

This Journal of Environmental Horticulture article is reproduced with the consent of the Horticultural Research Institute (HRI – <u>www.hriresearch.org</u>), which was established in 1962 as the research and development affiliate of the American Nursery & Landscape Association (ANLA – <u>http://www.anla.org</u>).

# HRI's Mission:

To direct, fund, promote and communicate horticultural research, which increases the quality and value of ornamental plants, improves the productivity and profitability of the nursery and landscape industry, and protects and enhances the environment.

The use of any trade name in this article does not imply an endorsement of the equipment, product or process named, nor any criticism of any similar products that are not mentioned.

# Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-07-19 via free access

# Height Control of *Picea spp.* and *Chamaecyparis lawsoniana* with Uniconazole and 6-Benzyladenine<sup>1</sup>

M.W. Duck<sup>2</sup>, B.M. Cregg<sup>3</sup>, R.T. Fernandez<sup>4</sup>, R.D. Heins<sup>5</sup>, and F.F. Cardoso<sup>6</sup>

Department of Horticulture

Michigan State University, East Lansing, MI 48824

## – Abstract –

The use of plant growth retardants (PGRs) could benefit conifer growers by enabling them to produce more uniform, live tabletop Christmas tree specimens. We applied two PGRs to determine effectiveness on height control and terminal bud density for the following species of conifer seedlings: Black Hills spruce (*Picea glauca var. densata*), Serbian spruce (*P. omorika*), Colorado blue spruce (*P. pungens*), and Port Orford cedar (*Chamaecyparis lawsoniana*). The chemicals were applied at 2-week intervals throughout an 8-week period for a total of four applications. Uniconazole was applied as a foliar spray and soil drench (5 and 1 ppm, respectively), 6-benzyladenine (BA) was applied as a foliar spray (500 and 1000 ppm), and the control did not receive a PGR application. Uniconazole was generally effective on the spruces but not on Port Orford cedar, whereas BA reduced height of all species and increased spruce bud densities. However, BA treatments were phytotoxic in all species tested. The drench of uniconazole caused minor phytotoxicity in Black Hills spruce, whereas foliar applications to Port Orford cedar had minor phytotoxic effects.

Index words: Sumagic®, spruce, plant growth regulator, benzyladenine.

Species used in this study: Port Orford cedar [*Chamaecyparis lawsoniana* (Murray) Parl.]; Black Hills spruce [*Picea glauca* (Moench) Voss var. *densata*]; Serbian spruce [*P. omorika* (Pancic) Purkyne]; and Colorado blue spruce (*P. pungens* Engelm.).

Plant growth regulators used in this study: uniconazole (Sumagic®), 6-benzyladenine (6-BA).

### Significance to the Nursery Industry

Container-grown tabletop Christmas trees have potential as new products for conifer nursery growers. However, intensively cultured conifers may grow too tall for use as tabletop trees. Plant growth retardants offer the possibility of controlling height without manual pruning. Uniconazole and 6benzyladenine were effective in controlling height of several species that can be grown as tabletop Christmas trees. The severe impacts of BA on growth of the spruces suggest that lower rates than those used here may provide adequate height control.

### Introduction

Greenhouse production of live tabletop Christmas trees can cause undesirable terminal shoot growth, resulting in an asymmetrical, unattractive plant. Many conifer species grow rapidly after seedlings become established (12, 20). The optimum growing conditions can further increase seedling growth, resulting in an undesirable growth habit. Consumers tend to prefer a natural, symmetrical specimen with full, yet open, branches (19). This growth habit allows ornaments to hang straight and shoot tips to look natural instead of having sheared or damaged tips. Plant growth retardant applications could eliminate shearing of seedlings, reducing labor costs but still resulting in a product appealing to consumers.

Although plant growth retardants (PGRs) are an important tool in growth regulation of ornamental crops (17), little work has been done to determine their effects on conifer species. Uniconazole is a common and effective PGR that could prove beneficial to conifer growers (1, 5, 7, 9) in the production of tabletop Christmas trees. It was introduced into the industry in the early 1980s as a foliar- or soil-drench-applied chemical that inhibits gibberellin (GA) biosynthesis (13, 17). The main benefits from its use are shortened internodes, darker green foliage, and an increase in epicormic bud development (10, 18). Compared to other PGRs, uniconazole can be applied at much lower rates to achieve comparable height control. Uniconazole is more effective when applied as a soil drench (2) because the chemical is transported throughout the plant via xylem tissue rather than phloem tissue. Therefore, when uniconazole is applied directly to the foliage, it cannot move throughout the plant, resulting in growth control only in tissue with which it comes into direct contact.

