Ten-year growth and survival of Douglas-fir seedlings treated with plant growth regulating substances at transplant

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Abstract: Commercially available plant growth regulators (PGRs) or moisture retention gels, applied to the roots of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) before planting, can modify indole-3-acetic acid (IAA) levels in roots, root growth responses, and tree survival. We treated two different 1+0 stock types (PSB313B and PSB323) of Douglas-fir with indole-butyric acid (IBA), ethephon (Ethrel®), alginate, or a combination of IBA and alginate. New root growth and IAA levels in roots were measured 2 weeks after planting, and aboveground growth and tree survival were monitored over 10 growing seasons after planting. Treatment with IBA or the combination of IBA and alginate increased IAA conjugate and free IAA levels in roots, root growth, and tree survival. Alginate treatment alone increased new root growth and tree survival, but did not increase free IAA levels in roots. Ethrel® treatment increased free IAA levels and root growth, but had no effect on IAA conjugates or tree survival. A cost analysis suggests that use of certain PGRs or alginate decreases the cost required to attain target stocking and increased tree size. Our results suggest that application of PGRs or other root-promoting materials to the roots of Douglas-fir before planting has the potential to be a cost-beneficial method for increasing root growth and tree survival.

Résumé : Les substances de croissance pour les plantes disponibles commercialement ou les gels pour la rétention d'humidité qui sont appliqués aux racines du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) avant la plantation peuvent modifier les niveaux d'acide 3-indole acétique (IAA) dans les racines, la réponse en croissance des racines et la survie des plants. Nous avons traité deux types de plants 1+0 (PSB313B et PSB323) de douglas de Menzies avec de l'acide indole butyrique (IBA), de l'éthéphon (Ethrel®), de l'alginate ou avec une combinaison de IBA et d'alginate. La croissance des nouvelles racines et le niveau de IAA dans les racines ont été mesurés deux semaines après la plantation. La croissance épigée et la survie des plants ont été notées pendant 10 saisons de croissance après la plantation. Les traitements avec IBA ou avec la combinaison de IBA et d'alginate ont causé une augmentation du niveau de conjugués de IAA et de IAA libre dans les racines, de la croissance des racines et de la survie des plants. Le traitement avec l'alginate seul a favorisé la croissance et la survie mais n'a pas eu d'effet sur le niveau de IAA libre dans les racines. Le traitement avec l'Ethrel® a provoqué une augmentation du niveau de IAA libre et de la croissance des racines mais n'a pas eu d'effet sur les conjugués de IAA ni sur la survie. Une analyse de coûts suggère que l'application de certaines substances de croissance ou d'alginate diminue le coût à consentir pour atteindre la densité relative cible et augmente la dimension des plants. Nos résultats suggèrent que l'application de substances de croissance ou d'autres substances qui favorisent l'enracinement, aux racines du douglas de Menzies avant la plantation, pourrait être une méthode avantageuse du point de vue du coût pour améliorer la croissance des racines et la survie des plants.

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Introduction

Rapid resumption of root growth is one of the principal processes responsible for tree survival after planting (Burdett 1987; Ritchie 1985; Ritchie and Dunlap 1980; Stone 1955). Several studies have attempted to predict the quality of forest tree seedlings by assessing root regeneration capacity i.e., the ability to initiate new roots upon planting (Stone et al. 1962; Burdett 1979; Ritchie 1985; McCreary and Duryea 1987). These studies concluded that the survival of a tree after planting is only partially a function of its ability to initiate new root growth and that root regeneration capacity is not the sole predictor of plantation performance. Although root regeneration capacity may not be considered an ultimate predictor of plantation performance, the ability to manipulate factors that regulate the quantity, quality, type, and speed of root growth has the potential to play an important role in increasing the survival and growth of planted trees (Scagel and Linderman 1998*a*, 1998*b*, 2000*b*).

Any number of factors may inhibit the initiation and elongation of new lateral roots, but in most cases, endogenous plant hormones are the primary factors responsible for the initiation of new root growth (MacIsaac et al. 1989; Pelosi et al. 1995; Karabaghli-Degron et al. 1998). While each hormone has a distinctive mechanism of action, interactions

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with other growth regulators and environmental factors frequently appear to influence the effect of any one hormone (Ross et al. 1983; Ribault and Pilet 1994). Indole-3-acetic acid (IAA) is the main auxin found in most plants. However, the response of plants to changes in endogenous IAA levels is likely to be dependent on absolute concentration, tissue sensitivity, and the levels of other plant hormones (Pilet 1992).

