Gibberellins and Stem Growth as Related to Photoperiod in Silene armeria L.¹

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ABSTRACT

Stem growth and flowering in the long-day plant Silene armeria L. are induced by exposure to a minimum of 3 to 6 long days (LD). Stem growth continues in subsequent short days (SD), albeit at a reduced rate. The growth retardant tetacyclacis inhibited stem elongation induced by LD, but had no effect on flowering. This indicates that photoperiodic control of stem growth in Silene is mediated by gibberellins (GA). The objective of this study was to analyze the effects of photoperiod on the levels and distribution of endogenous GAs in Silene and to determine the nature of the photoperiodic after-effect on stem growth in this plant. The GAs identified in extracts from Silene by full-scan combined gas chromatography-mass spectrometry (GC-MS), GA₁₉, GA₃₃, GA₄₄, GA₁₇, GA₁₉, GA₂₀, GA₁, GA₂₉, and GA₆, are members of the early 13-hydroxylation pathway. All of these GAs were present in plants under SD as well as under LD conditions. The GA₂₀ level was highest in plants in SD, and decreased in plants transferred to LD conditions. By contrast, GA₁₉, GA₂₀, and GA₁, initially increased in plants transferred to LD, and then declined. Likewise, when Silene plants were returned from LD to SD, there was an increase in GA₂₀, and a decrease in GA₁₉, GA₂₀, and GA₁, which ultimately reached levels similar to those found in plants kept in SD. Thus, measurements of GA levels in whole shoots of Silene as well as in individual parts of the plant suggest that the photoperiod modulates GA metabolism mainly through the rate of conversion of GA₂₀. As a result of LD induction, GA₁ accumulates at its highest level in shoot tips which, in turn, results in stem elongation. In addition, LD also appear to increase the sensitivity of the tissue to GA, and this effect is presumably responsible for the photoperiodic after-effect on stem elongation in Silene.

It is well established that in LDP photoperiodic control of stem growth is mediated by GAs². Several lines of evidence support this conclusion. Application of GAs under noninductive photoperiods stimulates stem elongation whereas treatments with inhibitors of GA biosynthesis suppress growth induced by LD conditions (17, 18). The promotive effects of LD on stem growth may be attributed to an increase in the levels of endogenous GAs (8, 9). In spinach, it has been shown that LD regulate GA metabolism by modulating the activity of two enzymes of the GA biosynthetic pathway, viz. GA₃₃-oxidase and GA₁₉-oxidase (4). These enzyme activities are present at high levels in plants under continuous light and increase the level of the active GA which, in turn, causes stem elongation.

In contrast to spinach, in the LDP Silene armeria interruption of LD by SD does not result in cessation of stem growth (1, 16). This requirement for a minimum number of LD for stem elongation to continue in SD suggests that following photoinduction GA metabolism is not altered. Previous work has shown that in Silene, LD increase GA turnover (14), as well as the endogenous GA-like activity (1).

In this paper, we report the main GAs identified in Silene armeria as 13-hydroxylated GAs. In addition, the effects of photoperiod on the levels of four physiologically important GAs, GA₃₃, GA₁₉, GA₂₀, and GA₁, as well as their distribution in different parts of the plant, are described.

MATERIALS AND METHODS

Plant Material

Seeds of Silene armeria L., strain S 1.2 (15), were sown on 1.5% agar. The seedlings were grown in plastic cups (240 mL) filled with soil. The plants were watered daily with half-strength Hoagland nutrient solution and kept in a growth chamber under SD conditions for approximately nine weeks until ready for experimentation. SD conditions consisted of 8 h light from fluorescent tubes and incandescent bulbs (350 μmol·m⁻²·s⁻¹) at 23°C, followed by 16 h darkness at 20°C. LD conditions consisted of the same main light period as SD, but supplemented with 16 h weak light from incandescent lamps (10 μmol·m⁻²·s⁻¹) at 20°C. Auxillary buds were removed at the beginning of the experiments and periodically thereafter. Development of the floral primordia was scored according to Takimoto (13).