Another PGR that has proven useful in the ornamentals industry is benzyladenine (BA). Unlike uniconazole, which inhibits the action of endogenous hormones, BA is a synthetic cytokinin that can mimic such hormones to stimulate plant growth. Cytokinins are responsible for promoting lateral branching (2, 5, 8), which makes BA a possible treatment for promoting greater bud densities. BA is effective in controlling growth and increasing bud densities of various conifers, but can produce undesirable effects such as deformed buds, reduced root growth, delayed budbreak, inhibition of secondary needle extension (3), and shortened, chlorotic needles (15, 16).

The objectives were to determine the effectiveness of uniconazole and BA applications in controlling height and increasing bud densities and to determine whether such applications were phytotoxic to some common landscape conifers used in the production of tabletop Christmas trees.

### **Materials and Methods**

Plant material and culture. The plant species we evaluated were Serbian spruce (Picea omorika), Black Hills spruce

<sup>&</sup>lt;sup>1</sup>Received for publication March 17, 2004; in revised form May 24, 2004. <sup>2</sup>Academic Specialist.

<sup>&</sup>lt;sup>3</sup>Assistant Professor.

<sup>&</sup>lt;sup>4</sup>Associate Professor.

<sup>&</sup>lt;sup>5</sup>Professor.

<sup>&</sup>lt;sup>6</sup>Veterinarian, M.Sc., Ph.D. Animal Breeding and Genetics Researcher, EMBRAPA (Brazilian Agricultural Research Corporation), Bage, Brazil.

(*P. glauca* var. *densata*), Colorado blue spruce (*P. pungens*), and Port Orford cedar (*Chamaecyparis lawsoniana*). At the beginning of the trial trees ranged in height from 15 to 74 cm (38 to 88 in). Seedlings were received from a local commercial nursery (Vans Pines Nursery, West Olive, MI) and planted in April 2000 in 3.8 liter (#1) containers (1 gal) with a 7:3 (by vol) peat:perlite substrate (Peat-Perlite Mix, Michigan Grower Products, Galesburg, MI).

Seedlings were grown outdoors under natural conditions at the Michigan State University Horticulture Teaching and Research Center (HTRC) in East Lansing. In June 2000, seedlings were treated with Ronstar preemergent herbicide at 2.2 kg/ha (9624 lb/A) and provided 17-7-8, a 3- to 7-month granular fertilizer (Wilbro Horticultural Products, Norway, SC) at 10 g/seedling (0.35 oz/seedling). Seedlings were irrigated with well water as needed. On January 30, 2001, once sufficient natural chilling had occurred, seedlings were transferred to a 16 hr (extended photoperiod using high-pressure sodium lamps)/20C (68F) greenhouse. Seedlings were irrigated as needed with a nutrient solution of well water [electrical conductivity of 0.65 mS/cm and 105, 35, 23 (mg/liter) Ca, Mg, and S, respectively] acidified with H<sub>2</sub>SO<sub>4</sub> to a titratable alkalinity of CaSO, at 130 mg/liter, containing watersoluble fertilizer [125–12–125–13 mg/liter N–P–K–Ca plus 1.0-0.5-0.5-1.0-0.2-0.1 mg/liter Fe-Mn-Zn-Cu-B-Mo (MSU Special, Greencare Fertilizers, Chicago, IL)].

*PGR treatments.* We used a completely randomized design with 10 plants per species and treatment. Beginning on February 7, the chemicals were applied at 2-week intervals throughout an 8-week period for a total of four applications. Uniconazole (Sumagic®, Valent USA Corporation, Walnut Creek, CA) was applied either as a foliar spray to run-off at 5 ppm or a soil drench (150 mL per drench) at 1 ppm. Although uniconazole is considered to be more effective as a drench, we tested it as a foliar application as well due to ease of application. 6-BA (Valent USA Corporation, Walnut Creek, CA) was applied only as a foliar spray (500 and 1000 ppm), and the control received no PGR treatment. All foliar applications contained a wetting agent (Capsil™, Aquatrols Corporation of America, Inc., Cherry Hill, NJ). A barrier was used during application of the PGRs to avoid chemical drift.