Several researchers have applied auxins to the root systems of tree seedlings (Carlson and Larson 1977; Hartwig and Larson 1980; Selby and Seaby 1982; Seaby and Selby 1990; Pendl and D'Anjou 1987; Tuskan and Ellis 1991; Carter and Tripepi 1989; Scagel and Linderman 2000*a*, 2000*b*). However, the effect of exogenously applied auxins on root growth has been variable (Coffman and Loewenstein 1973; Kelly and Moser 1983; Zaerr 1967; Scagel and Linderman 2000*a*, 2000*b*). Kelly and Moser (1983) found that root application of indole-butyric acid (IBA) to *Liriodendron tulipifera* L. increased root regeneration in both spring- and fall-planted seedlings. Struve and Moser (1984) and Struve and Arnold (1986) increased root regeneration of oak seedlings up to sixfold by application of auxins to roots. Simpson (1986) increased lateral root production in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings by soil-drench application of the auxins IBA and naphthalene acetic acid (NAA) to seedlings. We have recently found species-specific responses to application of auxins in root growth and tree survival of container-grown Douglas-fir, lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Scagel and Linderman 2000*a*, 2000*b*). Certain reports have also suggested that similar increases in root growth may result from ethylene application (Graham and Linderman 1981; Rupp and Mudge 1985; Stein and Fortin 1990*a*, 1990*b*; Scagel and Linderman 2000*a*, 2000*b*). In contrast, Zaerr (1967) and Lavender and Hermann (1970) obtained no effect of exogenous IBA on new root growth of several conifer species.

Abiotic and biotic factors other than hormone levels play a part in the regulation of root growth and tree survival after planting (Reid et al. 1991). Application of a hydrophilic gel to the root system prior to planting has the potential to increase the moisture availability around the newly planted root system (Miller and Reines 1974; Kudela 1976) and increase rhizosphere microbial populations or levels of root growth promoting substances, which, in turn, stimulate tree growth through mechanisms not associated with PGRs (Natsume et al. 1994).

Most studies have assessed the influence of exogenous application of auxins or moisture retention gels on tree growth parameters, but few have assessed changes in endogenous hormone status (Zaerr and Lavender 1980; Baraldi et al. 1995). A number of studies have described the effects of exogenous application of PGRs on root growth under controlled growth conditions (Selby and Seaby 1982; Seaby and Selby 1990; Kelly and Moser 1983; Simpson 1986; Scagel and Linderman 2000*a*); however, there have been few planting trials that have examined long-term field survival of PGR-treated seedlings. In a recent paper, we (Scagel and Linderman 2000*b*) describe the growth and survival of container-grown conifers 3 years after application of PGRs to the roots, either prior to cold storage or immediately before planting, in a high elevation clearcut. Here, we report how application of specific PGRs and a moisture retention gel to the root systems of Douglas-fir can influence root IAA content, and tree growth and survival 10 years after planting in a clearcut.

Materials and methods

Study location

The experimental planting site is located in Block-16, 10 km north of Boston Bar (B.C., Canada), just off the Trans-Canada Highway. The site has a south-facing midslope of 20–30% with a sandy-loam Dystric Brunisol over a thick colluvium. The upper 15–20 cm of the soil profile has 15% coarse fragments, but the soil below is 75% coarse fragments. Based upon sites of similar slope, moisture regime, and aspect, this site had the potential to develop a substantial brush cover and was expected to develop a substantial and prolonged moisture deficit during the summer (Goldstein 1990; Green and Klinka 1994). The planting site was harvested by clearcut in the winter of 1998, and the experimental planting was established in May 1988 without any site preparation. Throughout the length of the study, no vegetation control (chemical or manual) was done in the experimental planting sites.

Planting stock attributes, culture, and treatment conditions

Two stock types of Douglas-fir were used: interior Douglas-fir (PSB 323, 1+0) and coastal Douglas-fir (PSB313B, 1+0). The PSB313B 1+0 has been the most frequently prescribed stock type for these sites (see Scagel et al. (1992) for a review of stock type and planting characteristics). The PSB323 stock type has a larger root mass than the PSB313B stock type. The remainder of the stock used in this trial was used in a later planting at Ryan River (Section 88-A19215 described in Scagel and Goldstein 1990).

Treatments were applied in the spring (May 1988) immediately before planting and consisted of Stim-Root® (Plant Products Co. Ltd., Brampton, Ont.), Ethrel® (Rhône–Poulenc Canada, Inc., Mississauga, Ont.), the moisture retention gel alginate, or a combination of Stim-Root® and alginate. The Stim-Root® treatment consisted of a commercial preparation of IBA at 500 ppm applied to the roots as a powder. The combination treatment of Stim-Root® and alginate consisted of a commercial preparation of IBA at 500 ppm applied to roots for 10 s in a carrier of 5.0% alginate (calcium alginic acid, Protanal SF®, MultiKem Corp., Ridgefield, N.J.). Ethrel®, a commercial formulation of ethephon (2-chloroethyl phosphonic acid), is a slow-release ethylene compound that was applied for 10 s at 0.05 ppm in water. Treatment with alginate consisted of submerging the tree root systems for 10 s in a commercial formulation of 5.0% calcium alginic acid.

