Control of longitudinal and cambial growth by gibberellins and indole-3-acetic acid in current-year shoots of *Pinus sylvestris*

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Received June 6, 1996

Summary We investigated the involvement of gibberellins (GAs) and indole-3-acetic acid (IAA) in the control of longitudinal and cambial growth in current-year shoots of *Pinus sylvestris* L. Elongating terminal shoots, located at the apex of previous-year (1-year-old) branches in the uppermost whorl on the main stem, were variously decapitated (apical 5 to 10 mm removed), defoliated (all developing needle fascicles removed) and treated with exogenous GA₄/₇ or IAA, or both. Shoot length and the radial widths of xylem and phloem were measured, and the concentrations of GA₁, GA₃, GA₄, GA₉, and IAA in the stem were determined by combined gas chromatography–mass spectrometry with deuterated GAs and [¹³C₆]-IAA as internal standards. Decapitation decreased the production of xylem and phloem and the IAA concentration, but did not alter either longitudinal growth or the concentrations of GAs. Defoliation markedly inhibited shoot elongation, as well as cambial growth, and reduced the concentrations of GA₁, GA₃, GA₄, GA₉, and IAA. Application of GA₄/₇ to defoliated shoots promoted longitudinal growth and phloem production, without affecting xylem production or IAA concentration. Application of GA₄/₇ and IAA together to decapitated + defoliated shoots increased shoot elongation, xylem and phloem production and IAA concentration, whereas applying either substance alone had a smaller effect or none at all. We conclude that, for elongating current-year shoots of *Pinus sylvestris*, (1) both the shoot apex and the developing needle fascicles are major sources of the IAA present in the stem, whereas stem GAs originate primarily in the needle fascicles, (2) GAs and IAA are required for both shoot elongation and cambial growth, and (3) GAs act directly in the control of shoot growth, rather than indirectly through affecting the IAA concentration.

Keywords: decapitation, defoliation, phloem, Scots pine, shoot elongation, vascular cambium, xylem

Introduction

Experiments investigating the relationship between endogenous gibberellin (GA) concentrations and shoot growth, and the effects of applying GA₁, GA₃, GA₄, GA₄/₇ or inhibitors of GA biosynthesis on shoot growth, indicate that GAs play a major role in the mechanisms regulating shoot elongation and the production of xylem and phloem by the vascular cambium in woody species (Junttila 1991, Little and Pharis 1995, Moritz 1995, Olsen et al. 1995, Wang et al. 1995a, 1995b). Because it is widely considered that GA₁, and perhaps also GA₉, are the GAs that are active *per se* in the control of shoot growth, Pharis et al. (1991) proposed that inherently rapid growth in woody species, as reflected in height growth, stem volume and stem dry weight, is causally related to the endogenous concentrations of these GAs. In contrast, Lanner (1993) argued that shoot growth, particularly the elongation of stem units in fixed-growth *Pinus* spp. shoots, is regulated by the amount of auxin, presumably indole-3-acetic acid (IAA), exported from developing needle fascicles. Primary evidence for this view was the finding that the removal of the apical meristem from elongating *Pinus ponderosa* Dougl. ex Laws. shoots did not decrease longitudinal growth, whereas defoliation had a marked inhibitory effect (Lanner and Connor 1988). However, the relative impacts of decapitation and defoliation on the concentrations of IAA and GAs in the stem have not been investigated in elongating woody shoots. Moreover, although it is well established that IAA is important for cambial growth in shoots of both conifers and woody angiosperms (Little and Pharis 1995), and for shoot elongation in nonwoody angiosperms (Yang et al. 1993, McKay et al. 1994), its involvement in the control of longitudinal growth in woody species is uncertain. Thus, exogenous IAA has been observed both to promote the elongation of hypocotyl sections excised from various *Pinus* spp. (Zakrzewski 1975, Carpita and Tarmann 1982, Terry et al. 1982) and to inhibit the elongation of current-year *Pinus sylvestris* L. shoots when applied around the circumference of the subjacent previous-year (1-year-old) shoot (Sundberg and Little 1990). In addition, both a positive relationship and no relationship have been reported between the concentration of endogenous IAA and the rate of shoot elongation in woody species (Dunberg 1976, Wood 1983, Sandberg and Ericsson 1987, Bata et al. 1989, Rodriguez et al. 1991, Browning et al. 1992, Yang et al. 1992, Rinne et al. 1993).