For GA analysis, the whole shoot, except senescing leaves, was harvested. However, in the experiment on distribution of GAs, selected organs were collected. From each plant in the rosette stage the following organs were harvested separately: (a) apical tip, consisting of 5-mm long vegetative shoot tip with a pair of 6-mm long young leaves attached; (b) four pairs of light-green expanding young leaves (4.5–5.5 cm long); (c) six pairs of dark-green mature leaves (8–9 cm long); (d) stems, 1 to 2 cm long. From each elongated plant at anthesis the following were collected: (a) floral structures at anthesis or

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² Abbreviations: GA(s), gibberellin(s); amu, atomic mass unit; m/z, mass/charge; MeTMSI, methyl trimethylsilyl ether; KRI, Kovats Retention Index; SIM, selected ion monitoring; Tcy, tetcyclacis.
preanthesis stage (1 cm long); (b) the first, second, third, and fourth pair of the dark-green mature basal leaves; (d) stem, including internodes and peduncles (45–50 cm long).

Spinach (Spinacea oleracea) was grown as described (4). All samples were frozen immediately in liquid nitrogen, lyophilized, and stored at −20°C until analysis.

**Tetcyclacis Treatments**

When plants were kept continuously under SD or LD conditions applications of 10 mL Tcy (10−5 M) per plant were made to the soil on alternate days, beginning at the start of the experiment. If LD treatments were followed by SD, the inhibitor was applied starting at the beginning of the SD treatment.

**Extraction and Purification Procedure**

Freeze-dried samples were homogenized in cold 80% aqueous methanol in a Waring blender and the solvent was removed via a Büchner funnel. The residue was resuspended in the same solvent at 4°C overnight. The combined filtrates were reduced to the aqueous phase in vacuo at 35°C. An equal volume of 0.1 M KPi buffer at pH 8.2 was added, and the pH adjusted to 8.2. The extract was partitioned against hexanes (1:1, v:v), diethyl ether (5:1, 2:1, v:v), and again against hexanes (1:1, 2:1, v:v). The aqueous phase was adjusted to pH 2.8 using 6 N HCl, centrifuged, and purified by charcoal: Celite (1:2) adsorption chromatography (9). The GAs were eluted with 80% acetonitrile. The acetone was removed under reduced pressure, the aqueous residue adjusted to pH 2.5, and partitioned against ethyl acetate (5:1, 2:1, v:v). The organic fraction was further purified by silicic acid:Celite (1:2) adsorption chromatography as described (9). Additional purification was achieved by anion exchange chromatography.

The dried eluate from the silicic acid column was redissolved in a few drops of methanol, 0.1 M KPi (pH 8.2) was added, and the pH of the solution was adjusted to 8. The solution was applied to a column (1 x 10 cm) of QAE-Sephadex-A25 that had been equilibrated with 1.0 M Na-acetate. The column was washed with 5 volumes of water (pH 8). After application of the sample, the column was washed with water at pH 8 (30 mL). The GAs were eluted with 1 N acetic acid (40 mL). The eluate was reduced to dryness on a rotary evaporator.

**Reverse Phase HPLC**

Fractionation of GAs was carried out by reverse phase HPLC as described before (8). The extracts were injected onto an analytical column (30 x 0.4 cm) packed with μBondapak C18 which was attached to a C18 Guard-PACK precolumn. A 30 min linear gradient of 20 to 80% methanol in 1% aqueous acetic acid at a flow rate of 2.0 mL/min was used. Fractions were collected at 1 min intervals.

**Bioassay**

In preliminary experiments, HPLC fractions were assayed for GA-like activity using the d-5 corn bioassay as described previously (7).

**Qualitative Analysis by GC-MS**

HPLC fractions were collected, dried, and dissolved in methanol; they were combined in 14 groups of two to four fractions which were methylated with ethereal diazomethane. The samples were trimethylsilylated by adding 10 μL of pyridine-hexamethyldisilazane-trimethylchlorosilazane (9:3:1). The derivatized samples were analyzed using a JEOL AX 505 double focusing GC-MS system. The samples were coinjected with Parafilm (3) into an HP ULTRA 2 fused silica capillary column (25 m x 0.32 mm, 0.52 μm film thickness) at an oven temperature of 50°C in splitless mode. The oven temperature was increased at 40°C/min to 220°C, and then at 6°C/min to 280°C. The He inlet pressure was 70 kPa and the injector, interface, and source temperatures were 280, 290, and 250°C, respectively. Positive ion electron impact mass spectra at 70 eV were acquired scanning from 50 to 800 amu at 1 s per scan cycle.

