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Physiology and Growth of Containerized Coastal Douglas Fir Seedlings Given Different Durations of Short Days to Induce Dormancy

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Abstract. **We compared the effects of different durations of short days (SDs) as a dormancy-induction regime on bud development, bud endodormancy, and morphology of first-year containerized coastal douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] seedlings in the nursery together with seedling survival and growth after one growing season in a common garden. In early July, four durations of 8-h SDs were applied: 3, 4, 5, and 6 weeks. During the first week of SDs, budscale initiation started and was completed; then initiation of needles for next year's leading shoot (leader) began. Needle initiation was completed 10 weeks after the start of the regime in seedlings given 5 or 6 weeks of SDs and 13 weeks for those given 3 or 4 weeks of SDs. In early October, duration of SDs had no effect on bud endodormancy; 50% to 88% of terminal buds were endodormant. On this date, seedling height and shoot dry weight were unaffected by duration of SDs, whereas root dry weight and shoot diameter were significantly reduced in seedlings given 6 weeks of SDs compared with other durations. After one growing season, duration of SDs had no effect on seedling survival, leader length, shoot dry weight, root dry weight, or shoot diameter. We recommend the 3-week duration of SDs for coastal douglas fir crops.**

A critical phase of forest nursery culture is dormancy induction because it signals the end of height growth and the start of bud development. Forest nurseries in British Columbia, Canada, use short days (SDs) and/or moderate moisture stress as dormancy induction regimes [S. Joyce and S. Kiiskila, British Columbia Ministry of Forests and Range (BCMOFR), personal communication, 2009]. Studies have compared the effects of a SD regime with a moderate moisture stress regime on seedling morphology and physiology in the nursery as well as performance after planting for western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] (Grossnickle et al., 1991a, 1991b; O'Reilly et al., 1989a, 1989b, 1994a, 1994b), western red cedar (*Thuja plicata* Donn ex D. Don) (Krasowski and Owens, 1991; Krasowski et al., 1990), and coastal douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] (MacDonald and Owens, 2006). Control of height growth using SDs in recalcitrant, high-latitude British Columbia seedlots of sitka spruce [*Picea sitchensis* (Bong.) Carrière], sitka spruce × white spruce [*Picea glauca* (Moench.) Voss] hybrids, and sitka spruce × engelmann spruce (*Picea engelmanni* Parry) hybrids and its effects on subsequent performance have also been described (Hawkins and Draper, 1991; Hawkins et al., 1996; Krasowski et al., 1993).

Coastal douglas fir is one of the most important and valuable trees in temperate forestry both within its natural range and as an exotic (Hermann and Lavender, 1990). Within western North America, the variety extends from California to British Columbia (long. 37°–53° N, lat. 119°–128° E) (Kaundun et al., 1998). Coastal douglas fir is very important to the economy of British Columbia because its wood is valued in the global market for high-quality structural lumber (Aubry et al., 1998). In British Columbia, 51.1 million containerized coastal douglas fir seedlings were planted on government lands between 2000 and 2008 (A. Powelson, BCMOFR, personal communication, 2009).

The SD dormancy-induction regimes used by British Columbia nurseries are variable. Some nurseries use multiple applications of SDs, separated in time, whereas other nurseries use a single application. In coastal douglas fir seedlings, increasing the number of applications of SDs decreased shoot diameter, increased photosynthetic efficiency after –18 °C freezing in early fall, and decreased days to budbreak in late winter/early spring (Turner and Mitchell, 2003). In addition, abnormal bud development after multiple applications of SDs can occur in coastal douglas fir seedlings (MacDonald, unpublished results), which necessitates culling of affected seedlings during morphological grading (R. Merrell, BCMOFR, personal communication, 2009). For nurseries using a single SD application, the number of weeks used varies. However, the BCMOFR—which administers contracts for nursery crops, including cultural guidelines, and subsequently evaluates the crops—needs more than anecdotal information on the effects of different durations of SDs on seedling attributes.

