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Modification of root IAA concentrations, tree growth, and survival by application of plant growth regulating substances to container-grown conifers *

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Abstract. Tree survival after planting is partially a function of the tree's capacity to produce new roots. In a field trial we assessed the potential to modify the IAA concentration in roots, root growth responses, and plant survival by root application of plant growth regulators (PGRs) such as IBA, NAA, and ethylene, or alginate, a moisture retention material. Container-grown Douglas-fir, Englemann spruce, and lodgepole pine were lifted before and during prescribed lifting windows and treated with Stim-root®, Ethrel®, Hormogel®, or alginate before or after cold-storage, then planted in a clearcut. Lifting trees outside of the prescribed lifting window decreased IAA concentrations in roots of Douglas-fir, Englemann spruce, and lodgepole pine. Treating plants with different PGRs after cold storage increased root IAA concentrations and root growth after planting compared to treating plants prior to cold storage. Root growth and above ground plant growth and survival were well correlated to IAA concentrations in roots of Douglas-fir and Englemann spruce. IAA concentrations in roots of lodgepole pine correlated with root growth, but did not correlate with survival. A cost analysis of treatment effects on growth and survival showed that certain post-cold storage PGR treatments can decrease the cost necessary to attain target stocking and increase the size of the trees. Our results suggest that application of PGRs or other root-promoting materials to tree roots before planting has the potential to be a cost-beneficial method for increasing root growth and tree survival.

Introduction

Many warm, dry sites in the British Columbia (B.C.) interior and coast-interior transition of Canada have short growing seasons and summer drought conditions that result in low plantation survival and reduced site productivity (Scagel et al. 1992). Contributing factors to poor plantation performance include species and stock type selection, nursery practices, stock handling, planting technique, and the severe environment of the planting site. However, the underlying cause of seedling mortality after planting is usually the "quality" of the planting stock in relation to environmental demands of the planting site (Lavender 1990). Several studies have attempted to predict forest tree seedling quality by assessing root growth capacity, the ability to initiate new roots upon planting (Stone et al. 1962; Burdett 1979; Ritchie 1985; McCreary and Duryea 1987; Simpson and Ritchie 1997). These studies concluded that survival after planting is only partially a function of a tree's ability to initiate roots, and root growth capacity is not the sole predictor of plantation performance. Although root growth 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.

Specific hormones and plant growth regulators (PGRs) mediate growth and development (Ross et al. 1983). Endogenous hormone levels may be influenced by plant metabolic condition (e.g., age, cold hardiness, and dormancy), external physical environment (e.g., photoperiod, drought and temperature), and exogenous sources of PGRs (e.g., human application, rhizosphere microorganisms). The control of root growth is frequently associated with two PGRs: auxin and ethylene. Horticulturists commonly use commercially available PGRs to induce rooting of cuttings and promote seedling growth, and there is a potential for similar responses in forestry (Zaerr 1967; Alvarez and Linderman 1983; Kelly and Moser 1983; Selby and Seaby 1983; Simpson 1986). Pendl and D'Anjou (1978) and Simpson (1986) have used PGRs experimentally in forestry, and Zaerr and Lavender (1980) summarized the use of PGRs in forestry. Although the variability of plant responses to PGRs can be high, refinement of PGR application techniques and an understanding of the optimal timing for application could increase the effectiveness of using PGRs in forestry.

Several researchers have documented the effects of auxin (natural or their synthetic analogs) on root initiation and proliferation for different tree species (Selby and Seaby 1982; Ross et al. 1983; Simpson 1986) and certain reports have suggested similar roles for ethylene (Graham and Linderman 1981; Rupp and Mudge 1985; Stein and Fortin 1990a, 1990b; Blake and Linderman 1992). Although some reports describing adventitious rooting of cuttings have attempted to correlate endogenous auxin levels and metabolism with root formation, conflicting information exists concerning changes in the naturally occurring auxin indole-acetic acid (IAA) (Moncousin 1988; Blakesley et al. 1991). Most studies investigating the effects of PGR treatments on tree growth have not indicated whether treatments have actually modified hormone levels in the plant.

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).

In this paper, we report how applying specific PGRs and moisture retention gels to root systems of conifers with different survival potentials can influence tree growth and survival after planting. Our objective was to test the following interrelated hypotheses: (1) exogenous application of plant growth regulators and moisture retention compounds to roots of conifers can change the IAA content in roots after transplanting, (2) changes in root IAA content of conifers can increase root growth after transplanting, and (3) increases in root growth after transplanting can increase the aboveground growth and survival of conifers.

Materials and methods

Study location and plot layout

A plantation was established May 18–21, 1988, in the Durrand Creek Area, approximately 8 miles south of Savona, B.C. (50°46′00″ N, 120°52′00″ W). The site is in the very dry cool Montane Spruce (MSxx) classified biogeoclimatic zone (Meidinger and Pojar 1991) at 1550 m. Prior attempts at plantation establishment in this area resulted in 30–40% mortality (Gary Hunt, formerly of Balco-Canfor Reforestation, Kamloops, Canada, personal communication). Trees were planted in three blocks, at a two-meter spacing with two meters between rows. Each block consisted of 60 rows and 50 trees per row with one row per species and treatment combination.

Planting stock attributes, culture, and treatment conditions

Container-grown trees (1 + 0) of interior Douglas-fir *(Pseudotsuga menzesii* (Mirb.) Franco.), Englemann spruce (*Picea englemannii* Parry.), and lodgepole pine (*Pinus contorta* Dougl.) were obtained from the former Balco-Canfor nursery in Kamloops, B.C., Canada. Seedlings were either lifted on October 10, 1987 (early lift treatment) or lifted at dates prescribed by the B.C.

Ministry of Forests based on cold-hardiness testing (normal lift treatment) (November 9, 1987 for Douglas-fir and Englemann spruce or November 26, 1987 for lodgepole pine). The date of the early lift treatment chosen based on the nursery's experience on when all three species would not be ready for cold storage. At early- and normal-lift times, trees were either placed directly into −4 °C cold storage or treated before cold storage.

Treatments with PGRs consisted of submerging tree root systems for 10 sec in one of Hormogel®, Stim-root® (Plant Products Co. Ltd., Brampton, ON, CA), Ethrel® (Rhône-Poulenc Canada, Inc., Mississauga, ON, CA), or alginate (calcium alginic acid, Protanal SF®, MultiKem Corp., Ridgefield, NJ, USA). Hormogel® treatment was an experimental combination of 500 mg l^{-1} indolebutyric acid (IBA) and 500 mg l^{-1} naphthaleneacetic acid (NAA). Stim-root® treatment consisted of a commercial preparation of IBA at 500 mg l^{-1} applied to roots in a carrier of 5.0% alginate. Ethrel®, a commercial formulation of Ethephon (2-chloroethyl phosphonic acid), is a slow release ethylene compound that was applied at 50 μg l^{-1} for 10 sec in water. Treatment with the moisture retention gel alginate consisted of submerging tree root systems for 10 sec in a commercial formulation of 5.0% calcium alginic acid. Control plants received no treatment to the root systems.

Trees were treated either pre-cold storage or post-cold storage. Pre-cold storage treatments were applied as root dips to groups of five trees before normal production wrapping and packaging. Post-cold storage treatments were applied as root dips to groups of five trees before planting, after unwrapping bundles of thawed trees at the field site.

Collection of morphological and survival data

At planting (May 18, 1988), height and root collar diameter were measured on all trees and a representative sample of 50 trees for each species from each lifting time. An early survey of tree survival was done eight weeks after planting (July 4, 1988).

One growing season after planting (October 2, 1988), height, leader length, and root collar diameter were measured on all trees and survival were recorded. One year after planting (June 12, 1989) tree survival were recorded. Further morphological and survival data were collected on October 5–7, 1989 and November 1–3, 1990 after two and three seasons of growth, respectively.

When measuring height and leader length on trees with grazed or broken terminals, the length of the longest lateral branch was recorded. If grazing occurred early in the season, a dominant lateral was generally obvious. However, late season damage necessitated measuring laterals with no clear dominance. Although these later values were generally lower than the average for the remaining seedlings in the treatment, the values were not significantly lower (as determined by *t*-tests comparing means with and without the lateral measurements); therefore we retained the values in the data set. Plant size (D^2H, cm^3) was calculated for each plant by height × (stem diameter)^2.

Root growth, mycorrhizal status, and IAA analyses

At planting, sample plants from five randomly selected experimental trees per treatment-species combination (3-species × 5-growth regulator treatments × 2-lift times × 2-treatment times) were taken to assess root growth, mycorrhizal status, and root IAA content. These trees were planted in a greenhouse bed containing a sandy loam soil, grown under conditions of 20 °C, 18-h days, and 16 °C, 6-h nights and harvested after two weeks.