To clarify the involvement of GAs and IAA, and to investigate their possible interaction (Wang et al. 1995a, 1995b), in the regulation of longitudinal and cambial growth in current-
year conifer shoots, we determined the relationships among shoot elongation, xylem and phloem production, and stem concentrations of GAs and IAA in elongating *Pinus sylvestris* shoots subjected to decapitation and defoliation. The amounts of GA$_4$ and GA$_8$, as well as of GA$_1$ and GA$_3$, were measured because it is known that the GA$_9$ → GA$_4$ → GA$_1$ pathway is an important route for GA biosynthesis in conifer shoots (Moritz et al. 1989, Moritz and Odén 1990, Odén et al. 1995, Wang et al. 1996). In addition, we investigated the effects on shoot elongation, cambial growth and stem IAA concentration of applying GA$_{4/7}$ to defoliated shoots, and GA$_{4/7}$ and IAA, alone and together, to decapitated + defoliated shoots.

**Materials and methods**

**Plant material and treatments**

Four experiments were performed with Scots pine (*Pinus sylvestris*) trees that were about 10 years old and were located in a natural stand at the Swedish University of Agricultural Sciences, Umeå, Sweden (63°50’ N, 20°15’ E). In the shoot elongation period, groups of five or six vigorous trees about 2-m tall and bearing four or five similar-sized previous-year (1-year-old) branches in the uppermost whorl on the main stem were chosen. One branch per tree in a particular group was assigned to a specific treatment, described below, such that the average length of the current-year terminal shoot elongating at the branch apex was the same for each treatment.

In Experiment 1, five trees with four branches in the uppermost whorl were selected, and one elongating current-year terminal shoot per tree was either (1) left untreated (control), (2) decapitated (DC), i.e., the apical 5 mm was removed with a scalpel and 0.8 g lanolin was applied to the cut surface, (3) defoliated (DF), i.e., all expanding needles (3- to 4-mm long) were removed and 200 µl of water containing 0.05% Tween 20 was painted over the whole shoot, or (4) decapitated + defoliated (DC + DF). In Experiment 1A, a supplement to Experiment 1, five trees with three branches in the uppermost whorl were selected, and one elongating current-year terminal shoot per tree was either (1) left untreated (control), (2) decapitated, or (3) defoliated, as described in Experiment 1, except that 10 mm rather than 5 mm was removed from the apex of decapitated shoots. In Experiment 2, six trees with five branches in the uppermost whorl were selected, and one elongating current-year terminal shoot per tree either was left untreated (control) or was defoliated (DF) and painted with 200 µl of water containing 0, 0.1, 1 or 10 mg GA$_{4/7}$ 1$^{-1}$ and 0.05% Tween 20. In Experiment 3, five trees with five branches in the uppermost whorl were selected, and one elongating current-year terminal shoot per tree either was left untreated (control) or was decapitated + defoliated (DC + DF) and treated apically with 0.8 g lanolin containing 0 or 1 mg IAA g$^{-1}$ and painted on all sides with 200 µl of water containing 0 or 1 mg GA$_{4/7}$ 1$^{-1}$ and 0.05% Tween 20. In all experiments, the lengths of the current-year terminal shoots were measured, and the shoots were harvested to measure cambial growth and the concentrations of IAA (Experiments 1, 1A, 2 and 3) and GA$_1$, GA$_3$, GA$_4$, and GA$_9$ (Experiment 1). At the time of harvest, the basal 2 cm of each shoot was removed for the cambial growth measurement, and the remaining portion was defoliated (if needles were present) and saved for hormone extraction. The sample for hormone measurement was obtained by peeling the bark, scraping the exposed surface on the xylem side with a scalpel, and pooling the bark peelings and the scrapings. This material was frozen in liquid nitrogen and stored at −80 °C until analyzed.

**Measurement of shoot elongation and cambial growth**

The length of each current-year terminal shoot was expressed as a percentage of its initial length (mean of 63, 120, 54 and 74 mm in Experiments 1, 1A, 2 and 3, respectively), to obviate initial differences in shoot size.

