbage and lettuce. Ordinarily, stem elongation or bolting from a rosette is accompanied by flower formation. Which of these processes starts first, whether the one is the cause or the effect of the other, are questions which are difficult to answer.

The dramatic effect of gibberellins on stem elongation of rosette plants is generally known. Sometimes this stem elongation is accompanied by flower formation under non-inducing circumstances, however sometimes it is not, and this is one of the many

[1] Publication 391, Laboratorium voor Tuinbouwplantenteelt, Wageningen, the Netherlands

arguments for concluding that stem elongation and flower formation are not necessarily linked.

For investigations on the effects of gibberellins on flower formation and on stem elongation, *Silene armeria L.* is quite a useful experimental plant. As a rule, in short days it forms a rosette, which in long days elongates its stem, while almost simultaneously flower buds are formed (Liverman, 1952). Gibberellins almost always have a stem-elongation effect, with the one striking exception of 'Dwarf' (Wellensiek, 1972). With regard to the flower-forming effect of gibberellins, the experimental results have remained conflicting, until a double specificity was discovered. Michniewicz & Lang (1962) established a chemical specificity: among 9 gibberellins only GA_7 induced flowers. Wellensiek (1969) demonstrated a genetical specificity: the flower-inducing effect of GA_3 depends on the genotype.

The present paper deals primarily with details about the flower-forming effect of GA_3. During these investigations clear differences regarding stem elongation were observed and a consideration of the mutual relationships between GA_3, flower formation and stem elongation turned out to be worth-while.

Materials and methods

From Liverman's material, obtained through the courtesy of Anton Lang, several lines with different characteristics were selected. In earlier work (Wellensiek, 1969, 1970; Wellensiek & van Brenk, 1971) the lines Early 1, Late 1 and Early 2 were used. During the course of the investigations renumbering became necessary and symbols with S (= Silene) and figures were introduced. In the present paper will appear:

Line S1.1, formerly E_1 = Early 1
Line S1.2, formerly L_1 = Late 1
Line S2.1
Line S3.1
Line S4.1, formerly E_2 = Early 2.

Apart from different reactions to GA_3 these lines differ in rate of flower bud formation and in critical day-length, but the latter topics will not be discussed. Notwithstanding careful selection not all lines are completely homozygous, so that sometimes small aberrations from type are found.

The experiments were carried out in the greenhouse. The usual methods of sowing and growing were used. Unless otherwise stated, the treatments started with vegetative plants of at least 8 weeks old, grown in short days.

Short day (SD) means 8 hours of sunlight, long day (LD) means 16 hours of sunlight, both supplemented and extended with strong artificial light, if needed.

Gibberellic acid (GA_3), obtained as berelex from I.C.I., was applied by administering near the growing-tip 0.3 ml with a Cornwall syringe No 1240 S. The concentrations and the frequency of application will be specified when discussing the separate experiments. The difficulty to obtain very high concentrations like 10 000 ppm was overcome by adding 1.3 ml 50 % KOH per liter, resulting in pH = 7.

Parameters were: number of flowering plants per treatment if not 100 %; date of appearance of first flower bud, from which was derived the number of days from the beginning of a treatment until visible flower bud; stem length in cm at various moments.

Experiments, results and conclusions

GA_3 and flower formation

GA_3 effects in different genotypes. A weekly treatment with 0.3 ml 100 ppm GA_3 was given to plants of 4 lines in continuous SD. The treatments were stopped after flower formation or in case of no flowering after 13 weeks, when no more flower formation could reasonably be expected. The results are given in Table 1. Apart from 1 plant flowering out of order, the lines S1.1 and S3.1 have not reacted with flower formation, while S2.1 and S4.1 convincingly have. The former are classified as GA–, the latter as GA+.

Table 1. Numbers of flowering plants out of 10 and average numbers of days for flower formation from beginning of weekly treatments with 0.3 ml 100 ppm GA_3 in 4 lines, with their classification.