The percentage of the root system initiating new roots was used to estimate root growth potential. Root systems were visually divided into four vertical sections, and the percentage of white roots greater than 1.0 cm in length was recorded for each section (as described in Scagel and Linderman 2000a). Total root system ranking was determined by averaging the four ratings of the root subsections. During this procedure, the percentage of root tips colonized by mycorrhizal fungi was also determined as described in Scagel and Linderman (1998a). Percentage mycorrhizae colonization was determined by counting the number of primary laterals on a seedling and the number of these that were mycorrhizal. Representative mycorrhizae were sectioned and examined for Hartig net development under a light microscope to confirm mycorrhizal status.

All root samples for IAA analysis were rinsed, 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 (1990). IAA purification was performed as previously described (Scagel 1994; Scagel and Linderman 1998a, 1998b). 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 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) (v:v:v). Detection was at 280 nm and quantification was made by area integration through the Waters Data System. Values are given in ng g^{-1} root dry weight.

After one growing season (October 1988), three randomly selected seedlings were harvested from each treatment-species combination (3-species × 5-growth regulator treatments × 2-lift times × 2-treatment times) for assessment of root growth, mycorrhizal colonization, and root IAA content. Sample processing and analysis was carried out as described above for the sample trees taken at planting.

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, Vancouver, B.C., personal communication), Balco-Canfor Reforestation Centre (Gary Hunt, Kamloops, Canada) 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, \$CN tree^{-1}) for each species and treatment combination are listed in Table 1. The planting density (PD, number of trees ha^{-1}) necessary to achieve a target stocking density of 1000 trees ha^{-1} was calculated from (1000/((100 $-$ mortality) $\times$ 0.01)). The cost to plant (CTP, \$CN ha^{-1}) necessary to achieve the target stocking density was calculated by PD multiplied by TC. The cost of each surviving tree (CSS, \$CN tree^{-1}) at target stocking density was calculated from CTP divided by 1000. The cost per unit tree growth (SCSS, \$CN cm^{-3}) at target stocking density was calculated from CSS divided by average plant size (D^2H) of surviving seedlings three years after planting.

Experimental design and statistical analysis

This experiment consisted of three replicate blocks with 50 seedlings per species for each growth regulator treatment (5) at each lift-time (2) and growth regulator treatment time (2). Treatments were arranged randomly between rows in each block. For each tree species, data were subjected to Analysis of Variance (ANOVA) using the Statistica® statistical package (Statsoft, Inc., Tulsa, OK, USA, 1996). Where necessary, data were square root transformed to equalize variances. Contrast analyses were used for planned comparisons of means to address the following questions: (1) How do PGR-treated plants compare to controls when trees were lifted outside of their normal lifting window? (2) How do PGR treated plants compare to controls when trees were lifted at the industry-prescribed time? (3) Does the time of treatment (pre or post-cold storage) influence the response to different PGRs? (4) Does the time of treatment influence the response to lifting trees outside their normal lifting window? Contrasts used for comparisons included: (1) means of each PGR treatment compared separately to controls for each lift time (PGR $\times$ Lift Time interaction); (2) means of PGR treatment compared at different treatment times (PGR $\times$ Treatment Time interaction); and (3) means from lift times compared at different treatment times (Lift $\times$ Treatment Time interaction). Pearson's correlation coefficient (r^2) was used to detect linear

Table 1. Estimated cost per tree (CT) for each species and treatment combination ($CN/seedling).

Species and PGR treatment[1]	Cost ($CN/seedling)
Interior Douglas-fir	
Control	0.717
Alginate	0.746
Ethrel®	0.786
Stim-root®	0.748
Hormogel®	0.748
Englemann spruce	
Control	0.710
Alginate	0.734
Ethrel®	0.779
Stim-root®	0.741
Hormogel®	0.741
Lodgepole pine	
Control	0.731
Alginate	0.760
Ethrel®	0.800
Stim-root®	0.762
Hormogel®	0.762

[1]Where Control = no treatment (treatment and application cost $0.000/seedling), Alginate = Calcium Alginic Acid ($0.029/seedling), Ethrel® = Ethylene ($0.069/seedling), Stim-root® = IBA ($0.031/seedling), and Hormogel® = IBA + NAA ($0.031/seedling).

relationships between root IAA concentration, root growth, tree growth, and survival.

Results

IAA concentrations in roots

Early lifting decreased both the IAA conjugates and free IAA concentration in roots of Douglas-fir, Englemann spruce, and lodgepole pine two weeks after planting (PGR × Lift Time Contrasts, Table 2). Although response varied between species, applying some PGR treatments to trees that were lifted early increased IAA conjugates and free IAA in roots when compared to controls (Figure 1A and Figure 1B). When trees were lifted early, Stim-root® increased IAA conjugates and free IAA in roots of all three tree species, Hormogel® increased IAA conjugates in roots of all three tree species, and ethrel and alginate only increased IAA conjugates in roots of lodgepole pine and Englemann spruce.

Application of certain PGR treatments to trees lifted during the dates suggested by industry increased the IAA conjugate and free IAA in roots of Douglas-fir, Englemann spruce, and lodgepole pine two weeks after planting, when compared to controls (Figure 3A and Figure 3B). Stim-root® increased IAA conjugates and free IAA in roots of all three tree species. Applying Ethrel® or Stim-root® increased IAA conjugates and free IAA in roots of Douglas-fir. All PGR materials increased the IAA conjugates in roots of lodgepole pine, but only Hormogel® or Stim-root® increased free IAA in roots. All PGR materials increased the free IAA in roots of Englemann spruce, but only Stim-root® or alginate treatments increased IAA conjugates in roots.

Although, post-cold storage PGR treatment generally increased the IAA conjugates and free IAA in roots of Douglas-fir, Englemann spruce, and lodgepole pine two weeks after planting (Lift × Treatment Time Contrasts, Table 2), the influence of PGR treatment time on IAA conjugates and free IAA in roots varied between PGR treatment materials (PGR × Treatment Time Contrasts, Table 2). When compared to pre-cold storage application of PGRs, PGR treatments after cold storage increased IAA conjugates and free IAA in roots of Douglas-fir. Application time of alginate or ethrel did not influence IAA conjugates and free IAA in roots of lodgepole pine. Applying PGR treatments after cold storage to Englemann spruce had more influence on IAA conjugates than free IAA in roots.

Four months after planting, there were no significant treatment effects on the concentration of IAA conjugates or free IAA in roots of Englemann spruce, but roots of Douglas-fir and lodgepole pine treated with Stim-root® and Ethrel® had significantly higher concentration of IAA conjugates and free IAA (data not shown). One year after planting, lift time, PGR treatment time, and PGR treatment material had little effect on the concentration of free and conjugate IAA in roots of any of the three tree species (data not shown).

New root growth

Early lifting decreased new root growth of Douglas-fir, Englemann spruce, and lodgepole pine two weeks and four months after planting (Lift × Treatment Time Contrasts, Table 3). Although response varied between species, application of some PGRs to trees that were lifted early increased new root growth at two weeks (Figure 1C) but did not increase new root growth four months after planting (Figure 1D). When trees were lifted early, Stim-root®, alginate, and Ethrel® stimulated new root growth on Douglas-fir and lodge-