Cambial growth was measured as the radial widths of xylem and phloem, which were recorded at eight equidistant points around the circumference of transverse handcut sections obtained 2 cm from the basal end of the current-year terminal shoot. The sections were stained in a saturated aqueous solution of phloroglucinol in 20% hydrochloric acid and mounted in glycerol on microscope slides. The xylem measurement started from the outside of the pith and included only those xylem cells that reacted with the stain, i.e., in which at least some lignification had occurred. The phloem measurement spanned the cambium to the outside of the phloem, with the phloem accounting for at least 95% of the total width measured.

**Measurement of IAA**

The concentration of IAA was determined as described by Sundberg (1990). In brief, after homogenizing the stem sample in liquid nitrogen, an aliquot (about 0.5 g fresh weight) was extracted at 4 °C for 2 h in 0.05 M sodium phosphate buffer, pH 7.0, containing 0.02% diethyldithiocarbamic acid (Sigma, St. Louis, MO) as antioxidant and 50 ng [1$^{13}$C$_6$]-IAA (Cambridge Isotopes Laboratories, Andover, MA) as internal standard. The extract was purified by neutral and acidic diethyl ether partitioning, and the acidic ether-soluble part was methylated and subjected to reverse-phase high-performance liquid chromatography (HPLC). The HPLC mobile phase consisted of 50% methanol in 1% acetic acid and was delivered at a flow rate of 1 ml min$^{-1}$ by Waters M 501 pumps and a M 680 gradient controller (Waters Associates AB, Partille, Sweden). The sample was introduced by a Waters 712 WISP onto a 10 cm × 8 mm i.d. 4-µm Nova-Pak C$_{18}$ cartridge fitted in a RCM 8 × 10 module (Waters Associates AB). The IAA-methyl ester fraction was collected, silylated and injected splitless into a Hewlett-Packard 5890 gas chromatograph (GC) (Hewlett-Packard, Palo Alto, CA) fitted with a fused silica glass capillary column (25 m long, 0.25 mm i.d.) with a chemically bonded 0.25 µm SE-30 stationary phase (Quadrex, New Haven, CT). Helium was used as a carrier gas at a flow rate of 1 ml min$^{-1}$. The GC was linked to a Hewlett-Packard 5770 mass selective detector equipped with a 9133 data system. Quantifications were made by gas chromatography-selected
ion monitoring-mass spectrometry (GC–SIM–MS). The ratio of m/z 202:208 was used to calculate the endogenous concentration of IAA by the isotope dilution equation (Cohen et al. 1986).