Data collection and analysis. At the beginning of the trial, initial heights of all seedlings were measured, and terminal bud counts were recorded on the spruce seedlings. Height was measured throughout the trial at 2-week intervals (corresponding to each of the PGR applications). Phytotoxic effects (needle browning, discoloration, distorted growth) were noted at the time of height measurements. Seedlings were scored as 0 (no phytotoxicity symptoms) or 1 (evidence of phytotoxicity) Final height and terminal bud count were recorded at the completion of the experiment on May 2, 2001. Since initial seedling size varied by species, comparison of growth effects were based on relative growth rate (RGR) (8, 21) calculated as:

 $RGR = [ln (final height) - ln (initial height)] \div d$ 

Bud density for each section of new growth was calculated from bud count data by dividing the number of buds by shoot length.

Data for relative growth rate, bud density, and phytotoxicity were analyzed by using the mixed procedure (PROC MIXED) (SAS/PC software, SAS Institute Inc., Cary, NC). Normal distribution on the residual terms for RGR data was achieved after three extreme outliers were removed. However, significance levels did not change; therefore, data analysis was performed on the complete data set. Normal distributions for bud density and phytotoxicity data were achieved after log transformation and one extreme outlier was removed. Removal of the outlier did not change significance levels, so only a log transformation was performed. Means were separated by Tukey's Studentized Range test.

### **Results and Discussion**

Each of the main effects examined (species and PGR) affected (P < 0.0001) mean RGR and mean bud density (Table 1). Uniconazole reduced shoot height of Serbian spruce but had no effect on Black Hills spruce, Colorado blue spruce, or Port Orford cedar (Table 2). Uniconazole did not affect bud density for any species tested. Applications of BA increased bud density, reduced height growth (Fig. 1), and caused phytotoxic effects for every species tested (Table 3). Because of these significant interactions between main effects, making generalized recommendations for the overall experiment is difficult; therefore, results are presented for each species.

Black Hills spruce. Both BA treatments caused severe injury in Black Hills spruce seedlings (Table 3). The most severely damaged foliage turned brown and then died. Symptoms appeared after the final 500 ppm application, with 80% of those seedlings dying within the following 10 weeks. Seedlings treated with BA at 1000 ppm developed phytotoxic symptoms after the third application, and 100% of them died within the 10-week monitoring period. Needles that formed after BA treatments began were somewhat stunted compared with those of control seedlings, and needles grew parallel with rather than perpendicular to the stems. Only one seedling developed minor phytotoxic symptoms in the uniconazole drench treatment. All PGR treatments reduced relative height growth (Fig. 2). Bud density was increased by both BA treatments, but uniconazole treatments had no effect (Table 2). New buds occurred in clusters on growth that developed after BA treatments began. Areas of increased bud development were deformed and unattractive.

Serbian spruce. Phytotoxic effects of BA applications also occurred in Serbian spruce seedlings (Table 3), although symptoms differed from those observed with Black Hills spruce seedlings. New growth of affected seedlings was lightpink to purple. Discoloration in seedlings treated at 500 ppm was minor and began to disappear after final measurements

 Table 1.
 Analysis of variance for mean relative growth rate (RGR) (cm/d) and bud density (buds/cm) of four conifer species.

	RGR		Bud density	
Effect	df	F	df	F
Plant growth retardant	4	107.5 <sup>z</sup>	4	27.1 <sup>z</sup>
Species	3	82.3	2	28.1
$PGR \times Species$	12	6.2	8	12.5

<sup>z</sup>All effects significant at P < 0.0001.

Table 2.	Mean plant height,	number of buds.	and bud densities	for conifer seedlings	treated with BA or uniconazole.