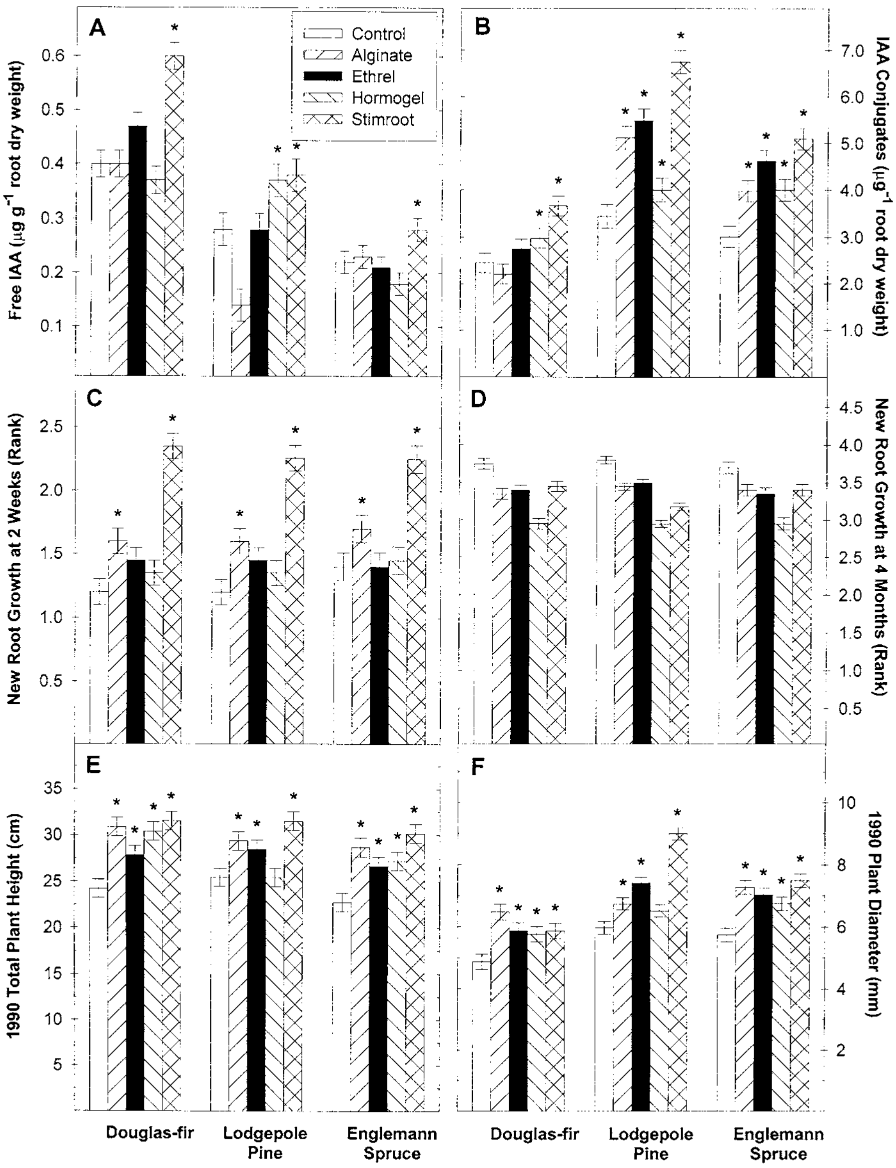

Figure 1. Influence of PGR treatments on trees lifted earlier than the industry suggested date. Free IAA (A) and IAA conjugate content (B) two weeks after planting, new root growth two weeks (C) and four months (D) after planting, and plant height (E) and diameter (F) three years after planting. Asterisks represent means significantly greater than controls ($p < 0.05$) within each conifer species based on contrast analysis. Control = no treatment, Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.

Table 2. Contrast means and significance levels (*p*-values) from contrast analysis on the free IAA and IAA conjugate content of roots from container grown conifers two weeks after PGR treatment and planting into soil in a clearcut.[1]

Treatments		IAA content of roots (μg g^{-1} root dry weight)					
		Douglas-fir		Lodgepole pine		Englemann spruce	
		Free[2]	Bound	Free	Bound	Free	Bound
PGR × Treatment Time							
Means							
Control[3]	Pre[4]	0.46	2.31	0.29	3.28	0.20	3.27
	Post	0.47	2.54	0.31	3.59	0.21	3.48
Alginate	Pre	0.39	2.41	0.27	5.60	0.27	3.86
	Post	0.46	2.97	0.27	5.56	0.25	4.59
Ethrel®	Pre	0.52	3.01	0.31	5.78	0.25	3.51
	Post	0.55	3.92	0.34	6.66	0.28	4.40
Hormogel®	Pre	0.36	2.77	0.35	4.22	0.23	3.06
	Post	0.52	3.55	0.61	5.85	0.33	5.41
Stim-root®	Pre	0.63	3.55	0.35	6.57	0.35	5.53
	Post	0.68	4.80	0.41	8.09	0.38	5.69
ANOVA variance components							
MS		0.501	11.83	2.06	67.02	0.32	118.91
MSE		0.001	0.221	0.003	0.742	0.002	0.393
$F_{4,2940}$		809.45	54.67	659.42	90.05	194.3	305.96
Contrasts and significance levels							
Control (Pre vs Post)		*0.815*	*0.236*	*0.427*	*0.845*	*0.649*	*0.321*
Alginate (Pre vs Post)		*<0.001*	*<0.001*	*0.875*	*0.844*	*0.065*	*<0.001*
Ethrel® (Pre vs Post)		*<0.001*	*<0.001*	*0.118*	*<0.001*	*<0.001*	*<0.001*
Hormogel® (Pre vs Post)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Stim-root® (Pre vs Post)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.021*	*0.351*
Lift × Treatment Time							
Means							
Early Lift[5]	Pre Cold	0.41	2.52	0.27	4.38	0.21	3.50
	Post Cold	0.48	3.11	0.30	5.15	0.24	3.96
Normal Lift	Pre Cold	0.53	3.10	0.38	5.81	0.32	4.18
	Post Cold	0.59	4.15	0.48	6.95	0.34	5.47
ANOVA variance components							
MS		0.033	40.72	0.804	25.03	0.01	128.55
MSE		0.001	0.221	0.003	0.742	0.002	0.393
$F_{1,2940}$		52.86	188.15	255.95	33.63	4.52	330.76
Contrasts and significance levels							
Early Lift (Pre vs Post Cold Storage)		*<0.001*	*<0.001*	*0.010*	*<0.001*	*0.037*	*<0.001*
Normal Lift (Pre vs Post Cold Storage)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.046*	*<0.001*
Pre Cold Storage (Early vs Normal Lift)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Post Cold Storage (Early vs Normal Lift)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*

[1]Contrast means, ANOVA variance components, and significance levels (*p*-values) comparing means of PGR treatments at different treatment times (PGR × Treatment Time interaction); and means of lift times at different treatment times (Lift × Treatment Time interaction). MS = Treatment mean square, MSE = Error mean square.
[2]Free = Free IAA, Bound = IAA Conjugates.
[3]Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.
[4]Pre-Cold = pre-cold storage treatment with PGR types, Post-Cold = post-cold storage treatment with PGR types.
[5]Early Lift = plants lifted earlier than industry suggested date, Normal Lift = plants lifted during industry suggested dates.