Plot layout and aboveground morphological data collection

The start of each row was marked with wire flags, with the species, treatment, and row number indicated on a metal tag. Trees were planted at 2-m spacings along the rows, with 2 m between rows. The first and last trees in each row as well as every third tree along each row were flagged. There were three rows (blocks) per species and treatment combination and 15 trees per row (15 trees × 3 rows = 45 trees per treatment per species). This site has been used for tours for the B.C. Ministry of Forests and the Pacific Phytometric Consultants (Scagel et al. 1992).

Morphological observations (survival, browse, forking, lamas growth) and measurements (total height (*H*), annual main stem growth increment, root collar diameter (*D*)) were taken in the fall of 1988, 1989, 1990, 1993, 1995, and 1997. On trees with grazed

or broken terminals, the length of the most dominant lateral branch was recorded. Plant size (V, cm^3) was estimated for each plant by using the equation for the volume of the frustrum of a right cone ($V = [\pi(H/3)(D/20)^2] + [(D/40) + 25]$, Husch et al. 1972). The change in above- and below-ground biomass during the first 2 weeks after planting was assessed on five randomly sampled experimental seedlings per treatment – stock type combination (five treatments × two stock types) from the planting sites, using the plants sampled for IAA analyses.

Root growth assessment

Samples for root growth assessment were taken from five randomly sampled experimental seedlings per treatment – stock type combination (five treatments × two stock types) at planting sites (May 1988). Trees were planted in a greenhouse soil bed under conditions of 20°C, 18-h days, and 16°C, 6-h nights and harvested after 2 weeks. The percentage of the root system initiating new roots was used to estimate root growth potential. Root initiation was estimated by the percentage of the root system with roots less than 0.5 cm in length, and new root growth was estimated by the percentage of the root system with new roots greater than 1.0 cm in length (as described in Scagel and Linderman 2000*a*).

IAA analyses

Samples for IAA analysis were taken from new roots on five randomly sampled experimental seedlings per treatment – stock type combination (five treatments × two stock types) in the planting sites 2 weeks after planting. Immediately after harvest, samples were immersed in liquid nitrogen and stored at –20°C in the dark. All tissue was freeze-dried before extraction. Extraction was performed using a modified method of Cohen et al. (1987) and Miller et al. (1990). Root tissue was ground in 80% 2-propanol in 0.2 M imidazole buffer. $^{13}C_6$ (benzene ring) IAA (0.1–1 $\mu g \cdot (g\ tissue)^{-1}$) and 50 000 – 1 000 000 cpm of ^{3}H-IAA were added, and the extract was allowed to equilibrate for 1 h. Two replicates each were purified and quantified for the endogenous concentration of free IAA and the conjugated forms (1M NaOH hydrolysable ester forms of IAA). IAA purification was performed as previously described (Scagel 1994; Scagel and Linderman 1998*a*, 1998*b*). Extracts were purified by HPLC on a C_{18} reverse-phase column (4.6 × 125 MM, Whatman Partisil DS-3) with flow rate of 1 $mL \cdot min^{-1}$, and 20% acetonitrile and 1% acetic acid as the mobile phase. Radioactive fractions were pooled, dried, resuspended in methanol, and methylated with diazomethane. After methylation the extracts were analysed by isocratic reverse phase on a Water Associates Bonpak C_{18} column (0.39 × 30 cm) equilibrated in water – acetonitrile – acetic acid (80:20:1) (by vol.). Detection was at 280 nm and quantification was made by area integration through the Waters Data System. Values are given in $ng \cdot (g\ root\ dry\ weight)^{-1}$.

Cost analysis

Assumptions for cost analysis (Scagel et al. 1992; Scagel 1994) are based on data from the B.C. Ministry of Forests (H. Hahn, personal communication), Balco–Canfor Reforestation Centre (Kamloops, B.C.), and a similar analysis by Schaap and DeYoe (1986). The estimated cost per tree was derived from the cost to purchase the seedling, prepare the tree for planting, and plant the tree. Estimated cost per tree (TC, Can$/tree) for each species–treatment combination are listed in Table 1. The planting density (PD, trees/ha) needed to achieve a target stocking density of 1000 trees/ha was calculated from ((1000/(1 – mortality)) × 0.01)). The cost to plant (CTP, Can$/ha) needed to achieve the target stocking density was calculated as PD × TC. The cost of each surviving tree (CSS, Can$/tree) at target stocking density was calculated as CTP/1000. The size cost i.e., the cost per unit tree growth (SCSS, Can$/$cm^3$), at target stocking density was calculated as CSS divided by average plant size (V) of surviving seedlings 3 years after planting.