Line	Treatment	Flowering	Days	Class
S1.1	$-GA_3$	0	–	GA—
	$+GA_3$	0	–	
S3.1	$-GA_3$	0	–	GA—
	$+GA_3$	1	75.0	
S2.1	$-GA_3$	1	72.0	GA+
	$+GA_3$	10	72.4	
S4.1	$-GA_3$	1	78.0	GA+
	$+GA_3$	10	68.5	

An experiment on GA_3 induction and desinduction in the same 4 lines was performed by applying 0.3 ml 100 ppm GA_3 in SD in 4 weekly successions, followed directly by LD, or followed by 4 weeks of SD, without GA_3, and next LD. Of course all plants flowered in LD, so that in Table 2 only the average numbers of days until flower formation in LD and the GA_3 effects have to be mentioned. It appears that the GA_3 effects in the 'LD directly' group are small, but even the smallest value is highly significant, so that at least some induction has occurred. The results after 4 weeks SD are completely different, for the GA_3 effects on S1.1 and S3.1 have totally disappeared and

Table 2. Average numbers of days for flower formation in LD and GA_3-effects as differences of $-GA_3$ and $+GA_3$ in 4 lines after 4 weekly treatments with 0.3 ml 100 ppm GA_3 in SD, either directly followed by LD or after 4 weeks SD; n = 12–16.

Line and class		LD directly			LD after 4 weeks SD		
		$-GA_3$	$+GA_3$	effect	$-GA_3$	$+GA_3$	effect
S1.1	GA—	25.4	22.3	+3.1	24.0	24.3	– 0.3
S3.1	GA—	25.8	24.1	+1.7	26.6	29.4	– 2.8
S2.1	GA+	21.0	20.0	+1.0	16.8	4.1	+12.7
S4.1	GA+	22.0	16.5	+5.5	22.0	4.9	+17.1

even have become negative. On the other hand, the GA_3 effects in S2.1 and S4.1 have increased very considerably.

We conclude that the partial GA_3 induction, which is apparent immediately after the GA_3 application, disappears, is desinduced during the subsequent 4 weeks of SD in the 2 GA⁻ lines, while the induction proceeds in the GA⁺ lines. Similar results were obtained in other experiments.

Genetics of sensitivity to GA_3 induction. The cross between the GA⁻ line S1.2 and the GA⁺ line S4.1 was analysed and Table 3 summarizes the results. In F_1 GA⁺ dominates, while backcrosses and F_2 are in agreement with a monogenic difference. Hence complete floral induction by GA_3 depends on one dominant pair of genes, while the recessive condition means only partial induction.

Table 3. For parental lines S1.2 (GA—) and S4.1 (GA+), their F_1, backcross (BC) F_1 × S1.2, BC F_1 × S4.1 and F_2 the numbers of flowering and non flowering plants and the % of flowering plants. Weekly applications of 0.3 ml ppm GA_3 in SD until termination of experiment after 13 weeks.

	Flowering	Non-flowering	Total	% flowering
S1.2 (GA—)	2	64	66	3.0
S4.1 (GA+)	60	1	61	98.4
F_1	51	3	54	94.4
BC F_1 × S1.2	50	54	104	48.1
expected	(52)	(52)		
actual deviation/standard deviation = 0.4				
BC F_1 × S4.1	73	1	74	98.6
F_2	173	70	243	71.2
expected	(182)	(61)		
actual deviation/standard deviation = 1.3				

Effect of GA_3 concentration. Shock treatment. In a former paper (Wellensiek, 1970) the effects of one application of 0.3 ml GA_3 in concentrations 0, 200, 400, ..., 1800 ppm on S1.1 and S4.1 were compared. Although the accelerations of flower formation in LD were small, varying between 2 and 4 days, a concentration effect as such was quite clear. This led to the question whether in a GA⁺ line one application of a very high concentration might be effective in SD. Concentrations up to 5000 ppm remained uneffective, but concentrations of 10 000 ppm or more resulted in flower formation. Table 4 summarizes the results of 2 experiments. Both from the numbers of flowering plants per treatment and from the average numbers of days for flower formation in SD it appears that the reaction of S1.1 as GA⁻ line can be neglected, but that S4.1 as GA⁺ line convincingly reacted to one shock treatment in SD.