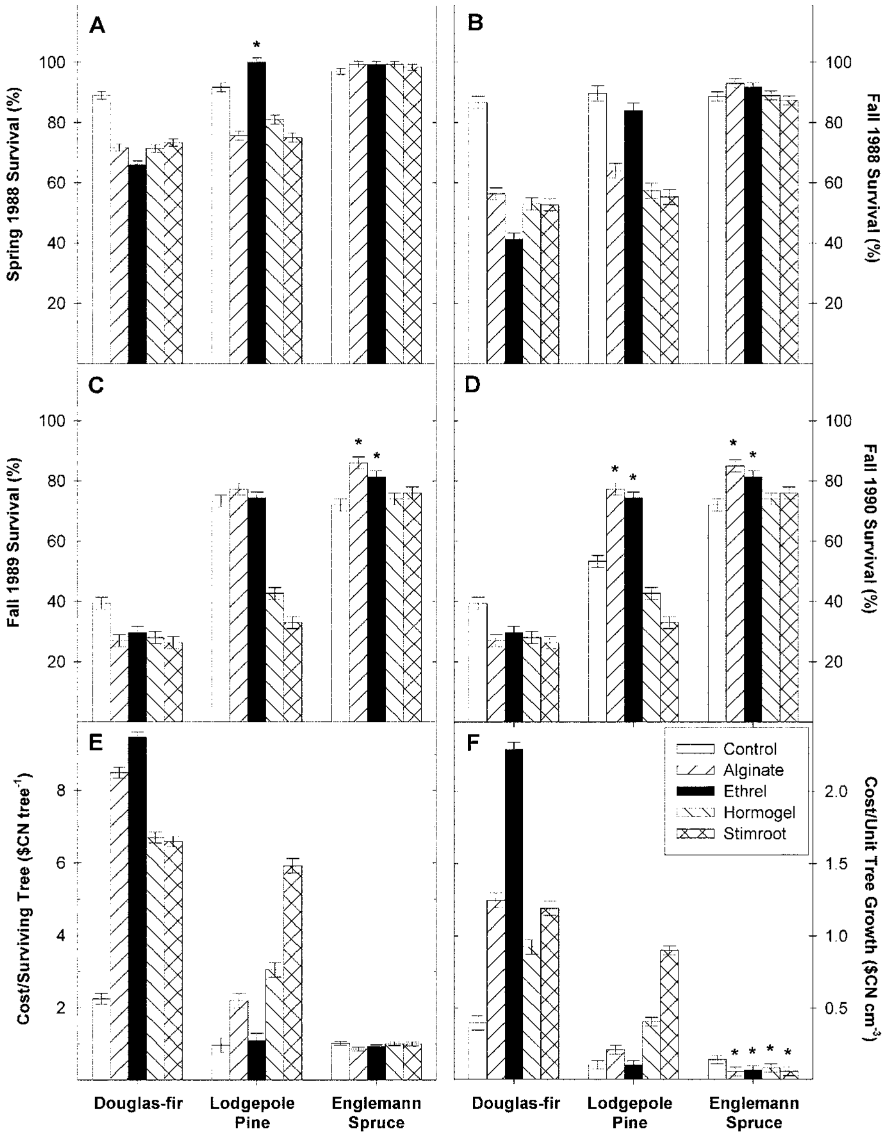

Figure 2. Influence of PGR treatments on trees lifted earlier than the industry suggested date. Survival four weeks after planting (A), survival one growing season after planting (B), survival two growing seasons after planting (C), survival three growing seasons after planting (D), cost of each surviving seedling (E), and cost per unit tree growth (F). Asterisks in A-D represent means significantly greater than controls ($p < 0.05$) within each conifer species based on contrast analysis. Asterisks in E–F represent means significantly less than controls ($p < 0.05$) within each conifer species based on contrast analysis. Control = no treatment, Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.

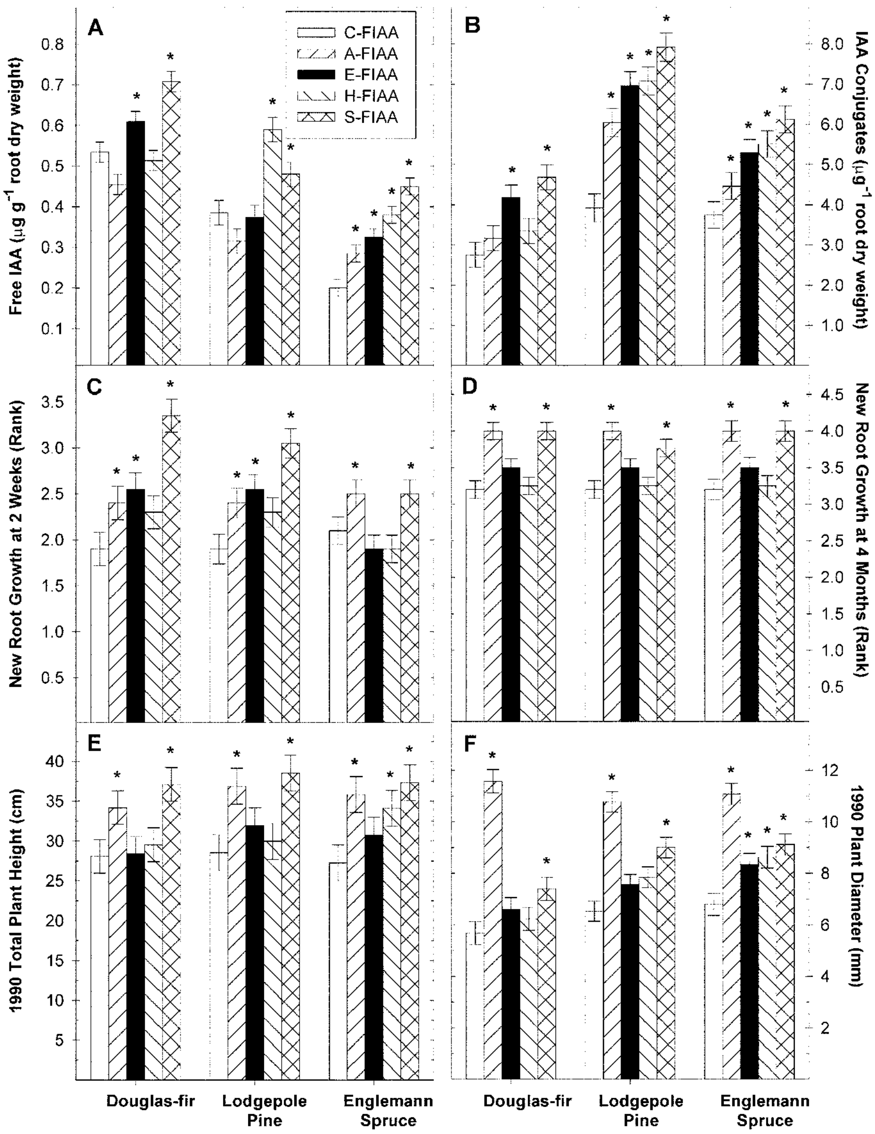

Figure 3. Influence of PGR treatments on trees lifted during the industry suggested dates. Free IAA (A) and IAA conjugate content (B) two weeks after planting, new root growth two weeks (C) and four months (D) after planting, and plant height (E) and diameter (F) three years after planting. Asterisks represent means significantly greater than controls ($p < 0.05$) within each conifer species based on contrast analysis. Control = no treatment, Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.

pole pine at two weeks after planting. New root growth in Englemann spruce two weeks after planting was only increased by Stim-root® and alginate treatments.

Applying certain PGR treatments to trees lifted during the industry suggested dates, increased the new root growth of Douglas-fir, Englemann spruce, and lodgepole pine two weeks or four months after planting, when compared to controls (Figure 3C and Figure 3D). Two weeks after planting, Stim-root® and alginate treatments increased new root growth in all three tree species and ethrel stimulated new root growth only in Douglas-fir and lodgepole pine. Four months after planting, at the end of the first growing season, differences in new root growth between PGR treatments were small with only alginate and Stim-root® treated plants having more root growth in all three tree species.

When compared to pre-cold storage treatments with PGRs, post-cold storage PGR treatment increased the new root growth of Douglas-fir, Englemann spruce, and lodgepole pine two weeks after planting (Lift × Treatment Time Contrasts, Table 3). Four months after planting, the influence of PGR treatment time on new root growth varied between PGR treatment materials (PGR × Treatment Time Contrasts, Table 3). Compared to pre-cold storage treatment of PGRs, applying Stim-root® or alginate after cold-storage did not influence new root growth of any tree species four months after planting.

We found that all trees sampled had some level of colonization by mycorrhizal fungi, although there were no differences between PGR treatments, lift times, or treatment times on the extent of root colonization by mycorrhizal fungi.

Above ground growth

Early lifting decreased height and diameter of Douglas-fir, Englemann spruce, and lodgepole pine after three growing seasons compared to trees lifted at the industry prescribed time (Lift × Treatment Time Contrasts, Table 4). Although response varied between species, treatment of trees that were lifted early with PGRs increased height and diameter of trees after three growing seasons when compared to controls (Figure 1E and Figure 1F). When trees were lifted early, Stim-root® and alginate treatments increased height and diameter of all three species. Ethrel® treatment increased height and diameter of early-lifted lodgepole pine and Englemann spruce, while Hormogel® increased both height and diameter on early lifted Douglas-fir and Englemann spruce.

Applying certain PGR treatments to trees lifted during the dates suggested by industry increased the height and diameter of Douglas-fir, Englemann spruce, and lodgepole pine after three growing seasons, when compared

Table 3. Contrast means and significance levels (p-values) from contrast analysis on the new root growth of container grown conifers two weeks and four months after PGR treatment and planting into soil in a clearcut.[1]

