

Morphology, Physiology, Survival, and Field Performance of Containerized Coastal Douglas Fir Seedlings Given Different Dormancy-induction Regimes

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Abstract. The effects of different dormancy-induction regimes on first-year containerized coastal Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] seedling morphology and physiology in the nursery, as well as seedling survival and performance after one growing season in a common garden, were investigated. In early July, three dormancy-induction regimes were applied: moderate moisture stress (MS), short day (SD), and short day with moderate moisture stress (SD+MS). In early October, seedling height, root collar diameter, and shoot dry weight were unaffected by regime, but root dry weight was reduced in seedlings from the MS and SD+MS regimes compared with the SD regime. At this time, morphogenesis was completed in all terminal buds of seedlings from both SD regimes, whereas it continued in all terminal buds of seedlings from the MS regime. Furthermore, 25% to 88% of terminal buds from the SD regimes were endodormant, but none from the MS regime were endodormant. In March, budbreak occurred at the same time in seedlings from the two SD regimes and was earlier than in seedlings from the MS regime; root growth capacity was unaffected by regime. After one growing season, there were no regime differences in seedling survival, root collar diameter, shoot dry weight, root dry weight, length of the current-year leader, or number of needles on the leader.

Coastal Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*] is one of the most important and valuable timber species in temperate forestry (Hermann and Laverder, 1990). Between 2000 and 2005, 38.1 million containerized coastal Douglas fir seedlings were planted on Crown lands in British Columbia [J. McClarnon, British Columbia Ministry of Forests (BCMOF),

personal communication, 2006]. Production of containerized coastal Douglas fir is increasing in the Pacific Northwest region of the United States despite that region's long tradition of bareroot nurseries. For example, one container nursery in Oregon shipped 6.5 million coastal Douglas fir seedlings over the course of 2004 and 2005 (K. Giles, PRT Oregon, personal communication, 2006). Currently, nurseries in both countries use moderate moisture stress (MS), short days (SD), or short days with moderate moisture stress (SD+MS) as a dormancy-induction regime for coastal Douglas fir (R. Merrell, BCMOF, and K. Giles, PRT, personal communication, 2006).

Earlier studies of western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] (Grossnickle et al., 1991a, 1991b; O'Reilly et al., 1989a, 1989b, 1994a, 1994b) and western red cedar (*Thuja plicata* Donn ex D. Don) (Krasowski and Owens, 1991; Krasowski et al., 1990) have reported the effects of these regimes on seedling morphology and physiology in the nursery and outplanting performance. Unfortunately, these results cannot be applied to coastal Douglas fir because the three species vary in architecture and shoot growth

pattern and, thus, they respond differently to nursery culture. Western hemlock is characterized by abundant current-year branching along its leader, and although a terminal bud does form, only part of next year's leader growth is preformed in the nursery; the remainder is neofomed on the planting site (O'Reilly et al., 1994b). [In the preformed component of the leader, leaves and their subtending internodes are initiated and undergo dormancy before elongating, whereas in the neofomed portion of the leader, they are initiated and elongate immediately (Halle et al., 1978).] Western red cedar also has abundant current-year branching along its leader, but the species does not form terminal buds. However, the shoot apical meristem is protected by the last formed scale-like leaves and thus, leader growth after planting is fully neofomed (Krasowski and Owens, 1991). In contrast, coastal Douglas fir has one strongly defined leader with little current-year branching on the leader and then only in proximal positions. Leader growth for the following year is preformed during nursery culture, but there may be late summer lammass growth on the planting site (Carlson and Preisig, 1981).

The objectives of this research were to examine the effects of MS, SD, and SD+MS dormancy-induction regimes on coastal Douglas fir seedling morphology and physiology in the nursery as well as seedling survival and performance after one growing season in a common garden. In the nursery component, a stock quality assessment approach was used, which measures both material (i.e., morphology and physiology) and performance (i.e., response to test conditions) attributes at select points in time (Grossnickle et al., 1991a; Grossnickle and Folk, 2005; Ritchie, 1984).

Materials and Methods

Nursery culture

Seedlings from one coastal Douglas fir seedlot (BCMOF Registered Seedlot No. 4505, 48°49' N, 123°56' W, elevation 610 m), which were part of the commercial crop grown at the Angus P. MacBean Nursery in Yellow Point, B.C., Canada (49°4' N, 123°55' W), were used. Stratified seeds were sown in early April 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 Plast Ltd., Edmonton, Alberta, Canada). The substrate mix was 2 peat:1 vermiculite (by volume 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. A mobile overhead boom system delivered misting and irrigation. Containers were misted during germination. Thereafter, during each irrigation, water was delivered until the substrate was saturated and gravitational water was draining

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from cavity bottoms. At container capacity (Handrek and Black, 1989), containers were weighed. Irrigation occurred when container mass, randomly sampled throughout the greenhouse, was 2 kg below the mass at container capacity.