Age and shock treatment. In order to study the possible influence of age on the effect of a GA_3 shock treatment, S2.1 plants of an age series 0, 2, 4, ..., 10 weeks were treated with an unusually large quantity of GA_3. Upon the suggestion of Dr J. van Bragt not one treatment with 10 000 ppm or more was given, but 3 treatments within 24 hours, each with 0.3 ml 8000 ppm. The '0 weeks' series was built up from seeds soaked in an 8000 ppm GA_3 solution for 5 days. The first lot failed and was replaced by another one, starting 1 week after the start of the first lot. Therefore, the actual difference in time between '0 weeks' and '2 weeks' is 3 weeks.

Table 4. Numbers of flowering plants out of 18 and average numbers of days for flower formation in SD in the GA– line S1.1 and the GA+ line S4.1 after 1 application of 0.3 ml GA_3 in the given concentration. Data of 2 experiments.

Concentration (ppm)	S1.1 (GA—)		S4.1 (GA+)	
	flowering	days	flowering	days
0	2	104.0	4	104.0
10 000	1	75.0	11	71.0
20 000	0	–	13	58.7
0	0	–	1	59.0
15 000	0	–	14	46.8

Only in the '10 weeks' age group flower formation took place. When after 12 weeks in SD no further flower formation could be expected, the 24 controls per age group, now representing an age series of 11, 14, 16 . . . , 22 weeks, were split up into 2 groups, one of which was shocked in the same way as described above. The results of both series are mentioned in Table 5. We see that relatively young plants did not react, but that from an age of 10 weeks flower formation occurred. The percentages of flowering at increasing ages tend to increase, but so irregularly, that no conclusion is justified. The existence of juvenility regarding a GA_3 shock, however, is beyond doubt. The limiting age approaches 10 weeks.

GA_3 and stem elongation

Concentration effect. Plants of the GA– line S1.1 and of the GA+ line S4.1 in SD received 1 application of 0.3 ml GA_3 in concentrations from 0 to 2000 ppm. The average stem lengths of the 14 plants per treatment after 8 weeks are shown in Table 6. The figures indicate an increasing effect of increasing concentrations, be it with some irregularities. The 2 lines do not present consistent differences.

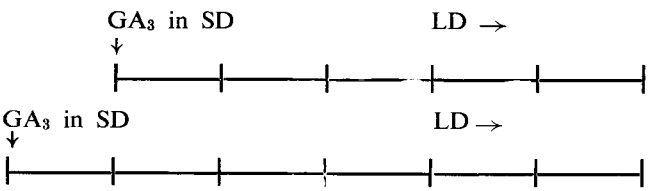
Table 5. Effect of 3 × 0.3 ml 8000 ppm GA_3, applied within 24 hours, on S2.1 plants of different ages. None of the controls –GA_3, not mentioned in the Table, flowered.

Age in weeeks	Final number	Flowering	% flowering	Days
0	24	0	–	–
2	24	0	–	–
4	23	0	–	–
6	24	0	–	–
8	23	0	–	–
10	23	10	43.5	79.8
11	12	4	33.3	64.0
14	12	7	58.3	63.7
16	12	4	33.3	62.3
18	12	9	75.0	56.7
20	12	5	41.7	52.4
22	12	11	91.7	62.5

Table 6. Average stem lengths in cm of S1.1 and S4.1, 8 weeks after 1 application of 0.3 ml GA_3 in given concentrations. n = 14; - = not measurable.