Table 1. Estimated initial cost per tree for each stock type and treatment combination.

Species and PGR treatment	Cost (Can$/seedling)
PSB323 interior Douglas-fir	
Control	1.039
Alginate	1.068
Ethrel®	1.108
Stim-Root®	1.083
Stim-Root® + alginate	1.1
PSB313B coastal Douglas-fir	
Control	0.609
Alginate	0.641

Note: Control is no treatment (treatment and application cost $0.000/seedling), alginate is calcium alginic acid ($0.029/seedling), Ethrel® is ethylene ($0.069/seedling), and Stim-Root® is IBA ($0.031/seedling).

Experimental design and statistical analysis

Not all stock type – treatment combinations were planted. Certain treatments for the PSB313 stock had to be excluded because of root rot problems in the nursery stock. The experiment was planted in an incomplete randomized block design of three replicate blocks with 15 seedlings per stock type for each growth regulator treatment. Treatments were arranged randomly between rows in each block. For each stock type, data were subjected to analysis of variance (ANOVA) using the Statistica statistical package (Statsoft Inc. 1996).

Contrast analyses were used for planned comparisons of means to address the following questions: (1) Do PGR-treated plants differ from controls? (2) How does application of Stim-Root® in a carrier gel compare with application of Stim-Root® alone? (3) How does application of Stim-Root® compare with application of Ethrel®? (4) Does stock type influence the response to different PGR materials?

Results

Stock type differences

The free IAA and IAA conjugate levels in the roots of field-grown plants 2 weeks after planting varied with stock type and alginate treatment (Table 2). Only free IAA levels from untreated PSB313B trees differed significantly from those of PSB323 trees. When trees were treated with alginate, free IAA levels in roots did not differ between PSB313B and PSB323 trees; however, IAA conjugate levels were higher in the roots of PSB323 trees (Table 2). New root growth was greater in PSB323 than in PSB313B trees, regardless of alginate treatment (Table 2).

Treatment effects on total height and root collar diameter were more apparent after the second field growing season, once mortality had reduced the dilution effects of less vigorous plants on treatment averages. Tree height and root collar diameter one and three growing seasons after planting were again greater in PSB323 than in PSB313B trees, whether they were treated with alginate or not (Table 3). However, 10 growing seasons after planting, neither height nor diameter of alginate-treated PSB323 and PSB313B trees differed significantly (Table 3).

Table 2. (A) Means and (B) significance levels (*p* values) from contrast analysis on the new root growth, total root dry weight, and free IAA and IAA conjugate levels of roots from conifers 2 weeks after PGR treatment.

(A) Treatment means.					
	Root IAA (μg·(g dry weight)$^{-1}$)		Root dry	New root growth (%)[b]	
Treatments	Free	Conjugate	weight (g)[a]	<0.5 cm long	>1.0 cm long
PSB313B					
Control	0.44	1.43	49.95	14.44	16.40
Alginate	0.43	1.36	48.04	15.97	28.82
SD	0.05	0.41	3.24	3.25	4.83
PSB323					
Control	0.40	1.42	52.53	23.31	27.48
Alginate	0.41	1.76	71.85	28.34	50.93
Ethrel®	0.52	1.55	60.12	30.13	31.23
Stim-Root®	0.79	2.57	82.80	28.65	51.19
Stim-Root® + alginate	0.46	1.84	71.58	30.71	41.89
SD	0.11	0.34	4.26	4.65	10.92
(B) Significance levels for contrasts.					
PGR treatment					
PSB313B					
Control vs. alginate	0.786	0.865	0.485	0.141	0.000
PSB323					
Control vs. alginate	0.719	0.001	0.000	0.009	0.000
Control vs. Ethrel®	0.009	0.294	0.002	0.001	0.083
Control vs. Stim-Root®	0.000	0.000	0.000	0.009	0.000
Control vs. Stim-Root® + alginate	0.263	0.001	0.000	0.001	0.000
Stim-Root® vs. Stim-Root® + alginate	0.000	0.000	0.000	0.463	0.000
Stim-Root® vs. Ethrel®	0.000	0.000	0.000	0.435	0.000
Stock type × PGR treatment					
Control					
PSB323 vs. PSB313B	0.039	0.829	0.348	0.000	0.000
Alginate					
PSB323 vs. PSB313B	0.629	0.000	0.000	0.000	0.000

Note: Control is no treatment, alginate is calcium alginic acid, Ethrel® is ethylene, Stim-Root® is IBA, and Stim-Root® + alginate is IBA and calcium alginic acid. PSB313B is 1+0 coastal Douglas-fir and PSB323 is 1+0 interior Douglas-fir.

[a]Total root system dry weight 2 weeks after planting in a clearcut.

[b]New root growth after planting in a greenhouse.

