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Effects of Light and Substrate on Planted Conifer Seedlings in Coastal British Columbia

Abstract

An experiment was carried out in the East Capilano Watershed, near Vancouver, British Columbia, to examine the effect of light and soil substrate on the survival and growth of Douglas-fir, western hemlock, and Pacific silver fir. Light availability in the old-growth forest understories was 3% of that in the clearcuts. The forest floor substrate had significantly higher concentrations of nutrients than those in the wood debris and mineral soil while, given the same soil substrate, these nutrients were not significantly different between the forest understories and the clearcuts. After two growing seasons, Douglas-fir had a significantly greater survival in the clearcuts than in the understories whereas western hemlock and Pacific silver fir had the same or better survival in the understories than in the clearcuts depending on the soil substrates. Douglas-fir and western hemlock had better growth in diameter, height, and total biomass in the clearcuts than in the understories. The effect of light on the growth of Pacific silver fir was, however, much less pronounced. In the clearcuts, growth of all three species was the best on the forest floor substrate, but the effect of soil substrate was much less notable in the understories. Light was the primary limiting factor for the survival and growth of the planted seedlings.

Introduction

In the wetter climates of coastal North America, coarse woody debris (CWD) forms a large portion of the organic matter pool on the forest floor (Harmon et al. 1986). Associated with these CWD accumulations is an abundance of tree regeneration growing upon stumps and downed logs in the understory of old-growth coastal forests (Taylor 1935, Minore 1972, Harmon et al. 1986, Harmon and Franklin 1989). The association between trees and woody microsites is so prevalent that the description embodied in the metaphor of a nurse log is commonly accepted (Maser et al. 1988).

Even though there appears to be an affinity of seedlings, particularly western hemlock (*Tsuga heterophylla*), for CWD, the nutrient availability associated with CWD compared to other forest floor sources is considered minor (Laiho and Prescott 1999, Krankina et al. 1999, Busse 1994), especially compared to the net N dynamics of the non-woody forest floor (Hope and Li 1997, Hart 1999). Heilman (1990) suggests that CWD is unimportant to tree growth relative to other detrital pools. However, Jurgensen et al. (1990) suggest that the importance of CWD to seedling survival and growth may be confounded by climate, which is important to tree survival and growth in the drier climates of Northern Rocky Mountain forests but unimportant or even detrimental in the wetter and colder climate of coastal Alaska. Further, the importance of CWD to seedling growth and survival under low light conditions may be different since the high association between decaying wood and regeneration has primarily referred to understory seedlings and saplings growing under the canopy of old-growth forests (Christy and Mack 1984, Harmon and Franklin 1989). Since foresters are interested in whether seedling growth increases or decreases by using well-rotted CWD as a regeneration medium, the question remains whether CWD is a necessary component for seedling survival and growth in clearcut and partially harvested managed forests.

The interaction of light and nutrients to seedling growth has been shown using nitrogen fertilizer treatments under controlled shaded conditions in

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greenhouses. Fertilized seedlings are larger than unfertilized seedlings in full light conditions, but are the same size under shaded conditions (Reed et al. 1983, Canham et al. 1996, Walters and Reich 1996). However, studies on the interaction of natural light conditions with natural forest substrates have more practical applicability.

Minore (1972) tested the interaction of artificial shaded conditions (using shade tents) with natural forest substrates for western hemlock, Douglas-fir (*Pseudotsuta menziesii*) and Pacific silver fir (*Abies amabilis*) seedlings. For all three species there was greater height and weight of the largest seedling growing in non-woody forest floors compared to woody substrates in full light, and much less pronounced differences under heavy shade (2% of full sunlight). However, shade tents artificially confound reduced light level treatments with changes in air and soil temperature and root medium, air turbulence, and relative humidity compared to natural shaded conditions (Waggoner et al. 1959). Further, Minore (1972) used the largest surviving seedling, as opposed to the mean, as the measure for comparison.

Research using natural light conditions and natural forest substrates in North American coastal forests tend to investigate the two conditions separately and not to look specifically at the interaction. Christy et al. (1982) did not detect significant differences between western hemlock seedlings growing in CWD and mineral soil under an old-growth canopy. In full light conditions, Kropp (1982) did not detect differences in height growth of western hemlock seedlings growing in CWD compared to seedlings growing in mineral soil. For Douglas-fir, where seedlings are primarily associated with mineral soils (Hermann and Lavender 1990), differences in total height of seedlings were not detected between decayed wood and mineral soil under full light conditions (Bernsten 1960).