Fertilizer was applied during each irrigation. A forestry seedling starter fertilizer (11N-17.9P-6.6K) with micronutrients was applied at a rate of 500-750 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 during June and July. From August on, a forestry seedling finisher fertilizer (8N-8.7P-24.9K) with micronutrients was applied at a rate of 750 mg-L⁻¹. Iron chelate (13% Fe) and a soluble trace element mix (13% S, 1.35% B, 2.3% Cu, 7.5% Fe, 8% Mn, 0.04% Mo, and 4.5% Zn) were applied, as needed, to adjust the foliar nutrition levels. Calcium nitrate (15.5% N, 20% Ca) was applied, as needed, to maintain the pH of the growing substrate between 4.5 and 5.5.

Dormancy-induction regimes

Two adjacent greenhouses identical in structure and orientation were used for the dormancy-induction regimes. For the MS regime, the polyethylene roof and sidewalls of the greenhouse were removed before the regime began. However, in the greenhouse used for the two SD regimes, the roof and sidewalls remained intact, protecting the computer-automated, blackout curtain system (with silver-colored exterior surface) that controlled photoperiod (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 the end of June, crop height averaged 16 cm and was within reach of the target specification (BCMOF, 2003). The three dormancy-induction regimes began in early July. The duration of the MS regime was 2 weeks and that of the SD regime was 4 weeks. The SD+MS regime was a combination, i.e., a 4-week SD regime with an initial 2-week MS regime.

The MS regime, developed by the BCMOF (Matthews, 1982) is the industry standard in British Columbia (R. Merrell, BCMOF, personal communication, 2006). Before the regime began, fertilizer application ended and the substrate was leached of mineral salts. Once the regime began, container weight was monitored until it was 3 kg below the mass at container capacity. At this container weight, predawn equilibrium water potentials of seedling shoots, determined by a pressure chamber technique (Ritchie and Hinckley, 1975), ranged from -1.0 to -1.5 MPa. Then, as soon as seedling shoot tips

wilted, containers were watered until the substrate was saturated and gravitational water was draining. During the 2 weeks of the MS regime, seedling shoot tips reached the wilting stage twice. After the regime ended, irrigation with the high-nitrate forestry seedling fertilizer (20N-3.4P-16.6K) with micronutrients, applied at a rate of 750 mg-L⁻¹, resumed when container weight was 2 kg below the mass at container capacity.

For both SD regimes, the photoperiod was 8 hours, from 8:00 AM to 4:00 PM. During the SD regime, irrigation with fertilizer continued to occur when container weight was 2 kg below the mass at container capacity. However, in the SD+MS regime, the first 2 weeks in SD were concurrent with a 2-week MS regime, which was identical to that described here. Seedling shoot tips wilted twice during this 2-week period. The SD+MS regime was separated from the remaining crop by a buffer, two containers wide, to prevent irrigation water from reaching the containers.

In early August, after the two SD regimes ended, containers were moved to the MS greenhouse (under ambient photoperiod and temperature). Containers from the three regimes were placed next to each other to ensure the same postinduction conditions. In addition, containers from the SD regimes were placed so as to maintain their original location within the greenhouse. In late October, the polyethylene glazing was installed on the greenhouse. From mid-November until late March, greenhouse temperature was maintained at 5 °C.

Experimental design

A modified split-plot experimental design was used in the nursery. There were two main plots in the greenhouse used for the SD and SD+MS regimes and one main plot in the greenhouse used for the MS regime. Each main plot consisted of four blocks, each corresponding to a metal pallet. Each pallet held 30 containers; the inner group of 12 containers comprised the experimental units and was surrounded by a buffer one container wide. Containers from which seedlings were sampled for the three assessments were

randomly selected in each block. The experimental design for the days to budbreak and root growth capacity tests, conducted in a controlled-environment chamber, was a split plot. The main plot consisted of five blocks, each containing a pot of seedlings for each regime. Pot placement was randomized within each block. The split-plot experimental design was also used in the common garden. The main plot consisted of two blocks, each containing three rows. Seedling placement was randomized within the rows.