Treatments		New root growth after planting (rank)					
		Douglas-fir		Lodgepole pine		Englemann spruce	
		2 Weeks	4 Months	2 Weeks	4 Months	2 Weeks	4 Months
PGR × Treatment Time							
Means							
Control[2]	Pre[3]	1.55	3.60	1.45	3.45	1.80	3.35
	Post	1.50	3.55	1.50	3.35	1.70	3.45
Alginate	Pre	1.85	3.60	1.85	3.70	2.00	3.65
	Post	2.15	3.75	2.15	3.75	2.20	3.75
Ethrel®	Pre	1.85	3.30	1.85	3.40	1.30	3.25
	Post	2.15	3.60	2.30	3.60	2.00	3.60
Hormogel®	Pre	1.40	2.95	1.40	2.95	1.30	2.95
	Post	2.25	3.25	2.25	3.25	2.05	3.25
Stim-root®	Pre	2.75	3.45	2.45	3.06	1.90	3.40
	Post	2.95	4.00	2.86	3.88	2.85	4.00
ANOVA variance components							
MS		14.93	13.01	14.20	24.68	28.31	13.43
MSE		0.09	0.24	0.12	0.26	0.08	0.24
$F_{4,2940}$		163.44	53.89	114.35	93.26	371.19	56.33
Contrasts and significance levels							
Control (Pre vs Post)		*0.954*	*0.293*	*0.927*	*0.542*	*0.542*	*0.413*
Alginate (Pre vs Post)		*<0.001*	*0.252*	*0.001*	*0.715*	*0.007*	*0.442*
Ethrel® (Pre vs Post)		*<0.001*	*0.022*	*0.001*	*0.145*	*<0.001*	*0.007*
Hormogel® (Pre vs Post)		*<0.001*	*0.026*	*<0.001*	*0.029*	*<0.001*	*0.021*
Stim-root® (Pre vs Post)		*0.013*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Lift × Treatment Time							
Means							
Early Lift[4]	Pre Cold	1.48	3.20	1.48	3.24	1.32	3.16
	Post Cold	1.70	3.56	1.66	3.51	1.96	3.56
Normal Lift	Pre Cold	2.28	3.56	2.16	3.46	2.00	3.56
	Post Cold	2.72	3.62	2.72	3.62	2.36	3.62
ANOVA variance components							
MS		9.07	16.87	25.60	2.59	14.7	21.67
MSE		0.09	0.24	0.12	0.26	0.08	0.24
$F_{1,2940}$		99.38	69.89	206.14	9.79	192.72	90.95
Contrasts and significance levels							
Early Lift (Pre vs Post Cold Storage)		*<0.001*	*<0.001*	*0.002*	*0.002*	*0.037*	*<0.001*
Normal Lift (Pre vs Post Cold Storage)		*<0.001*	*0.469*	*<0.001*	*0.077*	*0.046*	*0.466*
Pre Cold Storage (Early vs Normal Lift)		*<0.001*	*<0.001*	*<0.001*	*0.009*	*<0.001*	*<0.001*
Post Cold Storage (Early vs Normal Lift)		*<0.001*	*0.592*	*<0.001*	*0.213*	*<0.001*	*0.497*

[1]Contrast means, ANOVA variance components, and significance levels (p-values) comparing means of PGR treatments at different treatment times (PGR × Treatment Time interaction); and means of lift times at different treatment times (Lift × Treatment Time interaction). MS = Treatment mean square, MSE = Error mean square.
[2]Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.
[3]Pre-Cold = pre-cold storage treatment with PGR types, Post-Cold = post-cold storage treatment with PGR types.
[4]Early Lift = plants lifted earlier than industry suggested date, Normal Lift = plants lifted during industry suggested dates.

Table 4. Contrast means and significance levels (*p*-values) from contrast analysis on the height and diameter of container grown conifers three years after PGR treatment and planting into soil in a clearcut.[1]

Treatments		1990 height (cm) and diameter (mm)					
		Douglas-fir		Lodgepole pine		Englemann spruce	
		Height	Diameter	Height	Diameter	Height	Diameter
PGR × Treatment Time							
Means							
Control[2]	Pre[3]	24.46	5.21	27.44	6.13	24.96	6.17
	Post	25.83	5.34	26.58	6.18	25.09	6.35
Alginate	Pre	29.18	6.31	31.47	7.01	29.67	7.40
	Post	35.89	11.74	34.81	10.51	34.86	10.96
Ethrel®	Pre	23.93	5.29	26.34	6.14	24.58	7.05
	Post	31.36	6.77	33.09	7.83	32.64	8.33
Hormogel®	Pre	25.14	5.49	24.64	6.44	29.53	6.82
	Post	34.80	6.00	30.78	7.93	31.84	8.55
Stim-root®	Pre	28.77	6.93	30.31	6.67	31.45	7.71
	Post	9.89	7.22	39.55	9.47	36.05	8.91
ANOVA variance components							
MS		359.7	198.6	1250.6	153.2	1083.1	186.8
MSE		73.6	11.1	51.1	9.9	52.2	7.4
$F_{4,2940}$		4.88	17.84	24.45	15.47	20.75	25.18
Contrasts and significance levels							
Control (Pre vs Post)		*0.542*	*0.215*	*0.845*	*0.731*	*0.863*	*0.526*
Alginate (Pre vs Post)		*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
Ethrel® (Pre vs Post)		*0.000*	*0.014*	*0.000*	*0.000*	*0.000*	*0.000*
Hormogel® (Pre vs Post)		*0.001*	*0.634*	*0.001*	*0.000*	*0.000*	*0.000*
Stim-root® (Pre vs Post)		*0.000*	*0.046*	*0.000*	*0.000*	*0.000*	*0.000*
Lift × Treatment Time							
Means							
Early Lift[4]	Pre Cold	24.81	4.99	24.94	5.68	24.43	6.18
	Post Cold	32.74	6.18	30.71	7.35	29.75	7.54
Normal Lift	Pre Cold	27.78	6.34	31.14	7.27	31.60	7.88
	Post Cold	35.17	8.65	35.21	9.41	34.44	9.70
ANOVA variance components							
MS		868.8	364.6	248.1	1141.98	918.1	31.2
MSE		73.6	11.1	51.1	9.9	52.2	7.4
$F_{1,2940}$		11.80	32.74	4.85	115.35	17.58	4.2
Contrasts and significance levels							
Early Lift (Pre vs Post Cold Storage)		*<0.001*	*0.004*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Normal Lift (Pre vs Post Cold Storage)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Pre Cold Storage (Early vs Normal Lift)		*0.039*	*0.016*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Post Cold Storage (Early vs Normal Lift)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*

[1]Contrast means, ANOVA variance components, and significance levels (*p*-values) comparing means of PGR treatments at different treatment times (PGR × Treatment Time interaction); and means of lift times at different treatment times (Lift × Treatment Time interaction). MS = Treatment mean square, MSE = Error mean square.
[2]Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.
[3]Pre-Cold = pre-cold storage treatment with PGR types, Post-Cold = post-cold storage treatment with PGR types
[4]Early Lift = plants lifted earlier than industry suggested date, Normal Lift = plants lifted during industry suggested dates.

to controls (Figure 3E and Figure 3F). Stim-root® and alginate treatments increased height and diameter of all three tree species, while ethrel treatment had no influence on height or diameter and Hormogel® treatments increased height and diameter only on Englemann spruce.

When compared to pre-cold storage treatments with PGRs, applying any PGR treatment after cold storage increased both the height and diameter of Douglas-fir, Englemann spruce, and lodgepole pine after three growing seasons (PGR × Treatment Time Contrasts, Table 4).

Plant survival

Although response varied between species, applying PGR treatments to early-lifted trees decreased or had no effect on survival of trees one month after planting when compared to controls (Figure 2A). When trees were lifted early, no PGR treatment material increased survival of Douglas-fir or Englemann spruce one month after planting, and only ethrel treatment increased survival of lodgepole pine. Three growing seasons after planting, alginate and ethrel increased survival of early-lifted lodgepole pine and Englemann spruce compared to controls (Figure 2D). Over the three years of the experiment, Douglas-fir suffered more damage from frost and sun scald than either Englemann spruce or lodgepole pine (data not shown).

Applying PGR treatments to trees lifted during the dates suggested by industry had no effect on survival of any species four weeks after planting when compared to controls (Figure 4A). One growing season after planting, PGR treatment had little effect on the survival of Englemann spruce when compared to controls, while survival of Douglas-fir and lodgepole pine was reduced by some PGR treatments (Figure 4B). Three growing seasons after planting, Englemann spruce treated with any PGR material had higher survival than controls. Stim-root®, alginate, and Ethrel® treatments increased survival of Douglas-fir, and only Ethrel® application increased survival of lodgepole pine (Figure 4D).

Early lifting decreased survival of Douglas-fir, and pre-cold storage treated lodgepole pine and Englemann spruce one month after planting (Lift × Treatment Time Contrasts, Table 5). Three growing seasons after planting, early lifting only decreased survival of trees receiving pre-cold storage treatments with PGRs.