Nurseries face an operational tradeoff in selecting the duration of SDs to be used for coastal douglas fir crops. If the duration is too short, terminal buds will break and height growth will resume after the return to a long ambient photoperiod, thereby delaying shoot frost hardening and, thus, lift dates for early fall planting or freezer storage. If the duration is too long, then seedling biomass may be reduced and seedlings may not meet the BCMOFR morphological specifications for root dry weight and shoot diameter. The objectives of this research were to compare the effects of single applications of different durations of SDs on bud development, bud endodormancy, and morphology of coastal douglas fir seedlings in the nursery as well as on seedling survival and growth after one growing season in a common garden.

Materials and Methods

Nursery culture. Seedlings from one coastal douglas fir seedlot (BCMOFR Registered Seedlot No. 4505, long. 48°49′ N, lat. 123°56′ W, elevation 610 m) were used in this study. They were part of a commercial crop grown at the Angus P. MacBean Nursery in Yellow Point, British Columbia, Canada (long. 49°4′ N, lat. 123°55′ W). Stratified seeds were sown on 9 Apr. in British Columbia/Canadian Forest Service Plug Styrofoam Block (BC/CFS PSB) Styroblock 313A containers (198 cavities per container or 936 cavities/m^2, 60 mL volume per cavity, 13.3-cm cavity depth, 2.8-cm cavity top diameter) (Beaver Plastics Ltd., Edmonton, Alberta, Canada). The substrate mix was 2 peat:1 vermiculite (by volume)

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The use of trade names are necessary to report factually; however, the use of a name implies no endorsement by Natural Resources Canada of the product to the exclusion of others that may also be suitable.
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with a planned bulk density of 0.09 g·mL $^{-1}$. Nutricote Type 360 slow-release fertilizer (16N–4.4P–8.3K) (Chisso-Asahi Fertilizer Co., Ltd., Tokyo, Japan) was incorporated into the mix at a rate of 1.3 kg·m $^{-3}$. After germination, fertilizer was applied during each irrigation. A forestry seedling starter fertilizer (11N–17.9P–6.6K) with micronutrients was applied at a rate of 500 to 750 mg·L $^{-1}$ during April and May. Subsequently, a high nitrate forestry seedling fertilizer (20N–3.4P–16.6K) with micronutrients was applied at a rate of 750 mg·L $^{-1}$ from June until the end of dormancy induction. Iron chelate (13% Fe) and a soluble trace element mix (13% sulfur, 1.35% boron, 2.3% copper, 7.5% Fe, 8% manganese, 0.04% molybdenum, and 4.5% zinc) were applied, as needed, to adjust the foliar nutrition levels. Calcium nitrate (15.5% nitrogen, 20% calcium) was applied, as needed, to maintain the pH of the growing substrate between 4.5 and 5.5.

Although there was a limitation in using one seedlot, the results have broad geographical application because of the BCMOFR seed transfer rules (Snetsinger, 2007). This seedlot can be planted throughout the Maritime Seed Planning Zone (SPZ) from long. 48°25′ N to 51°49′ N (Vancouver Island and adjacent coastal mainland) at elevations from 260 m to 960 m as well as within the much smaller adjacent Georgia Lowlands SPZ (rain-shadow areas of southern Vancouver Island and adjacent Gulf Islands). In British Columbia, SPZs have been established to ensure that plantations are adapted to local climatic conditions (Ying and Yanchuk, 2006).