Greenhouse sampling

For each dormancy-induction regime, seedlings were sampled from each of the four blocks in the greenhouse. Seedling location within each container was randomly selected, but seedlings less than 16 cm were not sampled because they would have stopped height growth before the start of the regimes.

Nursery assessment in October

Twenty-four seedlings per regime (six from each block) were sampled in early October to assess seedling morphology, completion of terminal bud morphogenesis, and onset of terminal bud endodormancy. Seedling height and root collar diameter were measured before roots were washed clean of substrate. The terminal bud was excised and then the shoot was clipped from the root. Each component was bagged separately, immediately dried at 70 °C, and stored. Later, samples were dried at 80 °C to constant weight before weighing.

The terminal bud from each seedling was fixed at the time of excision and was later processed into slides using standard plant microtechnique protocols (Berlyn and Miksche, 1976). From the resulting slides for each terminal bud, the median longitudinal section (the section in the middle of the serial sections) was selected using a stereomicroscope. Then, anatomic observations on this section were made using a compound microscope. Bud morphogenesis was completed when the shoot apical meristem was at its annual minimum size or was ongoing when there was still space on the meristem for needle primordia to be initiated (Owens and

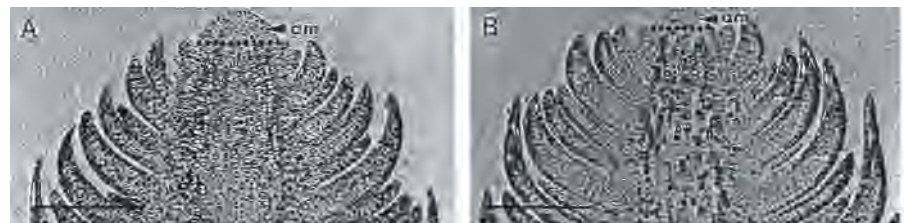


Fig. 1. Light micrographs of median longitudinal sections through the distal portion of the terminal bud in early October of coastal Douglas fir seedlings given different dormancy-induction regimes in July. The shoot apical meristem (am) is the dome of tissue above the dotted line drawn between the last-initiated primordia. Scale bar = 500 μ m. (A) Initiation of needle primordia by the shoot apical meristem is ongoing in a seedling from the moderate moisture stress (MS) regime. The shoot apical meristem is larger than in B and there is space for more needle primordia to form on each flank of the meristem. (B) Morphogenesis of the terminal bud is completed in a seedling from the short day (SD) regime that is also representative of a seedling from the short day with moderate moisture stress (SD+MS) regime. The shoot apical meristem is at its annual minimum size.

Molder, 1973 (see Fig. 1A, B). The onset of bud endodormancy was delineated by an absence of mitoses in the shoot apical meristem (Owens and Molder, 1973; see also Arora et al., 2003; Burr, 1990; Carlson et al., 1980; Krasowski and Owens, 1994; Laverder, 1991). Endodormancy is the suspension of growth in any plant structure containing a meristem that is regulated by physiological factors inside the structure (ASHS, 2002). The presence of each cell in mitoses within the meristem (defined as the dome above the most recently initiated needle primordia) and its location relative to the morphogenic zone of the meristem were recorded.

Assessment in March

After overwintering in the greenhouse, 20 seedlings per regime (five from each block) were sampled in mid-March for the days to budbreak and root growth capacity tests. Four seedlings were dibbled into each pot (3 L); pots were loosely filled with a 2 peat:2 vermiculite:1 sand (by volume) substrate mix. Pots were watered until the substrate was saturated and gravitational water was draining, and placed in a controlled-environment chamber (Convicon E15; Controlled Environment Ltd., Winnipeg, Manitoba, Canada) illuminated with a mixture of incandescent and cool-white fluorescent lamps giving an irradiance of 500 $\mu\text{mole}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Growing conditions were 20:20 °C day:night temperature and a 16-hour photoperiod. The substrate was maintained at saturation. Every 3 days, the terminal buds were examined and budbreak was recorded when the emerging shoot became visible just above the bud-scales. After 15 days, roots were washed clean of substrate and root growth capacity (Ritchie, 1984) was measured by counting the number of white roots ≥ 0.5 cm.

Assessment after one growing season

In late March, 24 seedlings per regime (six from each block) were sampled and identified using nursery tags. Seedlings were planted at 0.25-m spacing in a common garden, which had been recently ploughed and rotovated, in an abandoned farm field. In late October, seedling survival was recorded and then seedlings were excavated. If the seedling was alive, the root system was washed clean of soil. Then, root collar diameter and length of the current-year leader were measured, the root was clipped from the shoot, each component was bagged separately, and dry weights were determined as described here. Then, the number of needles on the current-year leader that were initiated during terminal bud morphogenesis in the nursery were counted.