Concentration (ppm)	S1.1 (GA—)	S4.1 (GA+)
0	-	-
200	7.8	8.3
400	9.6	9.7
600	14.4	15.6
800	16.6	16.0
1000	16.3	17.5
1200	18.8	13.8
1400	18.1	16.5
1600	16.5	15.1
1800	18.7	19.7
2000	23.0	21.3

Influence of SD on the stem-elongating action of GA_3. Originally for other purposes than to study stem elongation, plants of S1.1 a nd S4.1 in SD were treated once with 0.3 ml GA_3 of different concentrations. The concentration ranges for both lines were not completely identical. After 3 or after 4 weeks of SD the plants were transferred to LD, where rather great differences between the 3 weeks and the 4 weeks groups soon struck the eye. Measurements were done after 2 weeks in LD and the results are presented as an interesting side-observation, which, however, remains unexplained. For a good understanding the 2 treatments are schematically represented by the following time schemes, which run from the moment of the GA_3 treatment until the moment of measuring:



The results are compiled in Table 7, which shows that the figures rise from top to bottom, be it somewhat irregularly. This is a concentration effect, as expected. The remarkable observation, however, is that all figures after 4 weeks SD are much lower than the comparable figures after 3 weeks SD. The differences of S1.1 tend to decrease as the concentration increases, with a striking exception at 1000 ppm, but the differences of S4.1 remain on the same level. In other words: the stem-elongating effect of GA_3 has been lowered considerably by one more week of SD between the GA_3-application and the LD, hence during the 4th week of SD.

Age effect with shock treatment. In the experiments on age effect of GA_3 shock treatment regarding flower formation, stem lengths were determined. The data of the age group 11 - 22 weeks will be dealt with later. For the moment, the average stem lenghts of the plants in the age group 0 - 10 weeks are summarized in Table 8. None of the

Table 7. Average stem lengths in cm of S1.1 and S4.1 as a result of 1 application of 0.3 ml GA_3 in given concentration, followed by 3 or 4 weeks of SD, each followed by 2 weeks of LD, with the diferences. n = 18. Controls S1.1 and S4.1 without GA_3 had stems of 4.9 and 7.7 cm, respectively, after 2 weeks of LD.

Concentration (ppm)	S1.1 (GA—)			S4.1 (GA+)		
	after 3 weeks SD + 2 weeks LD	after 4 weeks SD + 2 weeks LD	difference	after 3 weeks SD + 2 weeks LD	after 4 weeks SD + 2 weeks LD	difference
400				15.9	12.2	3.7
600	15.6	7.3	8.3	15.2	11.9	3.3
800	16.7	9.6	7.1	16.7	12.7	4.0
1000	19.5	8.6	10.9	22.5	18.6	3.9
1200	20.7	14.1	6.6	24.6	20.4	4.2
1400	20.3	15.7	4.6			
1600	21.4	18.3	3.1			

plants in the age groups 0 and 2 weeks developed a measurable stem. For the rest the age effect is quite clear: the older, the longer stem. The increases in stem length from 4 to 8 to 15 weeks afther the GA_3 treatment are rather small, so that the maximum stem length is reached fairly soon. An exception is the 10 weeks age group from 4 to 8 weeks. This must be connected with the flower formation, which occurred in this age group only, but this will be discussed in the following item.

Table 8. Average stem lengths in cm after 4, 8 or 15 weeks in SD of S2.1 plants of indicated ages, treated with 3 × 0.3 ml 8000 ppm GA_3 applied within 24 hours. n = 24. None of the controls without GA_3 had a measurable stem; – = no measurable stem.