Measurement of GAs

To measure the concentrations of GA\(_3\), GA\(_4\), GA\(_7\) and GA\(_9\), an aliquot (about 1 g fresh weight) of the homogenized stem sample was extracted at 4 °C for 4 h in 80% aqueous methanol containing 0.02% (v/v) diethylthiocarbamic acid as antioxidant and 10 ng 17,17\(^{2}H\)\(_2\)-GA\(_3\), 100 pg 17,17\(^{2}H\)\(_2\)-GA\(_4\), 100 pg 17,17\(^{2}H\)\(_2\)-GA\(_7\) and 100 pg 17,17\(^{2}H\)\(_2\)-GA\(_9\) as internal standards. The methanol was filtered, and the tissue residue was washed with fresh 80% methanol and re-extracted under the same conditions. After evaporating the methanol from the combined filtrates at reduced pressure at 35 °C, the aqueous residue was applied in 0.5 M sodium phosphate buffer, pH 8.0, to a polyvinylpolypyrrolidone column (20 × 1.0 cm i.d.) and eluted with 0.1 M sodium phosphate buffer, pH 8.0. The eluate (0–75 ml) was acidified to pH 2.7 with 6 M HCl and extracted five times with 75 ml ethyl acetate. The acidic ethyl acetate extracts were combined, the remaining water was removed by freezing and filtering, and the organic phase was evaporated to dryness. The residue was dissolved in 5 ml water, adjusted to pH 8.0, and applied to a 40 × 20 mm i.d. QAE Sephadex A-25 column (Pharmacia, Uppsala, Sweden). The free GAs were eluted with 50 ml of 0.2 M formic acid, which is run through a 100-mg Bond Elute C\(_{18}\) column (Sorbent AB, Västra Frölunda, Sweden) that had been washed with methanol and 0.2 M formic acid. The column was eluted with 5 ml of methanol to collect the free GAs, and the methanol was evaporated to dryness. The samples were dissolved in about 100 μl methanol and subjected to HPLC. The chromatogram consisted of two Waters M 501 pumps connected to the column by a 7125 injector with a 250-μl loop (Rheodyne, Cotati, CA). The pumps were controlled by a Waters M 680 gradient controller. The samples were purified by a reversed-phase column packed with 5 μm Nucleosil C\(_{18}\) (200 × 4.6 mm i.d.) (Skandinaviska Genetec AB, Kungsbacka, Sweden). The mobile phase consisted of a 60-min linear gradient from water and acetic acid (99:1, v/v) to methanol and acetic acid (99:1, v/v). The samples were run at a flow rate of 1 ml min\(^{-1}\) and 1-ml fractions were collected. Fractions known to contain the GAs of interest were collected, methylated with ethereal diazomethane and trimethylsilylated in 15 μl N-methyl-N-trimethylsilyltrifluoroacetamide (MSTFA) and 15 μl pyridine at 70 °C for 30 min. The derivatization mixture was reduced to dryness and dissolved in about 10 μl n-heptane, and an aliquot was injected splitless into a Hewlett-Packard 5890 GC fitted with a fused silica glass capillary column (25 m long, 0.25 mm i.d.) with a chemically bonded 0.25 μm SE-30 stationary phase. The injector temperature was 270 °C. The column temperature was held at 60 °C for 2 min, then increased by 20 °C min\(^{-1}\) to 200 °C, and by 4 °C min\(^{-1}\) to 260 °C. The column effluent was introduced into the ion source of a JMS-SX102 mass spectrometer (JEOL, Tokyo, Japan). The interface and ion source temperatures were 270 °C and 250 °C, respectively. Ions were generated with 70 eV at an ionization current of 300 μA. Quantifications were made by selected reaction monitoring (Moritz and Olsen 1995). The reactions m/z 298 to m/z 270 and m/z 300 to m/z 272 for GA\(_3\), m/z 418 to m/z 284 and m/z 420 to m/z 286 for GA\(_4\), m/z 506 to m/z 448 and m/z 508 to m/z 450 for GA\(_7\), and m/z 504 to m/z 446 and m/z 506 to m/z 448 for GA\(_9\) were recorded. All data were processed by a JEOL MS–MP7010D data system.

Statistical analysis

Analysis of variance was applied to each data set, and where appropriate the difference between means was determined by Duncan’s multiple range test. In the Figures, within each measured variable, means accompanied by the same letter are not significantly different at \(P \leq 0.05\).

Results

In Experiment 1, the control shoots elongated throughout the experimental period, and by the end of the study they had increased threefold in length and produced wide bands of xylem and phloem at their base (Figure 1). Decapitation did

Figure 1. Longitudinal growth and production of xylem and phloem in current-year terminal shoots that were either untreated (control), de
capitated (DC), defoliated (DF) or decapitated + defoliated (DC + DF). Experiment 1, means ± SE, \(n = 5\).
not affect longitudinal growth, but it decreased production of xylem and phloem by about one-third. In contrast, defoliation almost totally arrested shoot elongation, and also reduced cambial growth. The combined decapitation + defoliation treatment inhibited longitudinal growth and xylem production to the same extent as the defoliation treatment, but it reduced phloem production more than defoliation did alone. Compared with controls, decapitation reduced the IAA concentration in the stem without altering the concentrations of GA₉, GA₄, GA₃ or GA₁, whereas the defoliation and decapitation + defoliation treatments decreased the IAA concentration to an even greater extent than the decapitation treatment and also lowered the concentrations of all the GAs (Figure 2). On a percentage basis, decapitation and defoliation both decreased the IAA concentration more than the concentration of any GA, and defoliation reduced the concentration of GA₉ more than GA₄, GA₃ or GA₁.