Species	Treatment (ppm) <sup>z</sup>	Mean shoot growth (cm) <sup>y</sup>	Mean number of buds (buds/shoot) <sup>x</sup>	Mean bud density (buds/cm)
Black Hills spruce	Control	12.8a	30.9a	2.4b
	BA 500 ppm	2.3b	14.3c	5.7a
	BA 1000 ppm	1.9b	16.0bc	3.4b
	Uniconazole 1 ppm	10.2a	28.3ab	2.5b
	Uniconazole 5 ppm	9.6a	26.4abc	2.8b
Serbian spruce	Control	11.0a	20.2b	1.9b
	BA 500 ppm	2.3c	26.9a	15.3a
	BA 1000 ppm	0.9c	10.0c	14.0a
	Uniconazole 1 ppm	8.0b	16.4b	2.2b
	Uniconazole 5 ppm	8.1b	19.8b	2.3b
Colorado blue spruce	Control	10.1a	19.2a	2.1bc
	BA 500 ppm	5.6b	16.9a	3.0a
	BA 1000 ppm	2.1c	4.7b	1.7c
	Uniconazole 1 ppm	11.2a	23.3a	2.1bc
	Uniconazole 5 ppm	8.8a	21.8a	2.5ab
Port Orford cedar	Control	5.6a	_	_
	BA (500)	2.4b	_	_
	BA (1000)	1.2b	_	_
	Uniconazole (1)	5.7a	_	_
	Uniconazole (5)	6.4a	_	_

<sup>z</sup>All PGR treatments were applied as foliar sprays except for uniconazole at 1 ppm (drench).

<sup>y</sup>Means within a species followed by the same letter are not different (P < 0.05). Means separated by Tukey's Studentized Range Test.

x Bud number and bud density not scored for Port Orford cedar



Fig. 1. Effects of plant growth retardant applications on height growth over time for Black Hills spruce, Serbian spruce, Colorado blue spruce, and Port Orford cedar seedlings.

were taken in May. However, all seedlings treated with BA at 1000 ppm developed severe phytotoxic symptoms, resulting in a large amount of dead foliage. Damage initially occurred on branch tips, but all of these seedlings eventually died within the 10-week monitoring period. No uniconazole treatment was phytotoxic. All PGR treatments reduced relative height growth (Fig. 2). Bud density was increased by both BA treatments, but uniconazole treatments had no effect (Table 2). New buds occurred in clusters on new growth that formed after BA treatments were applied. These areas were light-pink to purple, and bud clusters were somewhat deformed.

*Colorado blue spruce.* Seedlings developed phytotoxic symptoms following both BA treatments (Table 3). Symptoms were similar to those observed with Serbian spruce; however, tissue discoloration was light to dark red. Foliar damage was severe in both BA treatments, with all seedlings dying within the 10-week monitoring period after final measurements were recorded. Both BA treatments reduced height (RGR), but uniconazole did not affect RGR (Fig. 2). Benzyladenine application at 500 ppm increased bud density (Table 2). Increased bud formation occurred in clusters on growth that formed after BA treatments. Bud density was not affected by any other PGR treatment.

*Port Orford cedar.* Phytotoxic symptoms developed after the third application on seedlings treated with both rates of BA, and all treated seedlings died within the 10-week monitoring period (Table 3). New growth that formed during the trial was extremely stunted and was in clusterlike formations on the outermost branch tips. Uniconazole drench treatments were not phytotoxic; however, foliar applications of uniconazole caused minor phytotoxic symptoms on three of the 10 seedlings tested. Uniconazole treatments did not af-

Table 3. Mean phytotoxicity score of conifer seedlings treated with BA or uniconazole. Seedlings rated as 0 = no damage or 1= visible injury.

Treatment (ppm) <sup>z</sup>	Black Hills spruce <sup>y</sup>	Serbian spruce	Colorado blue spruce	Port Orford cedar
Control	0.0a	0.0a	0.0a	0.0a
BA 500 ppm	0.4bc	1.0b	1.0b	1.0b
BA 1000 ppm	1.0c	1.0b	1.0b	1.0b
Uniconazole 1 ppm	0.1ab	0.0a	0.0a	0.0a
Uniconazole 5 ppm	0.0a	0.0a	0.0a	0.0a

<sup>z</sup>All PGR treatments were applied as foliar sprays except for uniconazole at 1 ppm (drench).

<sup>y</sup>Means within a species followed by the same letter are not different (P < 0.05). Means separated by Tukey's Studentized Range Test.

fect seedling growth, but both BA treatments reduced shoot growth (Fig. 2).