Dormancy induction regimes and postinduction culture. Within the greenhouse used for the SD dormancy induction regime, photoperiod was controlled with a computer-automated blackout curtain system (VRE Greenhouse Systems, Stoney Creek, Ontario, Canada). To control temperature and humidity below the curtain system, four 1.5-m diameter exhaust fans (which were externally hooded with blackout curtain material to prevent light leaks) in the end walls vented when greenhouse temperatures reached 25 °C. Greenhouse space above the curtain system was vented by a jet tube suspended below the ridge. By late June, crop height averaged 16 cm and thus was approaching target height (17 cm). Earlier trials at our cooperating nursery had shown that seedlings continued to elongate after the SD cue was given; consequently, it is necessary to apply the SD regime before target height is attained so that the maximum height (25 cm) is not exceeded. On July 3, ambient photoperiod was 16 h 7 min. The SD regime began on 4 July (8-h photoperiod, 0800 IIR to 1600 IIR). Four durations of SDs were selected: 3, 4, 5, and 6 weeks. Shorter durations (2 weeks or less) were not used because experience at our cooperating nursery showed that budbreak occurred and shoot growth resumed after seedlings were returned to ambient photoperiod, delaying bud dormancy and frost hardiness. Based on a controlled environment study, McCreary et al. (1978) prescribed 8 weeks of SDs for coastal douglas fir seedlots from Oregon. We did not include a 7- or 8-week duration in this study because these durations reduced shoot diameter to values below minimum specifications in an earlier trial at our cooperating nursery (MacDonald, unpublished observations); thus, the seedlings would have been culled. A long-day control was also not included because that would not have induced dormancy. However, crop response to a control—a moderate moisture stress regime—compared with a SD regime (4-week duration) was reported in MacDonald and Owens (2006).

Containers were transferred to another greenhouse at the end of each duration. The roof and walls of that greenhouse had been removed, and thus temperature and photoperiod were ambient. Photoperiod on the day the 3-, 4-, 5-, and 6-week durations ended was 15 h 24 min, 15 h 7 min, 14 h 46 min, and 14 h 24 min, respectively. Irrigation with a forestry seedling finisher fertilizer (8N–8.7P–24.9K) with micronutrients, at a rate of 750 mg·L $^{-1}$, began. In late October, the polyethylene glazing was installed on the greenhouse. From mid-November until late March, irrigation did not occur and greenhouse temperature was maintained at 5 °C by heating and cooling. (This was a departure from the usual practice of freezer storage in British Columbia.) In late March, seedlings were planted in a common garden (without an irrigation system) in an abandoned agricultural field on the University of Victoria campus, Victoria, British Columbia (long. 48°25′ N, lat. 123°21′ W).

Experimental design in the greenhouse and common garden. A randomized complete block design was used in the greenhouse and common garden. In the greenhouse, the main plot consisted of four blocks, each corresponding to a pallet. Each pallet held 30 containers; the inner group of 16 containers comprised the experimental units and was surrounded by a buffer one container wide. In each block, three containers were randomly assigned to each duration of SDs, and the remaining four containers served as space holders. In the common garden, the main plot consisted of two blocks.

For each duration of SDs, seedlings were sampled from each of the four greenhouse blocks. Seedling location within each container was randomly selected; seedlings less than 16 cm were not sampled because they were thought to have ceased height growth and begun bud development before the start of the SD dormancy-induction regime.

Observations. On the day before the SD regime began and at regular intervals (weekly then biweekly) during bud development, seedlings were randomly sampled from each duration of SDs. Depending on quality of dissection, up to eight shoot tips were dissected and examined under scanning electron microscopy for illustrative purposes. In addition, 16 shoot tips were dissected and embedded in paraffin blocks. From these, 12 shoot tips per duration of SDs were further processed for serial sectioning and staining for light microscopy (the remainder was archived). Of these, the slides bearing the eight shoot tips that were free from processing artifacts were chosen. Then, the central-most longitudinal section of each shoot tip was selected, projected onto paper, traced, and stage of development was observed. Once needle initiation within the bud had started, the number of needle primordia along each flank of the developing telescoped leader (leading shoot) was counted. When all needle primordia had been initiated and the shoot apical meristem was at its annual minimum size (Owens and Molder, 1973), the shoot apical meristem was examined for presence of cells in mitosis using a compound microscope. Endodormancy is the suspension of growth in any plant structure containing a meristem that is regulated by physiological factors inside the structure (American Society for Horticultural Science, 2002). In this study, endodormancy is defined as an absence of mitotic activity in the shoot apical meristem within the terminal bud (Arora et al., 2003; Owens and Molder, 1973).

On 6 Oct., 24 seedlings were sampled from each duration of SDs. Seedling height, shoot diameter, shoot dry weight, and root dry weight were determined. Shoot diameter was determined on the hypocotyl where the color of the epidermis abruptly changes from green to brown at the top of the peat plug. On 30 Mar., 24 seedlings per SD duration were planted in a common garden. Subsequently, on 27 to 28 Oct., survival was recorded before seedlings were excavated. Then, seedling height, shoot diameter, shoot dry weight, and root dry weight were determined.