**Quantitative Analysis by GC-SIM**

For quantification purposes, [17,17-2H2]GA31 (99.0% enrichment), [17,17-2H2]GA19 (94.2% enrichment), [17,17-2H2] GA30 (99.3% enrichment), and [17,17-2H2]GA1 (99.2% enrichment) were added to the tissue homogenate as internal standards. The amounts to be added were estimated by preliminary experiments using ion current areas of the base peaks to provide approximate levels of the endogenous GAs. HPLC fractions were analyzed with the same GC-MS instrument and GC conditions described above for full-scanning GC-MS analysis, except that SIM with magnetic field switching was used. The instrument was calibrated between 300 and 600 amu with perfluorokerosene as reference. Each mixture of labeled/unlabeled GA or authentic GA was first injected for SIM peak adjustment and determination of the appropriate retention time window. Ions were monitored with dwell times of 100 ms as follows: for GA1/[17H2]GA1-MeTMSi, m/z 508, 506, 491, 448; for GA30/[17H2]GA30-MeTMSi, m/z 420, 418, 403, 375; for GA19/[17H2]GA19-MeTMSi, m/z 462, 436, 434, 375; and for GA31/[17H2]GA31-MeTMSi, m/z 450, 448, 419, 389.

For calculating the endogenous GA content, the contribution from natural isotopes from the unlabeled derivatized GAs was measured and the concentration of GA1, GA20, GA19, and GA31 estimated from the peak area ratios 506/508, 418/420, 434/436, and 448/450, respectively, by the formula in Fujikova et al. (2).

Quantification of the GAs was performed in at least two different experiments in which the observed ratio of internal standard to endogenous GA was close to unity.

**RESULTS**

**Effects of Photoperiod and Tetcyclacis on Stem Growth and Flowering**

Silene plants kept under SD conditions showed a rosette growth habit for at least 5 months with stems only 1 to 2 cm long. Stem elongation took place only after exposure to LD. In continuous LD, the growth curve showed a lag phase of 10
to 12 d, followed by 10 to 25 d of rapid growth with a steady 
growth rate of 2.0 to 2.5 cm/d (Fig. 1A). When plants were 
exposed to 0 to 20 LD and then returned to SD conditions, 
stem elongation occurred later and the growth rate was less 
than in continuous LD. Significant stem elongation was ob-
served after exposure to 3 LD (data not shown), whereas 20 
LD produced slightly taller plants than continuous LD treat-
ment. Between these two treatments Silene plants produced 
longer stems as exposure to LD increased (Fig. 1).

Applications of Tcy to plants exposed to continuous LD 
inhibited stem elongation by 80% (Fig. 1B). When the growth 
retardant was applied after LD induction had been completed, 
the inhibitory effect was less pronounced as the number of 
LD increased. Thus, stem elongation was reduced by 74% in 
plants exposed to 6 LD and then treated with Tcy, but only 
14% in plants kept under LD conditions for 20 d before Tcy 
applications started.

Floral initiation was determined according to the stages 
described for Silene by Takimoto (13). The first microscopic 
sign of floral initiation (stage 1) was observed after 8 LD 
(Table I), which indicates that cell division and the beginning 
of the cell elongation period had occurred earlier. During the 
following days, floral organs developed rapidly: stages 2, 3, 
and 4 were observed after 10, 12, and 14 LD, respectively. 
Anthers and pistils were visible under the dissecting micro-
scope after 16 to 18 LD (stage 5), and anthesis started after 
28 LD. The minimal number of LD to induce 100% flowering 
was 6 LD, but in some plants flowering was induced with as 
far as 3 LD, whereas plants kept in SD never produced any 
flower primordia. However, there was no obvious relationship 
between the degree of flowering and either the duration of 
LD exposure or the height of the plant. Further, plants treated 
with Tcy during or after LD induction produced open flowers 
earlier than the controls.