In Experiment 1A, the inhibition of longitudinal growth induced by defoliation was evident 1 week after the start of treatment, as were the reductions in cambial growth and stem IAA concentration caused by decapitation and by defoliation (Figure 3). In control shoots, the IAA concentration was three- to fourfold higher in the stem than in the developing needle fascicles. It was also observed that defoliating the upper half of an elongating current-year shoot decreased longitudinal growth and the stem IAA concentration more than did defoliating the lower half of an elongating current-year shoot (data not shown).

In Experiment 2, defoliation decreased shoot elongation, cambial growth, and the stem IAA concentration, as was also

![Figure 2](image1.png)

**Figure 2.** Concentrations of IAA, GA₉, GA₄, GA₃ and GA₁ in the stem of current-year terminal shoots that were either untreated (control), decapitated (DC), defoliated (DF) or decapitated + defoliated (DC + DF). Experiment 1, means ± SE, n = 5.

![Figure 3](image2.png)

**Figure 3.** Longitudinal growth, production of xylem and phloem, and IAA concentration in the stem (s) or needle fascicles (n) of current-year terminal shoots that were either untreated (control) (□, ■ for stems and needle fascicles, respectively), decapitated (DC) (□) or defoliated (DF) (○). Experiment 1A, means ± SE, n = 5.
observed in Experiments 1 and 1A, except that the decrease in xylem production was not statistically significant (Figure 4). Applying GA<sub>4/7</sub> to defoliated shoots promoted longitudinal growth, the optimal concentration being 1 mg GA<sub>4/7</sub> l<sup>-1</sup>. Exogenous GA<sub>4/7</sub> also stimulated phloem production, and the stimulation increased throughout the entire concentration range tested. The application of GA<sub>4/7</sub> did not increase xylem production or IAA concentration.

In Experiment 3, decapitation + defoliation in the absence of exogenous hormones reduced shoot elongation, xylem production and the IAA concentration as observed in Experiment 1; however, the treatment did not significantly decrease phloem production (Figure 5). Applying IAA or GA<sub>4/7</sub> alone to decapitated + defoliated shoots promoted the production of xylem and phloem, without significantly increasing longitudinal growth or the IAA concentration. In contrast, the application of IAA and GA<sub>4/7</sub> together increased shoot elongation, cambial growth and the IAA concentration.

**Discussion**

The relative importance of the shoot apex and the developing needle fascicles as sources of the GAs and IAA present in the stem of elongating current-year *Pinus sylvestris* shoots can be deduced from the extent to which decapitation and defoliation altered the concentrations of GAs and IAA in the stem. Decapitation did not affect the concentrations of GAs, whereas defoliation markedly reduced the concentrations of all GAs measured, particularly GA<sub>9</sub> (Figure 2). However, decapitation and defoliation both decreased the IAA concentration, and the impact of defoliation relative to decapitation decreased with increasing shoot length at the time of the treatment (compare Figures 2 and 3, in which the initial shoot length was 63 and 120 mm, respectively). High concentrations of GAs and IAA have been measured in current-year needles of several conifers, including *Pinus sylvestris* (Figure 3, Little and Wareing 1981, Savidge and Wareing 1984, Pharis et al. 1992, Wang et al. 1992). We conclude that the IAA found in elongating...
stems originates in both the shoot apex and needle fascicles, and the contribution by needle fascicles declines as the shoot ages, whereas needle fascicles are the major source of the GAs. Based on decapitation and defoliation experiments with 1-year-old shoots of conifers, it was concluded that expanding current-year shoots were the major source of IAA present in the 1-year-old stem, with the 1-year-old foliage being a relatively minor source (Little and Wareing 1981, Savidge and Wareing 1982, Sundberg and Little 1987, 1990). Whether the shoot apex and needle fascicles actually synthesize GA$_3$ and IAA, or supply a precursor or conjugate that is metabolized in stem tissues, has not been determined. Also, it is not known if the reduction in GA$_4$, GA$_3$ and GA$_1$ concentrations in the stem of defoliated shoots (Figure 2) is the result of (1) removal of the needle fascicles resulting in a decreased import into the stem of these specific GAs or their precursors (GA$_9$ for GA$_4$ and GA$_1$ and an unknown precursor for GA$_3$ (Wang et al. 1996)), or (2) an increase in their conjugation or degradation in the stem.