During the 10 growing seasons after planting, survival of the PSB323 trees was greater than that of the PSB313B trees, regardless of alginate treatment (Table 4). Over 50% of the PSB313B stock died in the first 2 years. In contrast, the PSB323 stock lost only a few trees every year for the first 5 years of the study. However, 10 growing seasons after planting, the size cost of surviving trees was not significantly different between the PSB323 and PSB313B stock types, regardless of alginate treatment (Table 4).

PGR treatment differences

Treatment of roots with Ethrel® or Stim-Root® at planting increased the free IAA levels in roots (Table 2). Treatment with Stim-Root®, alginate, or Stim-Root® and alginate also significantly increased IAA conjugate levels in roots of PSB323 trees 2 weeks after planting in the field, when compared with controls (Table 2). Roots from PSB323 trees treated with Stim-Root® had higher IAA conjugate and free IAA levels than roots from PSB323 trees treated with Ethrel® or Stim-Root® and alginate. The IAA levels of PSB313B trees 2 weeks after planting were not influenced by application of alginate (Table 2).

Treatment of PSB323 trees with Stim-Root® had a significant effect on root dry weight and morphology (Table 2). Treatment of roots with any PGR material increased belowground dry weight and the percentage of the root system with new roots on PSB323 trees 2 weeks after planting, when compared with controls (Table 2). PSB323 trees treated with Stim-Root® or alginate had a higher percentage of new roots (>1.0 cm in length) in their root system than plants treated with either Ethrel® or the combination of alginate and Stim-Root® (Table 2). The percentage of the root system on PSB313B trees with new roots greater than 1.0 cm in length was only significantly higher in trees treated with alginate (Table 2).

Treatment of roots with any PGR material increased the total height of PSB323 trees 10 growing seasons after planting, but only the trees that were initially treated with Ethrel® had significantly larger stem diameters (Table 3). Ten growing seasons after planting, neither total height nor stem

Table 3. (A) Means and (B) significance levels (*p* values) from contrast analysis on the total height and stem diameter of conifers 1, 3, and 10 growing seasons after PGR treatment and planting in soil in a clearcut.

(A) Treatment means.						
	Total height (cm)			Stem diameter (mm)		
Treatments	1988	1990	1997	1988	1990	1997
PSB313B						
Control	36.1	55.6	174.5	5.97	9.17	31.25
Alginate	37.1	83.4	225.6	7.5	13.16	48.45
SD	6.23	2.35	54.7	3.19	6.04	8.13
PSB323						
Control	53.6	82.1	213.5	9.96	14.33	46.66
Alginate	53.6	88.1	267	10.71	17.11	56.65
Ethrel®	47.7	84.9	291.6	9.65	15.59	61.1
Stim-Root®	51.4	86.3	266	10.53	15.89	53.41
Stim-Root® + alginate	51.1	75.9	233.1	9.97	17.58	51.71
SD	5.31	9.18	47.65	1.22	1.89	8.64
(B) Significance levels for contrasts.						
PGR treatment						
PSB313B						
Control vs. alginate	0.619	0.023	0.019	0.795	0.033	0.011
PSB323						
Control vs. alginate	0.553	0.557	0.015	0.866	0.872	0.167
Control vs. Ethrel®	0.375	0.793	0	0.659	0.522	0.042
Control vs. Stim-Root®	0.561	0.201	0.011	0.861	0.892	0.214
Control vs. Stim-Root® + alginate	0.559	0.241	0.023	0.039	0.048	0.145
Stim-Root® vs. Stim-Root® + alginate	0.981	0.951	0.863	0.026	0.066	0.792
Stim-Root® vs. Ethrel®	0.759	0.308	0.091	0.790	0.614	0.421
Stock type × PGR treatment						
Control						
PSB323 vs. PSB313B	0	0	0.183	0	0.007	0.045
Alginate						
PSB323 vs. PSB313B	0	0.006	0.146	0	0.002	0.181

Note: Control is no treatment, alginate is calcium alginic acid, Ethrel® is ethylene, Stim-Root® is IBA, and Stim-Root® + alginate is IBA and calcium alginic acid. PSB313B is 1+0 coastal Douglas-fir and PSB323 is 1+0 interior Douglas-fir. 1988 is fall 1988, 1 growing season after planting, 1990 is fall 1990, 3 growing seasons after planting, 1997 is fall 1997, 10 growing seasons after planting.

diameter differed between PSB323 trees treated with Stim-Root® and those treated with either Ethrel® or the combination of alginate and Stim-Root®. Treatment of roots with alginate, however, did increase the total height and stem diameter of PSB313B trees, 3 and 10 growing seasons after planting (Table 3).