Statistical analysis. Statistical analyses of data were conducted using SYSTAT 11 (SYSTAT Software, Inc., 2004). Data had normal distribution and homogeneity of variances and thus were not transformed. A general linear model analysis of variance (ANOVA) (SYSTAT Software, Inc., 2004) was used to analyze seedling height, shoot diameter, shoot dry weight, and root dry weight data. The model of the ANOVA follows:

$$Y_{ij} = \mu + D_i + B_j + DB_{ij} + \varepsilon_{k(ij)}$$

where μ is the mean; Y_{ij} is the measured variable for the $(ij)^{th}$ cell; D_i is the fixed effect of the duration of SDs, $i = 1, 2, 3, 4$; B_j is the random effect of blocking in either the greenhouse ($k = 1, 2, 3, 4$) or the common garden ($k = 1, 2$); DB_{ij} is the effect of the interaction between D and B; k is the seedling; and $\varepsilon_{k(ij)}$ is the experimental error. A sequential sums of squares was used to test hypotheses. Finally, where there were significant differences in main effects, a contrast analysis was run. Percentage data for onset of terminal bud endodormancy in the nursery and survival after one season were analyzed with Pearson χ^2 goodness of fit using a one-way log linear model. Significance was assigned at $P \leq 0.05$.

Results and Discussion

Bud development and bud endodormancy. The day before the SD dormancy-induction regime began in early July, the 12-week-old seedlings were in shoot neoformation (sensu Hallé et al., 1978); i.e., the shoot apical meristem initiates needle primordia (with subtending internodes) and they expand immediately. During the first week of SDs, neoformed needle initiation ended, and budscale initiation began and was completed (Fig. 1A). Next, initiation of needle primordia and thus shoot preformation (sensu Hallé et al., 1978) started (Figs. 1A and 2). During shoot preformation, needle primordia with internodes are initiated but do not expand. Rather, needle primordia stack up (Fig. 1B) forming a telescoped shoot, which enters endodormancy before expanding the next spring.

After the second week of SDs, rate of needle initiation increased within buds from all durations of SDs (Fig. 2). This rate of primordium initiation continued (Fig. 1B) for 6 weeks within buds given the 3-, 4-, and 5-week duration but only for 5 weeks within buds given the 6-week duration (Fig. 2). Thereafter, rate of needle initiation decreased (Fig. 2). Needle initiation was finished after 10 weeks in buds given the 5- and 6-week duration and after 13 weeks in buds given the 3- and 4-week duration (Fig. 2). Thus, bud development was completed by mid-September or early October. Duration of SDs had no effect on bud endodormancy (P = 0.26) in early October. For seedlings that received 3, 4, 5, and 6 weeks of SDs, 50%, 88%, 88%, and 75%, respectively, of the terminal buds were endodormant. In the buds that were not endodormant, the mitoses were in areas of the meristem that are not involved in needle initiation. Evidence of the breaking of terminal buds after return to ambient photoperiod was not observed.

The long period of bud development has implications for bud endodormancy in seedlings scheduled for late summer planting programs. Completion of bud development is a prerequisite for bud endodormancy (Arora et al., 2003; Owens and Molder, 1973). In turn, bud endodormancy is correlated with the overall resistance of coastal douglas fir seedlings to the stresses associated with lifting, handling, transport, and planting (Ritchie, 1984, 1986). Furthermore, seedlings with high stress resistance exhibit higher survival and growth rates after planting (Ritchie, 1986, 1989). To achieve dormant, stress-tolerant seedlings for late summer planting, it may be necessary to sow seed earlier in the spring, thereby increasing heating costs and thus seedling costs. Alternatively, silviculturalists could eliminate late summer planting in favor of early fall planting.