Identification of Gibberellins

Following reverse phase HPLC, biological activity was de-
ected in four zones (Fig. 2), viz. in fractions 15 to 16, 22 to 
25, 28 to 29, and 33 to 34. Based on the activity detected in 
the bioassay, 2 to 4 HPLC fractions were combined for analy-
ysis by full-scan GC-MS. Fractions without biological activity 
were also analyzed by GC-MS.

GA₁₂ and the following members of the early 13-hydroxy-
laction pathway, GA₃₃, GA₄₄, GA₁₇, GA₁₉, GA₂₀, GA₂₉, GA₁, 
and GA₅₆, were identified in extracts from Silene shoots (Table 
II) on the following basis: GA₅₃, GA₁₉, GA₂₀, GA₁, and GA₅₆ 
were identified by comparing mass spectra and KRIs with those 
of authentic, 13H₂ or 13C-labeled standards. GA₁₇, GA₄₄, 
and GA₂₀ were characterized by comparing the same param-
eters with those of GAs extracted from spinach (9). Finally, 
GA₁₂ was identified by comparing its mass spectrum and KRI 
with published data (5, 12).

In addition to the GAs of the early 13-hydroxylation path-
way, Silene extracts contained various uncharacterized GAs 
and related compounds. Two of these compounds had mass 
spectra indicative of dihydroxy-GA₁₂, with one of the two 
hydroxyl groups most likely at the C-13 position. The 
compound with the higher KRI has been found previously in 
maize (2, 6) and has been tentatively assigned the structure 
16,17-dihydro-17-hydroxy-GA₃₃. This compound probably 
arises from GA₅₃ by reduction of the 16,17-double bond, but 
it is also possible that it is an artefact that arises during the 
extraction and purification procedures. The other compound 
is an isomer of GA₁₈ and GA₃₄ (10), but with a KRI higher 
than that of GA₁₈. We propose 28-hydroxy-GA₃₃ as putative 
structure for this compound. Both compounds were present 
at very high levels in Silene extracts. They appear to be of 
wide occurrence, since they have also been detected in 
extracts from shoots of apple, spinach and Arabidopsis (M 
Talon, JAD Zeevaart, unpublished observations).

All GAs identified in Silene were present in extracts from 
plants grown under LD as well as under SD conditions. Thus, 
since no qualitative changes in the GA pattern were observed, 
we propose that the induction of stem elongation is related to 
quantitative changes in the GA levels.

Effect of Photoperiod on the Levels of Gibberellins

By using GAs labeled with stable isotopes as internal stand-
ards, the contents of GA₅₃, GA₁₉, GA₂₀, and GA₁ were mea-
sured in shoots of Silene by GC-SIM. The levels of these GAs

![Figure 1](https://example.com/figure1.png)

Figure 1. Effect of different photoperiodic treatments and tetacyclacis 
on stem elongation in Silene armeria. A. Stem growth of plants 
exposed to different numbers of LD, followed by SD. B. Same 
photoperiodic treatments as in A but, in addition, the plants 
were treated with tetacyclacis during the SD treatment. Applications 
of the retardant were made after the plants had been exposed to LD, 
beginning the first day of SD treatment, or of LD treatment if the 
plants were not returned to SD.
were estimated in preliminary experiments using ion current areas of the base peaks to estimate the amounts of standards to be added. Quantification of GA levels was repeated twice with similar results.