Treatment of roots with alginate, Stim-Root®, or the combination of alginate and Stim-Root® significantly increased survival of PSB323 trees, 10 growing seasons after planting (Table 4). Ten growing seasons after planting, survival of PSB323 trees treated with Stim-Root® was approximately 30% higher than that of trees treated with either Ethrel® or the combination of alginate and Stim-Root (Table 4). Although survival of the PSB313B stock was very low, PSB313B trees treated with alginate also had higher survival than control trees, 10 growing seasons after planting (Table 4).

After 10 growing seasons, the size cost of the surviving PSB323 trees was decreased by treatment of roots with Stim-Root® and Ethrel® (Table 4). The size cost of surviving PSB323 trees treated with Stim-Root® was similar to the cost of trees treated with either Ethrel® or the combination of alginate and Stim-Root®. Finally, PSB313B trees treated with alginate had a lower cost per seedling size than controls (Table 4).

Relationships between root IAA, root growth, and survival

Two weeks after planting, root IAA content of the PSB313B stock type was not correlated with any plant growth parameters or survival; however, root IAA content of the PSB323 stock type was significantly correlated with plant weight and survival (Table 5). New root growth of the PSB323 stock type was correlated with several plant growth parameters and plant survival (Table 5).

Thus, treatment of PSB323 trees with Stim-Root® or the combination of alginate and Stim-Root® increased IAA levels (both free and conjugate forms) in roots 2 weeks after planting, with associated increases in new root growth 2 weeks after planting and survival 10 growing seasons after planting. Alginate treatment also increased new root growth 2 weeks after planting and survival 10 growing seasons after planting, but without any increase in IAA content in the roots 2 weeks after planting. Ethrel® treatment increased

Table 4. (A) Means and (B) significance levels (*p* values) from contrast analysis on the survival and the size cost of surviving conifers 1, 3, and 10 growing seasons after PGR treatment and planting in soil in a clearcut.

(A) Treatment means.						
	Survival (%)			SCSS (Can$/cm^{-3})[a]		
Treatments	1988	1990	1997	1988	1990	1997
PSB313B						
Control	38.3	27.9	24.8	0.058 2	0.015 5	0.000 51
Alginate	74.2	44.6	38.3	0.045 8	0.007 4	0
SD	11.23	9.04	5.3	0.007 0	0.003 5	0
PSB323						
Control	84.7	69.0	52.9	0.028 0	0.008 1	0
Alginate	90.1	76.4	66.6	0.026 3	0.006 8	0.000 29
Ethrel®	91.0	63.7	55.7	0.032 6	0.007 8	0.000 15
Stim-Root®	89.4	84.5	84.5	0.025 8	0.006 8	0.000 19
Stim-Root® + alginate	87.3	69.0	69.0	0.032 5	0.011 1	0
SD	1.48	8.25	9.5	0.004 3	0.003 8	0
(B) Significance levels for contrasts.						
PGR Treatment						
PSB313B						
Control vs. alginate	0	0.000	0.000	0.313	0.050	0.91
PSB323						
Control vs. alginate	0.002	0.000	0.000	0.328	0.289	0.189
Control vs. Ethrel®	0	0.000	0.251	0.941	0.678	0.012
Control vs. Stim-Root®	0.008	0.000	0.000	0.062	0.325	0.016
Control vs. Stim-Root® + alginate	0.141	0.235	0.000	0.530	0.352	0.312
Stim-Root® vs. Stim-Root® + alginate	0.243	0.000	0.000	0.230	0.066	0.245
Stim-Root® vs. Ethrel®	0.384	0.000	0.000	0.049	0.625	0.688
Stock type × PGR treatment						
Control						
PSB323 vs. PSB313B	0	0.000	0.000	0.084	0.020	0.724
Alginate						
PSB323 vs. PSB313B	0	0.000	0.000	0.090	0.198	0.388

Note: Control is no treatment, alginate is calcium alginic acid, Ethrel® is ethylene, Stim-Root® is IBA, and Stim-Root® + alginate is IBA and calcium alginic acid. PSB313B is 1+0 coastal Douglas-fir and PSB323 is 1+0 interior Douglas-fir. 1988 is fall 1988, 1 growing season after planting, 1990 is fall 1990, 3 growing seasons after planting, 1997 is fall 1997, 10 growing seasons after planting.

[a]Cost per unit tree growth (Can$/cm^{-3}) at target stocking density.

free IAA content and new root growth 2 weeks after planting, but without any increase in survival at year 10.

Discussion

Conifer seedlings used in reforestation are often planted on harsh sites. The window of opportunity for planted trees to become established may be limited to a few weeks from snowmelt to the time when the soil is too dry and the climate too hot to support initial tree growth. To survive, newly planted trees must generate new roots that grow into the soil to acquire water and nutrients. We thus investigated the following interrelated theories: (1) Can exogenous application of PGRs and a moisture retention compound to roots of conifers change the IAA content in roots after transplanting? (2) Are changes in root IAA correlated with increased root growth after transplanting? (3) Are increases in root growth after transplanting correlated with 10-year growth and survival of trees? (4) Can exogenous application of PGRs and a moisture retention compound to roots increase 10-year growth and survival of trees?