Seedling morphology in the nursery. In early October, duration of SDs had a significant effect on root dry weight and shoot diameter, but not on shoot dry weight or seedling height (Table 1). Contrast analysis revealed that seedlings given 6 weeks of SDs had less root dry weight and smaller shoot diameter than those given 3, 4, and 5 weeks of SDs (Tables 2 and 3). Similarly, in norway spruce [*Picea abies* (L.) Karst.] (Konttinen et al., 2003) and sitka × white spruce (Eastham, 1991), shoot diameter was smaller on seedlings given longer durations of SDs compared with shorter durations. That seedling height in our study was unaffected by duration of SDs indicates that the internodes of needles (that were initiated before the SD regime began or before the change to budscale initiation during the first week of SDs) stopped elongating within the first 3 weeks of SDs. Similarly, height growth had stopped after 2 weeks of SDs in norway spruce (Konttinen et al., 2003), 18 SDs in white spruce (Coursolle et al., 1998a) and 3 weeks of SDs in sitka × white spruce (Eastham, 1991) seedlings.

We speculate that the reduction in root dry weight of coastal douglas fir seedlings given 6 weeks of SDs was caused by a reduction in daily photosynthesis. This reduction occurred both under the SD regime and after return to decreasing ambient photoperiod in mid-August.

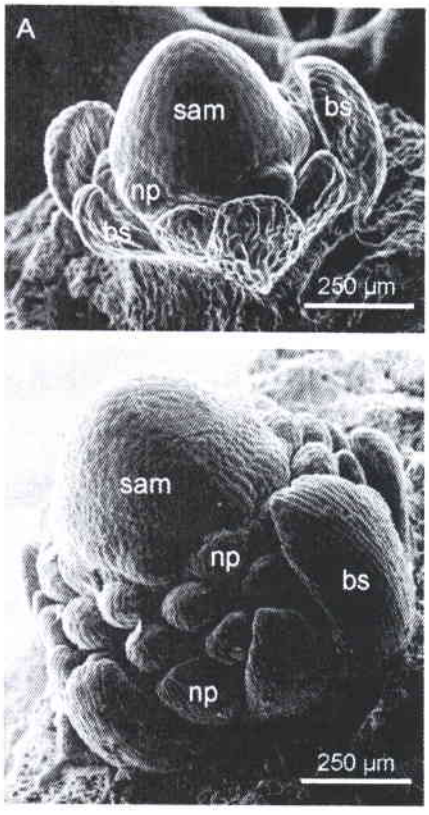

Fig. 1. Scanning electron micrographs of rudimentary terminal buds of coastal douglas fir seedlings, from which first-initiated budscales have been removed. (**A**) After 1 week of short days (SDs), the dome-shaped shoot apical meristem (SAM) has finished initiating budscales (BS) and is initiating needle primordia (NP). (**B**) The shoot apical meristem, after 4 weeks of SDs, is rapidly initiating needle primordia. As the needle primordia begin to stack up, the developing telescoped shoot is evident.

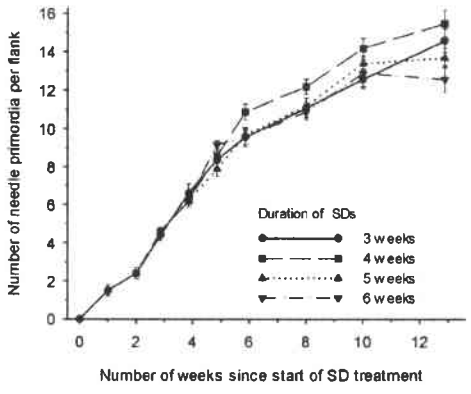

Fig. 2. Number of needle primordia initiated during bud development in coastal douglas fir seedlings. Needle primordia were counted along each flank of the developing telescoped shoot, as seen in a microscopic projection of the longitudinal section through the bud. Sampling started in early July, the day before the short day (SD) dormancy-induction regimes began. Seedlings were removed from SDs after 3, 4, 5 and 6 weeks. Final sampling was in early October. Values = mean ± SE, n = 8.