Statistical analysis

All data examination and analyses were conducted using SYSTAT 11 (SYSTAT Software, Inc., 2004). Data were not transformed because they had normal distribution and homogeneity of variances. Because of the operational constraint that crops had to be given a dormancy-induction regime, the set

of regimes we investigated is classified as an incomplete block design, and thus, a general linear model analysis of variance (ANOVA) (SYSTAT Software, Inc., 2004) was used to analyze seedling height, leader length, needle number, root collar diameter, shoot and root dry weight, days to budbreak, and root growth capacity data. The model of the ANOVA follows:

$$Y_{ij} = \mu + R_i + B_j + RB_{ij} + Ek(ij)$$

where μ is the mean; Y_{ij} is the measured variable for the (i, j) th cell; R_i is the fixed effect of dormancy-induction regime, $i = 1, 2, 3$; B_j is the random effect of blocking in the greenhouse, $k = 1, 2, 3, 4$; in the controlled-environment chamber, $k = 1, 2, 3, 4, 5$; or in the common garden, $k = 1, 2$; RB_{ij} is the effect of the interaction between R and B ; k is the seedling; and $Ek(ij)$ is the experimental error. A sequential sums of squares was used to test hypotheses. Finally, where there were significant differences in main effects, an orthogonal contrast analysis was run. Percentage data for completion of terminal bud morphogenesis, onset of terminal bud endodormancy, and survival after one season were analyzed with Pearson χ^2 goodness of fit using a one-way loglinear model.

Results and Discussion

Although all dormancy-induction regimes for coastal Douglas fir seedlings began in early July, the response of morphological and physiological attributes in early October was variable. Regime effects on seedling height, root collar diameter, and shoot dry weight were not significantly different (Table 1). In contrast, regime effects on root dry weight, completion of terminal bud morphogenesis, and onset of terminal bud endodormancy were significant (Table 1). Root dry weight

was significantly reduced in seedlings from the MS and SD+MS regimes compared with the SD regime (Tables 1 and 2). We speculate that this reduction was incited by fewer roots because of mortality in response to MS (van Eerden and Gates, 1990). Morphogenesis was completed in all buds from the two SD regimes, whereas it was still ongoing in all buds from the MS regime (Table 1, Fig. 1). Most buds from the SD regime were endodormant (defined by an absence of mitoses in the shoot apical meristem), only some buds from the SD+MS regime were endodormant, but no buds from the MS regime were endodormant (Table 1). Furthermore, in the buds from the three regimes that were not yet endodormant, the location of mitoses relative to the morphogenic zone within the shoot apical meristem varied by regime and was important because completion of morphogenic activity is a prerequisite for bud endodormancy (Arora et al., 2003; Owens and Molder, 1973). In seedlings from both SD regimes, mitoses were not in areas of the meristem involved in morphogenesis. In contrast, mitoses continued in the morphogenic zone within the meristem of seedlings from the MS regime.

The dormancy-induction regime had a significant effect on days to budbreak in mid-March (Table 3). Budbreak occurred at the same time in seedlings from the two SD regimes and was significantly earlier than in seedlings from the MS regime (Tables 3 and 4). In contrast, root growth capacity of seedlings from the three regimes was not significantly different (Table 3). Moreover, these values indicate that the seedlings had good physiological integrity (Grossnickle, 2000). Also, the root growth capacity values predicted high survival rates after planting because the test was conducted close to the planting date (Simpson and Ritchie, 1997).

Table 1. Material attributes of containerized coastal Douglas fir seedlings given different dormancy-induction regimes.^a

Attribute	Dormancy-induction regime ^b			P
	MS	SD	SD+MS	
Seedling ht (cm)	22.4 ± 0.4	23.6 ± 0.5	21.7 ± 0.5	0.3700
Root collar diam (mm)	3.2 ± 0.1	3.5 ± 0.1	3.3 ± 0.1	0.4980
Shoot dry wt (g)	1.37 ± 0.08	1.45 ± 0.07	1.25 ± 0.07	0.5251
Root dry wt (g)	0.62 ± 0.03	0.73 ± 0.03	0.59 ± 0.04	0.0754
Percentage of terminal buds that had completed morphogenesis	0	100	100	0.0001
Percentage of endodormant terminal buds	0	88	25	0.0001

^aThe assessments were made in early October. For each regime, percentage or mean \pm SE and P are presented, $n = 24$.