Our results provide additional evidence that GAs are involved in the control of both longitudinal and cambial growth in conifers (Little and Phariss 1995, Moritz 1995, Wang et al. 1995a, 1995b). First, comparing the control, decapitated and defoliated shoots in Experiment 1, stem GA concentrations were positively related to shoot elongation and, less obviously, to the production of xylem and phloem (Figures 1 and 2). Second, applying GA$_4$ alone to shoots deficient in endogenous GAs, i.e., defoliated shoots, stimulated longitudinal growth and phloem production (Figure 4). The most effective GA$_4$ concentration was lower for shoot elongation than for phloem production (1 mg l$^{-1}$ and 10 mg l$^{-1}$, respectively), which we attribute to the 10 mg l$^{-1}$ concentration resulting in a supra-optimal amount of GA reaching the shoot apex, but not the cambial region (Wang et al. 1992, 1996). Third, the application of GA$_4$ alone to shoots deficient in both GAs and IAA, i.e., decapitated + defoliated shoots, increased the production of xylem and phloem and also tended to promote shoot elongation (Figure 5). In all cases where the application of GA$_4$ alone stimulated shoot growth, the stem IAA concentration was not significantly increased (Figures 4 and 5), thus providing additional evidence that GAs control shoot growth directly, rather than indirectly through altering the IAA concentration (Wang et al. 1995a, 1995b).

Four observations support the view that IAA plays an important role in the regulation of both shoot elongation and cambial growth in conifers and, moreover, is required for the action of GAs in these processes. First, decapitation + defoliation concomitantly decreased xylem and phloem production, longitudinal growth and the stem IAA concentration, whereas applying IAA apically to decapitated + defoliated shoots increased cambial growth and partially restored shoot elongation and IAA concentration (Figures 1, 2 and 5). Similarly, it was observed that exogenous IAA countered the reductions in tracheid production and cambial region IAA concentration induced by debudding in previous-year conifer shoots (Little and Wareing 1981, Sundberg and Little 1987, 1990). Second, decapitation decreased both cambial growth and the stem IAA concentration (Figures 1 to 3). However, decapitation did not inhibit shoot elongation, presumably because the supply of endogenous IAA from the needle fascicles was sufficient to maintain normal subapical meristem activity, although it was limiting for cambial growth. Third, applying IAA together with GA$_4$ to decapitated + defoliated shoots enhanced the stimulatory effect of GA$_4$ or IAA alone on shoot growth (Figure 5). Similarly, exogenous GA$_3$ or GA$_4$ promoted cambial growth in 1-year-old shoots of Pinus sylvestris (Hejnowicz and Tomaszewski 1969, Wang et al. 1995a, 1995b) and other woody species (Little and Phariss 1995) only when a source of endogenous or exogenous IAA was present. Fourth, the 1 mg l$^{-1}$ GA$_4$ treatment promoted shoot elongation in defoliated shoots (Figure 4) relatively more than in decapitated + defoliated shoots (Figure 5). We speculate that this difference in response was caused by a greater supply of endogenous IAA in defoliated shoots than in decapitated + defoliated shoots, because decapitation removed only one IAA source whereas decapitation + defoliation removed two IAA sources. The marked increase in phloem to xylem ratio in defoliated shoots treated with 1 or 10 mg l$^{-1}$ GA$_4$ (Figure 4), and in decapitated + defoliated shoots treated with GA$_4$ alone (Figure 5), can be attributed to the induction of a high GA/low IAA ratio in the cambial region favoring phloem production (Digby and Wareing 1966).

We conclude that GAs and IAA are involved in the regulation of both longitudinal growth, as manifested in stem unit elongation, and cambial growth, as reflected in xylem and phloem production, in the current-year shoots of Pinus sylvestris. However, because the potential for shoot growth in Pinus spp. depends more on the number of stem units than on their length (e.g., Lanner and Connor 1988, Norgren et al. 1996), it remains to be determined if GAs and IAA also play a role in the mechanism controlling the initiation of stem unit primordia at the shoot apical meristem (Lanner 1993).

Acknowledgments

We thank Karin Ljung for technical assistance, Thomas Moritz for helpful advice, and the Swedish Council for Forestry and Agricultural Research and the Jacob Wallenberg Research Foundation/Lars-Erik Thunholm Foundation for Promotion of Scientific Research for financial support.

References


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