When compared to pre-cold storage treatments, applying PGR materials after cold-storage generally increased survival of Douglas-fir and lodgepole pine but had little effect on Englemann spruce (PGR × Treatment Time Contrasts, Table 5). One month after planting, the time of application with Stim-root® or alginate did not influence survival of Douglas-fir or Englemann spruce, while applying Stim-root® or alginate after cold storage increased

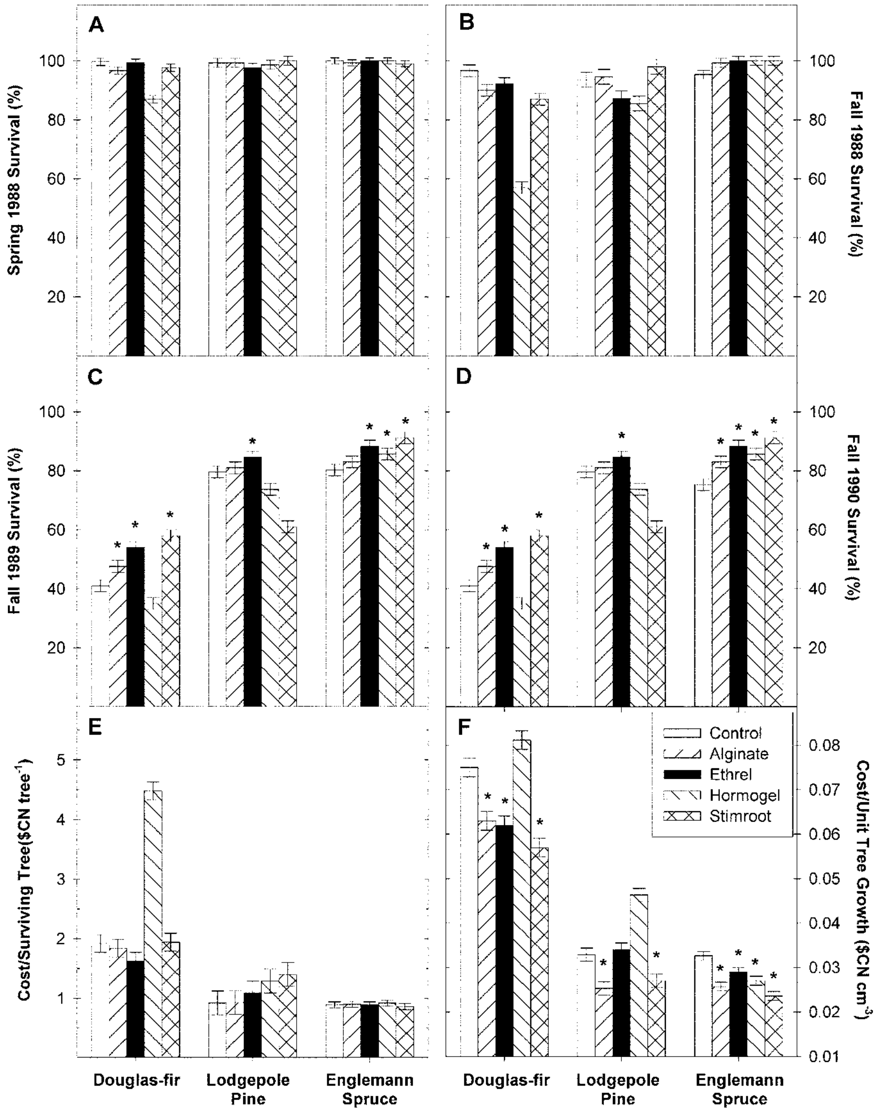

Figure 4. Influence of PGR treatments on trees lifted during the industry suggested dates. Survival four weeks after planting (A), survival one growing season after planting (B), survival two growing seasons after planting (C), survival three growing seasons after planting (D), cost of each surviving seedling (E), and cost per unit tree growth (F). Asterisks in A–D represent means significantly greater than controls ($p < 0.05$) within each conifer species based on contrast analysis. Asterisks in E–F represent means significantly less than controls ($p < 0.05$) within each conifer species based on contrast analysis. Control = no treatment, Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.

Table 5. Contrast means and significance levels (*p*-values) from contrast analysis on the survival of container grown conifers four weeks (1988) and three growing seasons (1990) after PGR treatment and planting into soil in a clearcut.[1]

Treatments		Survival (%)					
		Douglas-fir		Lodgepole pine		Englemann spruce	
		1988	1990	1988	1990	1988	1990
PGR × Treatment Time							
Means							
Control[2]	Pre[3]	78	31	85	64	96	65
	Post	75	39	80	63	96	67
Alginate	Pre	78	27	76	54	100	82
	Post	91	48	99	81	99	85
Ethrel®	Pre	71	30	97	64	99	86
	Post	94	53	99	69	100	84
Hormogel®	Pre	61	15	80	44	99	72
	Post	97	47	99	72	100	82
Stim-root®	Pre	85	29	85	50	98	74
	Post	91	51	100	83	100	86
ANOVA variance components							
MS		426.1	733.7	343.7	451.1	64.2	93.9
MSE		146.0	275.8	135.6	120.8	19.0	78.3
$F_{4,2940}$		2.91	2.65	2.53	3.73	3.38	1.19
Contrasts and significance levels							
Control (Pre vs Post)		*0.158*	*0.439*	*0.341*	*0.163*	*0.943*	*0.650*
Alginate (Pre vs Post)		*0.069*	*0.056*	*<0.001*	*0.006*	*0.204*	*0.401*
Ethrel® (Pre vs Post)		*0.001*	*0.024*	*0.730*	*0.053*	*0.522*	*0.746*
Hormogel® (Pre vs Post)		*<0.001*	*<0.001*	*0.007*	*<0.001*	*0.527*	*0.057*
Stim-root® (Pre vs Post)		*0.146*	*0.009*	*<0.001*	*<0.001*	*0.059*	*0.023*
Lift × Treatment Time							
Means							
Early Lift[4]	Pre Cold	60	14	71	39	98	73
	Post Cold	88	46	99	73	99	82
Normal Lift	Pre Cold	93	37	98	66	99	82
	Post Cold	99	53	99	78	99	84
ANOVA variance components							
MS		1815.0	2996.3	2720.3	1749.6	72.6	504.6
MSE		146.0	275.8	135.6	120.8	19.0	78.3
$F_{1,2940}$		12.43	10.86	20.06	14.48	3.82	6.44
Contrasts and significance levels							
Early Lift (Pre vs Post Cold Storage)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.047*	*0.010*
Normal Lift (Pre vs Post Cold Storage)		*0.146*	*0.029*	*0.732*	*0.004*	*0.839*	*0.512*
Pre Cold Storage (Early vs Normal Lift)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.006*	*0.008*
Post Cold Storage (Early vs Normal Lift)		*0.018*	*0.038*	*0.876*	*0.020*	*0.543*	*0.437*

[1]Contrast means, ANOVA variance components, and significance levels (*p*-values) comparing means of PGR treatments at different treatment times (PGR × Treatment Time interaction); and means of lift times at different treatment times (Lift × Treatment Time interaction). MS = Treatment mean square, MSE = Error mean square.
[2]Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.
[3]Pre-Cold = pre-cold storage treatment with PGR types, Post-Cold = post-cold storage treatment with PGR types.
[4]Early Lift = plants lifted earlier than industry suggested date, Normal Lift = plants lifted during industry suggested dates.

survival of lodgepole pine (PGR × Treatment Time Contrasts, Table 5). Three growing seasons after planting, survival of post-cold storage treated Douglas-fir and lodgepole pine was higher than trees treated prior to cold storage. PGR treatment time had little effect on survival of Englemann spruce.

Relationships between root IAA, plant growth, and survival

Free IAA and IAA conjugate concentrations in roots of Douglas-fir and Englemann spruce two weeks after planting were well correlated with new root growth, tree height, stem diameter, and plant survival three growing seasons after planting (Table 6). Free IAA content in roots of lodgepole pine two weeks after planting was only correlated to new root growth at that time. IAA conjugates in roots of lodgepole pine two weeks after planting were correlated to new root growth at that time, and height and diameter growth three growing seasons after planting (Table 6). Survival of lodgepole pine was not correlated to root IAA, new root growth, tree height or stem diameter.

Cost analysis of treatments

Early lifting increased the cost of each surviving tree (CSS) and the cost per unit tree growth (SCSS) of pre-cold storage treated Douglas-fir, lodgepole pine, and Englemann spruce (Lift × Treatment Time Contrasts, Table 7). Although response varied between species, application of PGRs to early lifted trees either increased or had no effect on CSS of all three tree species compared to controls (Figure 2E). When trees were lifted early, PGR treatment material either increased or had little effect on the SCSS of Douglas-fir and lodgepole pine. All but PGR treatment materials significantly decreased SCSS of Englemann spruce compared to controls (Figure 2F).

Applying PGRs to trees lifted during the dates suggested by industry did not decrease the cost of each surviving tree (CSS) of Douglas-fir, Englemann spruce, or lodgepole pine, three growing seasons after planting, when compared to controls (Figure 4E). Certain PGR treatments did, however, decrease the cost per unit tree growth (SCSS) three growing seasons after planting (Figure 4F). When compared to controls, trees treated with Stimroot® and alginate had lower SCSS for all three tree species. Any PGR treatment material decreased SCSS of Englemann spruce and all PGR treatment materials except Hormogel® decreased SCSS for Douglas-fir compared to controls.