Figure 3 shows the changes in the contents of the four GAs measured in plants grown under various photoperiodic combinations. Plants kept in LD contained high levels of GA13, lower amounts of GA19, and GA1, and very low levels of GA20. These levels showed little fluctuation in plants grown in SD. Continuous LD decreased the level of GA33 and increased the contents of GA19, GA20, and GA1. After 12 LD, levels of GA33 had declined to about half the level present in plants under SD. GA19 reached its highest level at 4 LD, whereas GA20 and GA1 peaked at 8 LD. Additional LD caused a decrease in the contents of these three GAs. The decline in the level of GA33 coincided with the increase in GA19 and the rise of the C19-GAs, GA20 and GA1, occurred slightly after that of GA19, suggesting a precursor-product relationship between these four GAs. Therefore, the effects induced by LD on the levels of endogenous GAs were clearly reversed by SD conditions. These results suggest that in Silene armeria, photoperiod modulates the levels of endogenous GAs mainly through the regulation of the rate of GA33 conversion.
**Effect of Photoperiod on the Distribution of Gibberellins**

To determine whether the photoperiod has an effect on the distribution of GAs among different parts of the plant, shoot tips, expanding leaves, mature leaves, stems, bracts, flowers, and peduncles were collected separately from *Silene* plants and analyzed for GAs. The plants were grown under (a) SD conditions, (b) SD followed by 8 LD, and (c) SD followed by LD until anthesis. The endogenous levels of GAs in these organs were first estimated, and then quantified twice with internal standards in two separate experiments with similar trends.

Figure 4 shows the distribution of GAs found at three different stages of development. In SD conditions, tips had the highest GA contents while mature leaves contained the lowest levels. Developing leaves and stems had relatively high amounts of endogenous GAs. In the four parts of the plants analyzed the C_{20}-GAs, GA_{53} and GA_{19}, were present at higher levels than the C_{19}-GAs, GA_{20}, and GA_{1}.

After exposure of *Silene* plants to 8 LD, GA_{33} had decreased in all organs, whereas the levels of GA_{19}, GA_{20}, and GA_{1} had increased. These increases were greater in shoot tips and young leaves than in stems and mature leaves (Fig. 4). Thus, in two separate experiments levels of GA_{19} had increased 4- to 5-fold in tips and expanding leaves, but only 2- to 3-fold in stems and mature leaves. There was also less increase in the content of GA_{20} in stems than in the rest of the organs. GA_{1} levels were highest in the shoot tips (13-fold increase) and growing leaves (8-fold increase), whereas the increases in GA_{1} in stems and mature leaves were only 6- and 3-fold, respectively, in comparison with the GA contents of these organs in SD.

The GA distribution pattern at anthesis (after 30 LD) was more similar to that found in plants in SD than in LD conditions. Flowers and flower buds had the highest contents of GAs, of which GA_{33} was the most abundant. Levels of GAs in the leaves were at their lowest values. Except for GA_{33}, low amounts of GAs were also present in the peduncles (Fig. 4).

Consistent with the results shown in Figure 3 for whole shoots, analysis of individual organs indicated that the transfer of *Silene* plants from SD to LD conditions decreased the levels of GA_{53}, while it increased the contents of GA_{19}, GA_{20}, and GA_{1}. However, these increases did not have the same magnitude in all parts of the plant. It is possible that the distribution or activity of GA_{33}-oxidase (or other GA oxidases) was not the same in the organs examined, or that the differences observed were, at least partly, due to transport of GAs.

GA levels in Figures 3 and 4 cannot be compared, since results in Figure 3 are for whole shoots, whereas only specific organs were analyzed in Figure 4. However, levels of GAs in shoots followed the same pattern observed for mature leaves (Table III). This is not surprising since mature leaves, on a dry weight basis, represent 75 to 85% of the total shoot weight. For the less abundant GAs, GA_{20} and GA_{1}, the levels detected in whole shoots were practically the same as those found in mature leaves. For GA_{33} and GA_{19}, which were present at relatively higher amounts in shoot tips, stems, and expanding leaves, the levels detected in whole shoots were greater than those found in mature leaves. For these GAs the contribution of the rest of the organs, in particular growing leaves, probably increased the average value of the whole shoot determination.

**DISCUSSION**

Exposure of *Silene armeria* to 3 to 6 LD results in significant stem elongation (16; Fig. 1A). Thus, stem growth induced by LD proceeds for a considerable period of time under subsequent SD conditions. This requirement for a minimal number of LD suggests that after moving *Silene* plants from LD to SD conditions, GA metabolism would continue as if the plants were still in LD. However, the results presented above do not support this proposal.