Age in weeks	Average stem lengths cm) after		
	4 weeks	8 weeks	15 weeks
0	–	–	–
2	–	–	–
4	2.3	3.3	3.8
6	4.0	5.1	6.7
8	7.3	10.3	10.6
10	13.1	36.4	39.8

Flower formation and stem elongation

The enormous stem elongation of plants after flower formation has started cannot escape observation. The relation between flower formation and stem elongation can be very well studied in those treatments where some of the plants flower, some not. The GA_3 shock treatments were used to this effect. As a first orientation the material, already discussed in Table 4 will be used. Of course S1.1 is of no value, because practically no flowering occurred, so that in Table 9 only data about S4.1 are presented. It needs no long argumentation to conclude that the flowering plants produced a very

Table 9. Average stem lengths in cm of S4.1 plants in SD and number of plants (in brackets) after 1 application of 0.3 ml GA_3 of given concentration, divided in non-flowering and flowering plants. Data of 2 experiments, measured 66 and 80 days after GA_3 application, respectively.

Concentration (ppm)	Non-flowering	Flowering	Difference
10 000	27.9 (7)	72.3 (11)	44.4
20 000	50.2 (5)	106.0 (13)	55.8
15 000	16.0 (2)	84.3 (14)	68.3

considerably longer stem than the non-flowering ones. Since all plants received the same GA_3 treatments, the differences are only caused by non-flowering or flowering.

More detailed data were collected from the plants of the second part of the experiment on age effect of GA_3 shock in S2.1, presented in Table 5. Stem measurements were done at 4 weeks and at 11 weeks after the shock treatment. At 4 weeks no flowering plants were present yet, but a classification into non-flowering and flowering was made later. Fig. 1 demonstrates that within each age group the stem length of the

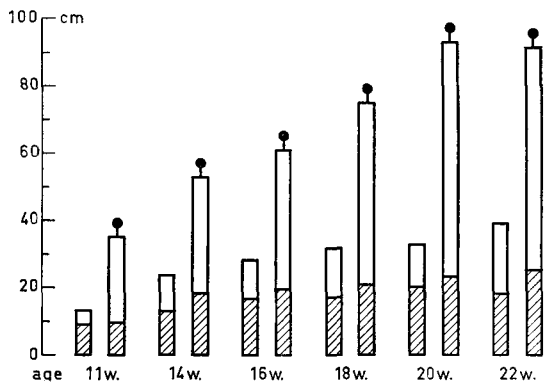


Fig. 1. Abscissa: Age of S2.1 plants in weeks (w.) when treated in SD with 3 × 0.3 ml 8000 ppm GA_3 within 24 hours.
Ordinate: Left of each pair of bars, average stem lengths of non-flowering plants. Right of each pair of bars with flowering symbol on top, average stem lengths of flowering plants.
Lower part of each bar length at 4 weeks after GA_3 treatment, upper part after 11 weeks.

Table 10. Increases in average stem lengths in cm between 4 and 11 weeks after treatment with 3 × 0.3 ml 8000 ppm GA_3 within 24 hours of S2.1 plants of indicated ages, separately for non-flowering and flowering plants; numbers of plants are in brackets.

Age in weeks	Non-flowering	Flowering	Difference
11	4.2 (8)	25.3 (4)	21.1
14	10.2 (5)	34.3 (7)	24.1
16	11.4 (8)	41.5 (4)	30.1
18	14.3 (3)	53.7 (9)	39.4
20	12.6 (7)	69.6 (5)	57.0
22	21.0 (1)	66.1 (11)	45.1

flowering plants was much greater than of the non-flowering plants. Although after 4 weeks the differences were already clear, much greater differences were found after 11 weeks. When the different age groups are compared, it appears that both among the non-flowering plants and among the flowering plants increasing age at the moment of GA_3 treatment means a longer stem. Only between 20 and 22 weeks discrepancies occur.

A further illustration from the same material is presented in Table 10, which again clearly shows (in rows) the differences between flowering and non-flowering plants, the differences increasing up to 20 weeks, and (in columns) between the age groups.