^bRegime: MS, moderate moisture stress; SD, short days; SD+MS, short days with moderate moisture stress.

Table 2. Analysis of variance table for root dry weight of containerized coastal Douglas fir seedlings in early October.

Source	df	MS	Test	F	P
Regime	2	0.1307	R/R × B	4.1011	0.0754
SD vs. SD+MS and MS	1	0.2526	R/R × B	7.923	0.0306
Block in greenhouse	3	0.0644	B/E	2.7492	0.0505
Regime × block	6	0.0319	R × B/E	1.3599	0.2455
Error	60	0.0234			
Total	72	0.2510			

Table 3. Performance attributes for containerized coastal Douglas fir seedlings given different dormancy-induction regimes.^a

Attribute	Dormancy-induction regime ^b			P
	MS	SD	SD+MS	
Days to budbreak	11 ± 0.6	5 ± 0.3	5 ± 0.3	0.0001
Root growth capacity	14 ± 0.1	16 ± 2.3	12 ± 2.3	0.5608

^aThe assessments were made in late March after 15 days under ideal growing conditions. For each regime, mean ± SE is presented, n = 20.

^bRegime: MS, moderate moisture stress; SD, short days; SD+MS, short days with moderate moisture stress.

Table 4. Analysis of variance table for days to budbreak of containerized coastal Douglas fir seedlings in early March.

Source	df	MS	Test	F	P
Regime	2	265.05	R/R × B	38.6230	0.0001
MS vs. SD and SD+MS	1	529.00	R/R × B	77.0856	0.0001
Block in chamber	4	3.38	B/E	1.0075	0.4137
Regime × block	8	6.86	R × B/E	2.0485	0.0618
Error	45	3.35			
Total	60	278.64			

Table 5. Survival and performance for containerized coastal Douglas fir seedlings given different dormancy-induction regimes.^a

Attribute	Dormancy-induction regime ^b			P
	MS	SD	SD+MS	
Percentage of seedlings surviving	100	100	100	—
Root collar diam (mm)	6.6 ± 0.2	6.7 ± 0.2	7.0 ± 0.2	0.6514
Shoot dry wt (g)	8.40 ± 0.42	7.84 ± 0.40	7.90 ± 0.52	0.4412
Root dry wt (g)	4.69 ± 0.23	4.68 ± 0.24	4.83 ± 0.32	0.6506
Leader length (cm)	8.0 ± 0.4	7.3 ± 0.3	7.7 ± 0.4	0.4686
Number of needles on leader	159.4 ± 6.5	165.7 ± 5.9	163.4 ± 7.0	0.7171

^aThe assessments were made in late October after one growing season in a common garden. Percentage or mean ± SE is presented, n = 24.

^bRegime: MS, moderate moisture stress; SD, short days; SD+MS, short days with moderate moisture stress.

Indeed, all seedlings from the three regimes survived one growing season in a common garden (Table 5). As in the nursery assessment, root collar diameter and shoot dry weight of seedlings were not significantly different (Table 5). However, unlike the nursery assessment, there were no significant differences in root dry weight (Table 5). The length of the current-year leader was not affected by regime nor was the number of needles on it (Table 5), despite differences in timing of the completion of terminal bud morphogenesis in the nursery (Table 1).

In summary, seedlings from the three dormancy-induction regimes had similar morphology in the nursery with the exception of root dry weight. However, after one growing season in a common garden, differences in root dry weight were no longer apparent, and seedlings had similar survival and performance. With respect to coastal Douglas fir seedling morphological specifications that are used to cull seedlings at lifting (BCMOF, 2003), the three regimes did not prevent the seedlings from achieving the 3.0-cm root collar diameter target specification nor did they result in seedlings that exceeded the 26-cm maximum height specification. However, there were differences in the timing of onset of bud endodormancy and of budbreak after overwintering, and these

are important considerations for seedlings destined for spring or autumn planting. For low-elevation spring planting, in which time for adequate root development before budbreak is important, seedlings given a MS regime are recommended. On mid- to high-elevation sites that are autumn planted, seedlings given a SD regime are recommended because earlier bud endodormancy is an advantage. Finally, we urge nurseries producing autumn-planting stock to conduct trials to determine both the critical night length for their seed sources and the timing of the SD regime needed to ensure bud endodormancy for their earliest shipping dates.

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