Table 1. Morphology of containerized coastal douglas fir seedlings given different durations of short days (SDs) to induce dormancy.[z]

	Duration of SDs (weeks)				
	3	4	5	6	P
Root dry wt (g)	0.73 ± 0.04	0.73 ± 0.03	0.60 ± 0.04	0.55 ± 0.04	≤0.01
Shoot diam (mm)	3.5 ± 0.1	3.5 ± 0.1	3.2 ± 0.9	3.1 ± 0.9	0.04
Seedling ht (cm)	21.0 ± 0.5	23.6 ± 0.5	22.9 ± 0.4	21.7 ± 0.5	0.06
Shoot dry wt (g)	1.32 ± 0.06	1.45 ± 0.07	1.31 ± 0.08	1.12 ± 0.08	0.09

[z]Samples were collected in early October during nursery culture. Dormancy induction (8-h SD) started in early July. For each duration, values = mean ± SE, n = 24.

Table 2. Analysis of variance table for root dry weight of containerized coastal douglas fir seedlings given different durations of short days (SDs) to induce dormancy.

Source	df	MS	Test	F	P
Duration of SDs	3	0.2037	R/R × B	17.73	≤0.01
3 + 4 + 5 weeks with 6 weeks[z]	1	0.3168	R/R × B	27.58	≤0.01
Block in greenhouse	3	0.0527	B/E	1.52	0.22
Duration × block	9	0.0115	R × B/E	0.33	0.96
Error	80	0.0346			
Total	96	0.3024			

[z]Contrast analysis.
MS = mean square.

Table 3. Analysis of variance table for shoot diameter of containerized coastal douglas fir seedlings given different durations of short days (SDs) to induce dormancy.

Source	df	MS	Test	F	P
Duration of SDs	3	0.9567	R/R × B	4.34	0.04
3 + 4 + 5 weeks with 6 weeks[z]	1	1.5022	R/R × B	6.79	0.03
Block in greenhouse	3	0.0869	B/E	0.39	0.76
Duration × block	9	0.2213	R × B/E	0.97	0.46
Error	80	0.2241			
Total	96	2.9943			

[z]Contrast analysis.
MS = mean square.

Table 4. Survival and growth of containerized coastal douglas fir seedlings[z] after one growing season in a common garden.

	Duration of short days (weeks)				
	3	4	5	6	P
Survival (%)	100	100	100	96	0.39
Leader length (cm)	8.5 ± 0.4	7.3 ± 0.3	8.1 ± 0.4	6.8 ± 0.3	0.18
Shoot diam (mm)	6.4 ± 0.2	6.7 ± 0.2	6.6 ± 0.2	6.5 ± 0.2	0.80
Shoot dry wt (g)	7.25 ± 0.37	7.84 ± 0.40	7.75 ± 0.39	7.19 ± 0.34	0.76
Root dry wt (g)	4.26 ± 0.22	4.68 ± 0.24	4.60 ± 0.26	4.42 ± 0.24	0.36

[z]Seedlings were given different durations of short days to induce dormancy during nursery culture the previous year. For each duration, values = percentage or mean ± SE, n = 24.

Furthermore, these seedlings had less time under ambient photoperiod for secondary growth before the vascular cambium became endodormant. Earlier, coastal douglas fir seedlings at our cooperating nursery that were given 4 weeks of SDs beginning in early August did not meet root dry weight specifications by early fall lift dates (MacDonald, unpublished observations). Similarly, root dry weight was less in *Larix occidentalis* Nutt. seedlings grown under low light intensity compared with high light intensity (Vance and Running, 1985). In that study, the reduction in photosynthesis affected photosynthate allocation to the roots more than to the shoots (Vance and Running, 1985).

Survival and growth after planting. After one growing season in a common garden, duration of SDs in the nursery had no effect on seedling survival, leader (leading shoot) length, root dry weight, shoot dry weight, or shoot diameter (Table 4). Likewise, leader length was unaffected by duration of SDs in norway spruce (Konttinen et al., 2003), white spruce (Coursolle et al., 1998b), or sitka × white spruce (Eastham 1991) after one growing season.

Recommendations. We recommend the 3-week duration of SDs for coastal douglas fir seedlots from British Columbia as well as those in adjacent Washington State. Container nurseries located at more southern latitudes in the United States are advised to verify that the 3-week duration causes irreversible bud development and an 8-h photoperiod is appropriate for their seedlots.

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