While there are several physiological and environmental factors that influence root growth after planting, it is generally accepted that IAA plays a significant role in regulating root growth and can, in turn, be influenced by many environmental, chemical, and biological factors (Blakesley et al. 1991; Reid et al. 1991; Ribault and Pilet 1994; VanIersel 1998). We changed the IAA concentration in conifer roots in our study by external application of IBA (a synthetic auxin), Ethrel® (a slow-release ethylene compound), and a moisture retention gel. It is a common practice in horticulture to stimulate root initiation on cuttings by application of hormone powders or solutions to the plants, and moisture retention gels are popular amendments to media formulations in container-grown horticultural crops (Hartmann et al. 1997). However, the application of PGRs or moisture retention gels to container-grown or forest trees prior to planting is not a common practice in forestry.

Application of certain PGRs increased root IAA levels 2 weeks after plants were treated with PGRs. Although the mechanisms by which these PGRs influence root IAA levels are unknown, the variable IAA levels we measured could well be a result of differences in the relative initial

Table 5. Probability values (p) for correlations (r^2) between root IAA concentrations, root growth, tree survival, and growth characteristics of PSB313B and PSB323 Douglas-fir after PGR treatment.

	Root IAA content		New root growth[a]		Survival[b]	
Characteristics	Free	Conjugate	<0.5 cm long	>1.0 cm long	1988	1997
PSB313B						
2 weeks after planting						
Bound root IAA	0.211					
New root growth <0.5 cm	0.110	0.608				
New root growth >1.0 cm	0.131	0.377	0.632			
Aboveground plant growth (dry weight)	0.967	0.393	0.164	0.717	0.368	0.337
Belowground plant growth (dry weight)	0.695	0.619	0.279	0.609	0.692	0.553
10 years after planting						
Total plant height	0.779	0.625	0.680	0.229	0.269	0.106
Plant diameter	0.491	0.884	0.701	0.125	0.379	0.210
Survival[b]						
Fall 1988	0.987	0.384	0.998	0.085		
Fall 1990	0.804	0.124	0.993	0.065	0.000	
Fall 1997	0.681	0.293	0.966	0.097	0.000	
PSB323						
2 weeks after planting						
Bound root IAA	0.000					
New root growth <0.5 cm	0.165	0.665				
New root growth >1.0 cm	0.114	0.000	0.095			
Aboveground growth (dry weight)	0.028	0.000	0.653	0.000	0.271	0.001
Belowground growth (dry weight)	0.000	0.000	0.024	0.000	0.123	0.000
10 years after planting						
Total plant height	0.061	0.853	0.539	0.452	0.128	0.233
Plant diameter	0.986	0.305	0.664	0.539	0.329	0.106
Survival[b]						
Fall 1988	0.639	0.283	0.012	0.392		
Fall 1990	0.027	0.000	0.067	0.000	0.000	
Fall 1997	0.006	0.000	0.077	0.000	0.000	

[a]New root growth 2 weeks after planting.
[b]1988 is fall 1988, one growing season after planting; 1990 is fall 1990, three growing seasons after planting; 1997 is fall 1997, ten growing seasons after planting. Correlation results for 1990 are only presented for root IAA content and new root growth.

IAA content of the trees at the time of treatment, variations in environmental conditions at the planting site, variations in tissue sensitivity to the concentration of PGR applied (Firn 1986; Pilet 1983), tissue receptivity to the type of PGR applied (Pilet 1992), or differences in initial seedling quality. Tuskan and Ellis (1991) were able to increase height and survival of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), by applying IBA in a gel carrier to roots prior to planting. In our study, roots from trees treated with Stim-Root® had higher levels of IAA conjugates and free IAA than roots from trees treated with a combination of Stim-Root® and alginate. Furthermore, using alginate as a carrier for the IBA-containing material decreased the tree's response (e.g., height growth) to the Stim-Root®. This effect of alginate may explain some of our previous studies (Scagel and Linderman 2000*a*, 2000*b*; Scagel 1994). For example, in a greenhouse study, Scagel and Linderman (2000*a*) found that IBA application dramatically increased root IAA, root growth, and aboveground growth of Douglas-fir, ponderosa pine, and western larch (*Larix occidentalis* Nutt.). However, in a field planting (Scagel and Linderman 2000*b*), IBA applied in alginate or a combination of IBA and NAA applied in a hydrophilic polymer to roots of Douglas-fir did not yield exceptional growth responses.