All GAs identified in *Silene*, GA_{12}, GA_{33}, GA_{45}, GA_{19}, GA_{19}, GA_{20}, GA_{1}, GA_{29}, and GA_{33} are members of the early 13-
Therefore, that although flowering and stem elongation in *Silene* are both induced by photoperiod, the flowering response is mainly a qualitative response to LD which in this strain is not induced by applied GA<sub>1</sub> (15), whereas stem elongation is related to the duration of the LD treatment.

Determination of GA levels in whole shoots of *Silene* (Fig. 3), as well as individual parts of the plant (Fig. 4), suggests that GA<sub>33</sub>-oxidase is under photoperiodic control, as is the case in spinach (4). The activity of this enzyme apparently increases when *Silene* plants are transferred from SD to LD, and, conversely, decreases in plants which have been returned from LD to SD. Thus, LD treatments resulted in a decline of the levels of GA<sub>33</sub> along with an increase in the concentrations of GA<sub>19</sub>, GA<sub>20</sub>, and GA<sub>1</sub> (Fig. 3). This increase was particularly large in the case of GA<sub>1</sub> (Table III), and in the elongating apices (Figs. 4 and 5). It appears, therefore, that LD enhance the flow through the GA biosynthetic pathway, increasing the levels of the active GA, GA<sub>1</sub>, which results in stem growth (Fig. 5). However, it must be realized that measurement of endogenous GA levels does not provide results on metabolic turnover rates.

It is clear from the data in Figure 3 that following return of *Silene* from LD to SD, GA levels, including those of GA<sub>1</sub>, were similar to those present in plants under SD conditions, where no stem growth takes place. However, following LD induction stem elongation did proceed in SD, although at a lower rate than in LD (Fig. 1A). Further, the results obtained with Tcy, an inhibitor of GA biosynthesis (19), indicate that following LD induction, GAs were required for stem elongation (Fig. 1B). It is of interest that the GA present in plants under SD did not promote stem elongation, whereas the same GA level in parts previously photoinduced and returned to SD did cause stem growth. It should be noted, however, that in *Silene* and *Agrostemma* treated with growth retardants, higher amounts of exogenous GAs were required in SD than in LD to induce the same stem elongation (1, 7). These observations suggest that LD have a twofold effect in *Silene*: (a) they cause an increase in the GA content by increasing the activity of GA<sub>33</sub>-oxidase, and (b) they increase the sensitivity of the tissue to GA. This interpretation may explain the photoperiodic aftereffect observed in *Silene*, although the biochemical basis of the increased sensitivity to GA is not known at present.

In conclusion, the early 13-hydroxylation pathway operates in the LDP *Silene armeria* under LD and SD conditions. LD probably modulate the levels of GAs through the regulation of the rate of GA<sub>33</sub> conversion. As a result of the LD induction, GA<sub>1</sub> accumulates at its highest levels in elongating apices. Thus, stem elongation occurs in LD because GA<sub>1</sub> reaches a certain threshold level. The effect of GA<sub>1</sub> may be further enhanced by an increase in sensitivity to GA which is also induced by LD.

**ACKNOWLEDGMENTS**

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Table III. Comparison of Levels of Gibberellins in Shoots and Mature Leaves of S. armeria Grown under Different Photoperiodic Conditions

<table>
<thead>
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<th>Gibberelin</th>
<th>SD Whole shoots</th>
<th>Mature leaves</th>
<th>8 LD Whole shoots</th>
<th>Mature leaves</th>
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Table III continued...

A convenient source of n-alkane standards for the determination of gas chromatographic retention indices. Phytochemistry 10: 1155–1157


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Figure 5. Proposed biosynthetic pathway for gibberellins identified in Silene armeria, along with levels of GA$_{33}$, GA$_{19}$, GA$_{20}$, and GA$_{1}$. (ng/g dry weight) found in shoot tips of plants grown in SD, or after exposure to 8 LD. NA = not analyzed.

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LITERATURE CITED