Benzyladenine. This synthetic cytokinin can mimic natural plant hormones by either increasing bud density or reducing shoot elongation (2, 11). Height was reduced in all species tested (Fig. 1), and bud density also increased in each of the spruce species (Table 2). However, BA treatments caused severe phytotoxic effects on all species (Table 3). Blake and South (3) reported similar findings on loblolly pine (Pinus taeda L.). BA reduced plant height when sprayed with 1000 ppm, but not 500 ppm. Little (14) dipped shoots of balsam fir [Abies balsamea (L.) Mill.] seedlings in a liquid solution of BA, which caused an increase in lateral bud number, branch diameter, and lateral shoot production. The most effective treatments in this study were those applied after the branches had reached 70% of their final length; phytotoxic symptoms were observed after multiple applications of BA whereas single treatments caused minimal or no phytotoxicity.

We applied a total of four applications in our trial, with phytotoxic symptoms occurring after the third treatment in most species. The frequency of phytotoxic effects may have been related to the number of application. Also, since seedlings were actively growing when treatments were applied, this new growth may have been too young and sensitive, re-



Fig. 2. Effects of plant growth retardant applications on mean relative growth rates of Black Hills spruce, Serbian spruce, Colorado blue spruce, and Port Orford cedar seedlings. Error bars represent SE of the mean.

sulting in damaged tissue similar to that observed by Little (14) in Fraser fir [*Abies fraseri* (Pursh) Poir.] seedlings.

Tissue discoloration occurred around the areas of increased bud development with Colorado blue spruce seedlings, and occurred on new growth of concolor fir seedlings. Prior research has also indicated this same red to purple discoloration on new growth of the following species: Serbian spruce seedlings, concolor fir [*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr.] (5), balsam fir (14), and Colorado blue spruce seedlings (16). Phytotoxic symptoms in fir seedlings were thought by Little (14) to be a result of applying BA too soon to new shoot growth.

Buds from areas of increased bud formation on spruce seedlings were somewhat deformed and occurred in clusters. Loblolly pine seedlings treated with BA at 1000 ppm experienced abnormal bud development, inhibition of secondary needle extension, and delayed budbreak (3). Shortened, unnatural needle growth, as observed with Black Hills spruce seedlings that we tested, was also detected in Scotch pine (*Pinus sylvestris* L.) seedlings treated with BA (15).

Uniconazole. Treatments of uniconazole reduced stem length of Black Hills and Serbian spruce. Hinesley (7) reported height growth of Fraser fir seedlings was reduced by 22 to 45% after the plants received soil drench treatments of uniconazole at 2, 4, or 16 ppm. Uniconazole reduced apical dominance, which favored lateral shoot growth over terminal shoot growth. A soil drench of uniconazole at rates of 1000 and 2000 ppm reduced height growth of 3-yr-old loblolly pine seedlings by 55% (1).

Unlike Black Hills and Serbian spruce, seedling growth of Colorado blue spruce and Port Orford cedar was not affected by uniconazole. Shoot growth was not affected in Colorado blue spruce seedlings receiving 15 ppm foliar applications of uniconazole, (5). Shoot dry weight of leyland cypress [*X Cupressocyparis leylandii* (A.B. Jacks. & Dallim.) Dallim. & A.B. Jacks] already established in the landscape was unaffected by foliar or soil drenches of uniconazole (9). However, growth of containerized Leyland cypress treated in the same manner as the field-grown specimens was reduced by 37 to 48%. Effectiveness of uniconazole applications on Colorado blue spruce and Port Orford cedar seed-lings could depend on age, application method, and rate of application.

Bud density of all species tested was unaffected by either uniconazole treatment. The main benefits generally observed from the use of uniconazole were shortened internodes, darker green foliage, and an increase in epicormic bud development. One reason we did not observe increased bud densities may be because of the time of year treatments were applied. Uniconazole treatment of Fraser fir seedlings in May increased lateral bud number (by 20 to 24%), whereas treatment in June and September reduced lateral bud formation 45 to 34% (7).