Discussion

The function of GA_3 in flower formation

There is no doubt that GA_3 must be considered as a floral-inducing factor, however according to Cleland & Zeevaart (1970) as a pharmacological factor rather than a physiological one, because no relation between internal level of GA and flower initiation was found. It is therefore not surprising that the action of GA_3 deviates from the physiologically inductive factors LD, high temperature and low temperature. These three are able to induce completely and after suboptimal induction the effects of all three are desinduced in SD (Wellensiek, 1966). Regarding GA_3, complete or only partial induction may occur, depending on the genotype. There are GA+ and GA– lines. From their data it is evident that Cleland & Zeevaart (1970) have used a genetically impure GA+ line. Furthermore, partial induction in GA+ lines is never followed by desinduction, but partial induction in GA– lines is followed by desinduction in SD. The negative effect of GA_3 after such a desinduction in Table 2 could perhaps be ascribed to a weakening of the plants through the stem-elongating action of GA_3. The absence of desinduction in the GA+ lines could point to an optimal induction – which is never followed by desinduction – but this is not evident, since in SD no flower formation occurred, unless after a shock treatment.

The genetically determined sensitivity to complete floral induction by GA_3 could suggest a destruction of an inhibition by the dominant gene. With other words: in partially sensitive lines, GA−, complete flower formation is inhibited, but in completely sensitive lines, GA+, this inhibition is nullified by the GA+ gene.

The effect of shock treatment with GA_3 in sensitive lines (Tables 4 and 5) shows that GA_3, once administered in a large enough quantity, shows long-lasting effects.

The duration of juvenility for shock treatment, in Table 5 established as longer than 8 weeks, cannot be considered as an absolute value, because doubtlessly the sensitive age is influenced by environmental factors. The existence of juvenility as such is beyond doubt, however. It suggests that the plant needs a minimal size to react to GA_3.

The stem-elongation properties of GA_3

Stem elongation after GA_3 treatment is often irregular, both within treatments and between treatments. Cleland & Zeevaart (1970) found the same high variability. This does not exclude that GA_3 has always at least some stem-elongating effect, except in very young plants and in the remarkable 'Dwarf' (Wellensiek, 1972), which was not included in the present material. An effect of the GA_3 concentration on stem elongation

(Table 6) is clear, without differences between GA− and GA+ lines.

The lowering of the stem-elongating effect of GA_3 in the 4th week of SD after the application of GA_3, as demonstrated in Table 7, is an observed fact, which deserves attention, but which is hard to understand. At first glance the phenomenon is similar to desinduction of partial induction, but desinduction regarding stem elongation is unlikely, because stem elongation must be considered as a direct action of GA_3, and not as an induction. This renders desinduction unacceptable.

Also for stem elongation after a GA_3 shock treatment the existence of a juvenile phase was found, in Table 8 longer than 2 weeks. This value is just as relative as in case of floral induction, while absence of a measurable stem in the lowest age groups does not necessarily mean absence of some stem elongation, since the plants could not be dissected without sacrificing them. Because the observations on stem elongation and flower formation were done with the same material, grown under the same conditions, the conclusion is justified that juvenility for stem elongation, if it exists, lasts (much) shorter than for flower formation. This is another argument that stem elongation and flower formation are not identical processes.

The stem-elongating effect of flower formation

The strong stem-elongation effect of flower fomation (Fig. 1) is so convincing that further discussion of the fact is unnecessary. A remaining topic of interest is the question when this influence starts. Cleland & Zeevaart (1970) found that the onset of floral initiation precedes stem elongation. This confirms unpublished results of C. G. Elings in 1967. The observations, dealt with in the experimental part, have shown that already 4 weeks after treatment with GA_3 in SD the influence of future flowering could be detected. This is long before flower buds became visible and suggests that the stem-elongating effect did not arise from the flower buds, but rather from the prefloral stage.

A completely analogous stem-elongating effect of flower formation was recently found in peas (Wellensiek, 1973) with totally different methods. In the present case of *S. armeria* non-flowering and flowering plants within one treatment were compared. In peas the ontogenetical development of individual plants with different genotypes was analysed.

There is no doubt that the present research has implications for the mechanism of flower formation in *S. armeria* in general, but a discussion of this topic is beyond the scope of the present paper.

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