When compared to pre-cold storage treatments with PGRs, applying PGR treatments after cold-storage generally decreased the cost of each surviving tree (CSS) and the cost per unit tree growth (SCSS) of Douglas-fir, and lodgepole pine after three growing seasons (PGR × Treatment Time Contrasts,

Table 6. Pearson correlation coefficients (r^2) and probability values (p), for linear correlations between root IAA concentrations, root growth, tree survival and growth characteristics of container grown conifers after PGR treatment and planting into soil in a clearcut.

	Characteristic									
	Root IAA content[1]				New root growth[2]				Survival	
Species	Free		Bound		2 Weeks		4 Months		Fall 1990	
Characteristic	r^2	p	r^2	p	r^2	p	r^2	p	r^2	p
Douglas-fir (n > 37)										
Root IAA content										
Bound	0.605	0.0002								
New root growth										
2 Weeks	0.811	<0.0001	0.740	<0.0001						
4 Months	0.455	0.0203	0.394	0.0586	0.478	0.0124				
Plant growth 1990[3]										
Height	0.808	0.2488	0.593	0.0168	0.509	0.0051	0.328	0.1024	0.042	0.430
Diameter	0.677	0.0017	0.615	0.0070	0.672	0.0002	0.599	0.0029	0.021	0.584
Survival[4]										
Spring 1988	0.268	0.1623	0.167	0.4309	0.170	0.2999	0.175	0.3691	0.429	0.026
Fall 1988	0.214	0.4696	0.124	0.4309	0.341	0.0853	0.155	0.5271	0.443	0.0286
Fall 1990	0.499	0.0267	0.088	0.4762	0.393	0.0664	0.106	0.6060		
Lodgepole pine (n > 38)										
Root IAA content										
Bound	0.492	0.0017								
New root growth										
2 Weeks	0.535	0.0005	0.558	<0.0001						
4 Months	0.028	0.4165	0.039	0.2364	0.271	0.0992				
Plant growth 1990										
Height	0.002	0.7881	0.438	0.0060	0.448	0.0048	0.419	0.0088	0.007	0.6185
Diameter	0.002	0.7797	0.439	0.0058	0.366	0.0237	0.187	0.2614	0.006	0.6511
Survival										
Spring 1988	0.045	0.2040	0.025	0.3473	0.046	0.1974	0.009	0.5723	0.428	<0.0001
Fall 1988	0.039	0.2332	0.052	0.7557	0.055	0.1570	0.061	0.1347	0.508	<0.0001
Fall 1990	0.006	0.6333	0.024	0.3513	0.029	0.3030	0.001	0.8196		
Englemann spruce (n > 50)										
Root IAA content										
Bound	0.770	<0.0001								
New root growth										
2 Weeks	0.599	<0.0001	0.645	<0.0001						
4 Months	0.642	<0.0001	0.549	<0.0001	0.646	<0.0001				
Plant growth 1990										
Height	0.316	0.0255	0.459	0.0008	0.649	<0.0001	0.301	0.0337	0.305	0.1533
Diameter	0.493	0.0003	0.508	0.0002	0.460	0.0008	0.349	0.0128	0.406	0.0034
Survival										
Spring 1988	0.221	0.1223	0.192	0.1810	0.384	0.0059	0.168	0.2445	0.549	<0.0001
Fall 1988	0.189	0.1864	0.030	0.7345	0.269	0.0583	0.406	0.0034	0.708	<0.0001
Fall 1990	0.399	0.0344	0.341	0.0918	0.465	0.0092	0.361	0.0674		

[1]Free = free IAA, Bound = IAA Conjugates two weeks after planting.
[2]2Weeks = two weeks after planting, 4 Months = four months after planting.
[3]Height = total plant height after three growing seasons, Diameter = stem diameter after three growing seasons.
[4]Spring 1988 = four weeks, Fall 1988 = one growing season, Fall 1990 = three growing seasons after planting.

Table 7. Contrast means and significance levels (p-values) from contrast analysis on the cost of surviving container grown conifers three (1990) years after PGR treatment and planting into soil in a clearcut.[1]

Treatments		1990 cost and cost per size of surviving plant					
		Douglas-fir		Lodgepole pine		Englemann spruce	
		CSS[2]	SCSS	CSS	SCSS	CSS	SCSS
PGR × Treatment Time							
Means							
Control[2]	Pre[3]	2.27	1.03	1.00	0.37	0.99	0.04
	Post	2.09	0.98	1.09	0.07	0.95	0.04
Alginate	Pre	8.51	1.29	2.19	0.21	0.91	0.06
	Post	1.82	0.06	0.94	0.04	0.85	0.03
Ethrel®	Pre	11.50	3.33	1.18	0.12	0.91	0.07
	Post	1.57	0.11	0.99	0.05	0.93	0.04
Hormogel®	Pre	24.58	3.68	3.25	0.43	1.03	0.08
	Post	1.60	0.13	1.08	0.06	0.89	0.04
Stim-root®	Pre	6.79	1.22	3.07	0.82	1.01	0.06
	Post	1.74	0.05	0.92	0.03	0.85	0.02
ANOVA variance components							
MS		218.9	0.450	11.23	0.020	0.015	0.00001
MSE		39.36	0.066	3.33	0.006	0.010	0.00004
$F_{4,2940}$		5.56	6.77	3.37	3.35	1.02	0.32
Contrasts and significance levels							
Control (Pre vs Post)		*0.704*	*0.866*	*0.961*	*0.976*	*0.957*	*0.964*
Alginate (Pre vs Post)		*0.072*	*0.018*	*0.024*	*0.049*	*0.425*	*0.067*
Ethrel® (Pre vs Post)		*0.009*	*0.001*	*0.858*	*0.772*	*0.734*	*0.133*
Hormogel® (Pre vs Post)		*<0.001*	*<0.001*	*0.045*	*0.0014*	*0.067*	*0.025*
Stim-root® (Pre vs Post)		*0.017*	*0.020*	*<0.001*	*0.001*	*0.031*	*0.086*
Lift × Treatment Time							
Means							
Early Lift[4]	Pre Cold	12.44	2.68	4.21	0.63	1.02	0.11
	Post Cold	1.76	0.14	1.08	0.07	0.91	0.06
Normal Lift	Pre Cold	9.03	1.30	1.27	0.08	0.91	0.05
	Post Cold	1.70	0.12	0.99	0.04	0.88	0.04
ANOVA variance components							
MS		1216.2	2.61	30.53	0.059	0.087	0.00027
MSE		39.36	0.066	3.33	0.006	0.0010	0.00004
$F_{1,2940}$		30.90	39.24	9.16	9.95	5.96	6.66
Contrasts and significance levels							
Early Lift (Pre vs Post Cold Storage)		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.013*	*<0.001*
Normal Lift (Pre vs Post Cold Storage)		*0.002*	*0.042*	*0.675*	*0.799*	*0.586*	*0.292*
Pre Cold Storage (Early vs Normal Lift)		*0.0145*	*0.019*	*<0.001*	*<0.001*	*0.013*	*<0.001*
Post Cold Storage (Early vs Normal Lift)		*0.979*	*0.961*	*0.896*	*0.879*	*0.598*	*0.058*

[1]Contrast means, ANOVA variance components, and significance levels (p-values) comparing means of PGR treatments at different treatment times (PGR × Treatment Time interaction); and means of lift times at different treatment times (Lift × Treatment Time interaction). MS = Treatment mean square, MSE = Error mean square.
[2]CSS = cost of each surviving tree ($CN tree^{-1}) and SCSS = cost per unit tree growth ($CN cm^{-3}) at target stocking density.
[3]Alginate = Calcium Alginic Acid, Ethrel® = Ethylene, Hormogel® = IBA and NAA, Stim-root® = IBA.
[4]Pre-Cold = pre-cold storage treatment with PGR types, Post-Cold = post-cold storage treatment with PGR types.

Table 7). The timing of PGR treatment had little effect on the CSS and SCSS of Englemann spruce. Stim-root® and alginate applications to Douglas-fir and lodgepole pine after cold storage decreased CSS and SCSS compared to trees treated prior to storage (PGR × Treatment Time Contrasts, Table 7).