Plant growth retardants could benefit tabletop Christmas tree producers by reducing the need to prune long terminal shoots and increasing lateral branch formation for fuller, more attractive specimens. Uniconazole treatments reduced shoot growth of Black Hills and Serbian spruce, had no effect on growth of Colorado blue spruce and Port Orford cedar, and did not increase bud density of any species tested. BA significantly reduced shoot growth of all species treated and also increased bud density of spruce seedlings. However, BA treatments at both rates were extremely phytotoxic in all species. Because all species we tested were very responsive to BA treatments, this PGR may have potential for controlling shoot height and increasing bud density in conifers. By reducing application rates and making fewer applications, height control and increased bud density might be achieved with less phytotoxicity. Studies should be performed with BA and uniconazole to determine more effective rates and the most effective timing of applications for BA in regard to age of new growth. Plant growth retardant protocols can then be developed for tabletop Christmas trees.

### Literature Cited

1. Barnes, A.D. and W.D. Kelley. 1992. Effects of a triazole, uniconazole, on shoot elongation and root growth in loblolly pine. Can. J. For. Res. 22:1–4.

2. Barrett, J.E. 1992. Mechanisms of action, p. 12–18. *In*: H.K. Tayama, R.A. Larson, P.A. Hammer and T.J. Roll. Tips on the Use of Chemical Growth Regulators on Floriculture Crops. Ohio Florists' Association, Columbus, OH.

3. Blake, J.I. and D.B. South. 1991. Effects of plant growth regulators on loblolly pine seedling development and field performance. Proc. 6th Biennial S. Silv. Res. Conf. 100–107.

4. Bryan, J.A. and J.R. Seiler. 1991. Accelerating Fraser fir seedling growth with benzylaminopurine sprays. HortScience 26:389–390.

5. Duck, M.W. 2002. Developing production systems for tabletop Christmas trees. M.S. Thesis. Michigan State Univ., East Lansing.

6. Hinesley, L.E. and R.W. Wright. 1988. Budset and growth of eastern white pine following application of 6-benzylaminopurine to trees fertilized with different levels of Nitrogen. J. Environ. Hort. 6:42-45.

7. Hinesley, L. E., S.L. Warren, and L.K. Snelling. 1998. Effect of uniconazole on shoot growth and budset of containerized Fraser fir. HortScience 33:82–84.

8. Hunt, R. 1982. Plant Growth Curves: The Functional Approach to Plant Growth Analysis. Edward Arnold, London.

9. Keever, G.J. and M.S. West. 1992. Response of established landscape plants to uniconazole. HortTechnology 2:465-468.

10. Kimball, S.L. 1990. The physiology of tree growth regulators. J. Arboriculture 16:39–41.

11. Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press, Orlando, FL.

12. Landis, T.D., R.W. Tinus, S.E. McDonald, and J.P. Barnett. 1992. The container tree nursery manual: Atmospheric environment. USDA Forest Service, Washington, DC.

13. Larson, R. 1992. History, p. 8–11. *In*: H.K. Tayama, R.A. Larson, P.A. Hammer, and T.J. Roll. Tips on the Use of Chemical Growth Regulators on Floriculture Crops. Ohio Florists' Association, Columbus, OH.

14. Little, C.H.A. 1985. Increasing lateral shoot production in balsam fir Christmas trees with cytokinin application. HortScience 20:713–714.

15. Mulgrew, S.M. and D.J. Williams. 1984. Promoting bud development and branching of Scotch pine with 6-BA. J. Arboriculture 10:294–297.

16. Mulgrew, S.M. and D.J. Williams. 1985. Effect of benzyladenine on the promotion of bud development and branching of *Picea pungens*. HortScience 20:380–381.

17. Rademacher, W. 1991. Biochemical effects of plant growth retardants. p. 169–200. *In*: Plant Biochemical Regulators. New York, Marcel Dekker, Inc.

18. Ruter, J.M. 1994. Growth and landscape establishment of *Pyracantha* and *Juniperus* after application of paclobutrazol. HortScience 29:1318–1320.

19. Sundback, E. 2002. The future is open. Michigan Christmas Tree J. 49:5–7.

20. Thomas, B. and D. Vince-Prue. 1997. Bud dormancy. p. 279–316. *In*: Photoperiodism in Plants. Academic Press, San Diego, CA.

21. Wang, G.G., J. Su, and J.R. Wang. 2000. Height growth of planted black spruce seedlings in response to interspecific vegetation competition: a comparison of four competition measures at two measuring positions. Can. J. For. Res. 30:573–579.