It is hypothesized that the form of IAA present in root tissue plays an important role in the regulation of root growth (Kleczkowski and Schell 1995). In some species, there is an inverse correlation between the level of IAA conjugates and growth rate (Bandurski and Schulze 1977), and the relative content of IAA conjugates and free IAA depends on the age and growth rate of plant cells (Ostin et al. 1998). Auxin available for uptake by plants is usually rapidly converted to catabolites or sugar conjugates (De Klerk et al. 1999). Conjugation of free IAA is, however, a reversible inactivation that can allow for future release of free auxin (Smulders et al. 1990). Our PGR applications influenced both IAA conjugates and free IAA in roots of treated trees, but not always to the same extent. For instance, Stim-Root® application increased both IAA conjugates and free IAA in roots after 2 weeks, while Ethrel® application only increased the free IAA content in roots. In another study, Scagel and Linderman (2000*b*) found similar results from Ethrel® application to Douglas-fir, lodgepole pine, and Englemann spruce.

Exogenous auxin often promotes induction of roots on cuttings and it has been shown to inhibit both the outgrowth

of root primordia (De Klerk et al. 1990) and root growth (Thimann 1936). Although some of our PGR treatments increased root IAA levels after 2 weeks, not all increases in root IAA were correlated with increased root initiation and growth. For instance, Stim-Root®-enhanced IAA conjugates and free IAA levels in roots were positively correlated with increased root initiation (new root growth <0.5 cm) and root growth (new root growth >1.0 cm). In contrast, Ethrel® enhanced levels of IAA, which were positively correlated with root initiation, had no effect on IAA conjugates, and had little effect on root growth.

Stimulation of root growth by Ethrel® has been reported previously (Graham and Linderman 1981; Alvarez and Linderman 1983; Blake and Linderman 1992; Scagel and Linderman 2000*a*, 2000*b*). In some plants, ethylene has been found to enhance tissue sensitivity to auxin (Liu and Reid 1992; Visser et al. 1996). In our study Ethrel® induced changes in root initiation 2 weeks after application and these changes were positively correlated with subsequent increases in aboveground plant growth. In the study presented here and in Scagel and Linderman (2000*b*), our results indicate that exogenously applied Ethrel® influenced root initiation indirectly by increasing levels of free IAA in roots. Our results with Ethrel® may help explain the earlier results of Graham and Linderman (1981), Alvarez and Linderman (1983), and Blake and Linderman (1992), where exposure of seedling roots to relatively low levels of ethylene gas stimulated root growth.

Although some of our PGR treatments increased root growth 2 weeks after treatment, not all increases in root growth were correlated with plant survival. The PGR treatments that increased the IAA content in roots, root initiation, and root growth were also correlated with increased aboveground growth. However, only application of PGR treatments containing IBA increased tree survival. This supports the conclusions of other researchers (Ritchie 1985; McCreary and Duryea 1987) that root initiation and new root growth are not the sole predictors of seedling quality and survival after transplant.

Application of a hydrophilic gel to the root system prior to planting has the potential to increase moisture availability around the newly planted root system (Miller and Reines 1974; Kudela 1976). We found that application of alginate to roots increased root initiation and root growth 2 weeks after application. Alginate also increased aboveground growth and survival of trees. However, alginate had no effect on the free IAA content of the roots. In another study, we (Scagel and Linderman 2000*b*) also found that alginate application to root systems of container-grown Douglas-fir, Englemann spruce, and lodgepole pine increased plant growth and survival of trees but had little or no early effect on root IAA content.

Reforestation efforts strive for the greatest survival and growth of planted trees at the least cost. Cost analysis of the treatments applied in this study indicates that treatment with certain PGRs or with alginate was cost effective, supporting the results of a previous study (Scagel and Linderman 2000*b*) with container-grown Douglas-fir on a high-elevation site in the interior of British Columbia, Canada.

The present study confirms the validity of applying root growth stimulating compounds to increase the growth and survival of conifer trees after planting. The results presented here were similar to those resulting from inoculation of trees with ectomycorrhizal fungi possessing differential capabilities to produce IAA and ethylene (Scagel and Linderman 1998*a*, 1998*b*). Rhizosphere microorganisms, such as ectomycorrhizal fungi, are known to produce plant growth regulators (PGRs), including IAA and ethylene, and can influence morphological changes in the root growth of conifers (Scagel and Linderman 1998*a*, 1998*b*). With refinement, treatment of plants with either PGR materials or inoculation with fungi or bacteria that produce or induce PGRs (Chanway 1997) could easily be incorporated into reforestation practices. Although the results of our present study and those of Scagel and Linderman (2000*b*) show obvious variability in responses to PGR treatment based on plant species, i.e., depending on stock type and environment, one should be able to fine tune PGR application concentrations and timing to reduce some of this variability.

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