Discussion

Influence of lifting time

Root IAA concentrations have been related to root formation and growth in some species (Blakesley et al. 1991). We attempted to change the IAA concentration in conifer roots in our study by external application of IAA precursors or inducers. We assumed that lifting container-grown conifers before the optimal time for lifting would reduce the amount of IAA in root tissue causing decreased root growth at planting. In general, we found that roots of early-lifted Douglas-fir, Englemann spruce, and lodgepole pine had lower free IAA and IAA conjugate contents two weeks after planting than roots from plants lifted at the normal time. Roots of early-lifted plants of all three tree species also grew less during the first two weeks after planting, and early lifting decreased tree growth and survival. Although applying certain PGR treatments to roots was able to partially offset the decrease in IAA, root growth, and tree growth resulting from early lifting, some PGR treatments did not increase survival of early-lifted trees. Treatments with PGRs should therefore not be considered an ameliorative treatment for stock lifted prior to appropriate lifting dates. The ability of certain PGRs to increase root growth by changing root IAA levels indicates that root IAA content may be a very important factor in early root growth and subsequent plant survival.

Influence of treatment time

Tissue sensitivity can influence the response of plants to PGRs (Pilet 1992). When we applied several commercial materials to root systems before cold storage or prior to planting, we found that some treatments increased root IAA concentrations, but treatment effects were dependant on the timing of application and were species specific. Differences due to timing of application may be a result of differences in tree developmental stage, the relative initial IAA content at the time of treatment, variations in the environmental conditions at the planting site, or differences in initial tree quality. Also, plants treated prior to cold storage may not be able to effectively take up and metabolize PGRs under low temperature conditions. The response of plants to auxin may also depend on the initial growth rate of the plant. At low concentrations auxin stimulates fast-growing roots more than slow growing roots (Pilet and Saugy 1987), indicating that the endogenous IAA content is different in slow- and fast-growing roots. Abscisic acid content of roots can also significantly decrease the effect of PGRs on endogenous IAA content and root growth (Pilet 1992). Treating plants after cold storage, in most cases, was more successful at increasing root IAA concentrations and root growth after planting, than treating plants before cold storage. Plants treated after cold storage may have had a better ability to absorb PGRs and synthesize IAA, or perhaps had higher levels of auxin cofactors, or lower levels of auxin antagonists. Auxin cofactors are known to reduce IAA oxidase activity (Bandurski and Schulze 1977), resulting in higher tissue IAA concentrations.

Ratios of the two forms of endogenous IAA, free and ester-linked, may also influence the regulation of root growth (Bandurski and Schulze 1977). Some researchers have found an inverse correlation between the level of ester-linked IAA and growth rate (Baraldi et al. 1995; Kleczkowski and Schell 1995). While others have reported that levels of conjugated IAA increase during adventitious root formation, levels were not always correlated to rooting (Blakesley 1994). In addition, although few conclusions have been made about the relative influences of these IAA forms, the available data show that the relative content of free and ester-linked IAA depends on the age and growth rate of the root cells. The results of our study showed that applying PGRs after cold storage increased both IAA conjugates and free IAA in roots of treated conifers when compared to plants treated prior to cold storage. In fact, plants treated with PGRs after cold storage generally had higher ratios of IAA conjugates to free IAA than plants treated with PGRs prior to cold storage.

Influence of PGR treatment

The effects of PGR treatments on root growth may be a function of the type of PGR and the concentrations applied (Pilet 1983; Firn 1986). When we applied a moisture retention gel (alginate) or one of three PGR treatments to root systems of three different conifer species, we found that some treatments increased root IAA concentrations, but treatment effects were dependant on the timing of application and were species specific. For species where Stimroot® and Ethrel® treatments increased root growth and survival, root IAA concentrations also increased. Other researchers have previously reported stimulation of root growth by Ethrel® (Graham and Linderman 1981; Alvarez and Linderman 1983; Blake and Linderman 1992). The results of our study suggest that exogenously applied ethylene (as Ethrel®) influences root growth indirectly by increasing root IAA concentrations, a phenomenon reported to occur on plants exposed to extreme stress from flooding (Wample and Reid 1978). This response could have been a direct effect of ethylene on root growth, or a response resulting from the concomitant rise in IAA content of these roots. Our results may explain the earlier results (Graham and Linderman 1981; Alvarez and Linderman 1983; Blake and Linderman 1992) where exposure of seedling roots to relatively low levels of ethylene gas stimulated root growth, a response that one would expect from elevated IAA in the roots.

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 applying alginate to roots increased root growth and plant survival but not always with a concomitant increase in root IAA concentrations. Scagel and Linderman (2000b) reported increased root initiation, root growth and survival of bare-root Douglas-fir after treating roots with alginate prior to planting, however, alginate had no effect on free IAA content of the roots. This indicates that alginate was capable of increasing root growth and survival by a mechanism not directly associated with the IAA content of the roots.

Influence on tree growth and survival

One of the objectives of this study was to determine whether exogenous application of PGRs could increase concentrations of IAA in the roots and subsequent growth and survival of conifers. Some of our PGR treatments not only elevated root IAA concentrations, but certain treatments also increased root growth and subsequent tree growth and survival. Increases in root IAA concentrations, root growth, and plant growth, were not always associated with increased tree survival. Genetic and developmental differences between species could account for the different responses, but environmental characteristics could also have played a major role. For example, the Durrand Creek site has prolonged summer drought conditions, while the spring is usually cold and wet. Treatment of trees to increase root IAA and root growth will only increase survival when survival is primarily a function of new root growth after planting. The experimental site at Durrand Creek was not considered optimal for growth of Douglas-fir due to the high incidence of early and late season frost damage and prolonged summer drought. PGR treatment increased survival of Douglas-fir one month after planting, but Douglas-fir suffered more damage from temperature extremes and sun scald than Englemann spruce. Although PGR treatment increased root IAA and root growth of Douglas-fir on this site, survival was primarily a function of the environment, rather than an increase in root development. In a similar study, we (Scagel and Linderman 2000b) found that PGR increased survival of bareroot Douglas-fir on a lower elevation site, more suitable for growth of Douglas-fir, in the coast-interior transition of British Columbia.

Even when survival is primarily a function of new root growth after planting, other environmental aspects may limit the effectiveness of PGR treatments on survival even when treatments increase root IAA and root growth. For example, treatment of lodgepole pine with Stim-root® and alginate prior to planting caused trees to flush earlier when compared to controls. Others have found that short-photoperiod treatments of trees following cold storage can effect root growth and cause an early flush after planting (Odlum et al. 1993; Hawkins et al. 1996). Earlier bud break caused PGR treated plants to be more susceptible to damage from browsing and late frosts than untreated controls, especially during the first growing season. We (Scagel and Linderman 2000b) found a similar increased in damage from browsing on bareroot Douglas-fir treated with different PGRs. Applying PGRs may increase root growth and cause trees to flush earlier than untreated trees. This may be detrimental if an early flush of growth occurs on trees planted on sites prone to frosts or damage from browsing early in the growing season. Species susceptibility to browse damage may also be a factor. In our study, Englemann spruce treated with Stim-root® and alginate also flushed earlier than controls, however browse damage was minimal.

Application to reforestation

Reforestation efforts strive for the greatest survival and growth of planted trees at the least cost. Using the appropriate lifting date (vs. early lifting) decreased the cost of each surviving tree (CSS) of controls by about 14% and the cost per unit tree growth (SCSS) by approximately 60%. Cost analyses of the treatments applied in this study suggest that treatment of Englemann spruce and lodgepole pine with certain PGRs were cost effective when the size of the surviving tree was considered. Although Stim-root® treatments decreased the SCSS of Douglas-fir three growing seasons after planting, other PGR treatments were not cost effective at increasing establishment of Douglas-fir in the type of environment on this experimental site. Cost analysis of other similar field trials (R.K. Scagel, unpublished results) showed 3–39% decreases in cost of surviving bare-root Douglas-fir (in projected target stocking) resulting from alginate or Stim-root® treatments. If the technology for PGR-mediated increased root growth and survival could be refined, planting costs could be decreased to achieve target density on difficult-to-regenerate sites where survival is primarily a function of initial root growth.

We believe that applying root-stimulating compounds to tree roots prior to planting can increase IAA levels in roots and root growth, and has the potential to increase tree survival under certain environmental conditions. With refinement, it would be logistically simple to incorporate this type of methodology into container-grown seedling production and reforestation systems. The application method is easy and rapid and when container-grown plants with firm root plugs are used, and does not appreciably change how plants are handled over normal container production practices. Although there is a great deal of variability in the response of different tree species, we believe this methodology can be fine-tuned by better defining optimum PGR concentrations and timing to reduce variability in responses. The results here were similar to those resulting from inoculation with PGR-producing or -inducing ectomycorrhizal fungi (Scagel 1994; Scagel and Linderman 1998a, 1998b), and exploitation of either type of treatment might have very profound effects on tree survival after planting.

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