This study explores whether the relative importance of CWD to seedling survival and growth suggested for the drier climates of the Rocky Mountain forests extends to wetter coastal climates, and tests the interaction between forest substrates and light to seedling survival and growth. The objective of this study was to determine whether there is a survival and growth advantage to seedlings when planted in decaying wood compared to non-woody humus forms and mineral soil under two light environments under a wet coastal climate. This study was undertaken using three species of the coastal forest of British Columbia (Douglas-fir, western hemlock, and Pacific silver fir), an area where the association between seedlings and saplings with CWD is particularly strong (Harmon and Franklin 1989).

Methods

Study Sites

Three study sites were located in one watershed north of Vancouver, British Columbia located in the Submontane variant of the Very Wet Maritime Coastal Western Hemlock biogeoclimatic subzone (CWHvm1) (Green and Klinka 1994). The climate associated with this variant is mild and humid (mesothermal) with warm summers and no dry season (Trewartha and Horn 1980). Heavy precipitation, upwards of 4000 mm annually, and the mild oceanic climate, with mean annual temperature approximately 8°C, are characteristic of this climate. The morphology and soil characteristics of the three sites were similar. Soils were identified as Humo-Ferric Podzols (Soil Classification Working Group 1998). Humus form groups were identified either as Hemimor or Humimor (Green et al. 1993), 10–15 cm thick. These groups included pockets of Leptomoder, 5 cm thick. The soil moisture regime was identified as fresh (no water deficit or excess), and the soil nutrient regime as medium using the methods outlined in Green and Klinka (1994).

Each site included a clearcut and an adjacent old-growth stand along the same south-facing slope (Table 1). Clearcutting occurred between 1990 and 1991. The clearcuts were 2-5 ha in area. Adjacent old-growth forest stands, dominated by Douglas-fir, western hemlock, Pacific silver fir, and western redcedar (*Thuja plicata*), were characterized by overstory canopy trees 60 m in height, 300-750 yr of age, and 100-200 cm diameter at 1.3 m above the germination point.

Experiment

In April 1995, six plots with irregular shapes of about 100 m^2 were established, one in the center of each clearcut and one in each of the adjacent forest understories. At least 100 m from the edge of clearcuts, understory plots were established under old-growth forest stands, which were rela-

TABLE 1. Characteristics of the study sites in coastal British Columbia.

	Site 1		Site 2		Site 3	
	Clearcut	Understory	Clearcut	Understory	Clearcut	Understory
Elevation (m)	585	625	560	560	560	570
Aspect (°azimuth)	160	180	148	152	160	142
Slope (%)	32	32	18	15	35	35

tively uniform in stand structure, understory vegetation, and light conditions.

The understory vegetation within each plot was cleared. Three types of substrates were collected and put into a planting pot (20 cm top diameter, 17 cm base diameter, 25 cm height). The substrates were:

- woody debris of decay class IV and V (as defined by Maser and Trappe 1984);
- non-woody forest floor (L, F, and H horizons);
- mineral soil (Ahe and Bf or Bhf horizons).

One sample of each substrate was taken from each plot to determine its nutrient properties. The planting pots were placed together, and, for the open grown seedlings, a berm was constructed around the pots with the spaces between the pots filled with a combination of mineral soil, wood, and humus material. Within each plot, 60 seedlings of each species were then planted in 60 separate pots, with 20 of the pots containing one of the three substrates (3 species x 3 substrates x 20 pots). In April 1995, 1-yr-old styrofoam container-grown seedlings of western hemlock and Pacific silver fir, and 2-yr-old bareroot seedlings of Douglas-fir were planted with one seedling in each planting pot. The container cavity size for the western hemlock and Pacific silver fir seedlings was 2.5 cm in diameter, 11.4 cm in depth and 39 mL in volume. In each of the six plots, a completely randomized design was implemented for species and substrates.

The choice of pots was made for two reasons: 1) to isolate the seedling roots, and 2) to reduce variability. Under natural conditions, the variability in response in growth in each substrate may be confounded with not being able to isolate the substrate the roots actually grow in. A seedling may be planted in decaying wood but the roots may proliferate in the adjacent non-woody humus or mineral soil. In addition, the variation in the measures of growth in the understory can be reduced when using pots by grouping the pots within light conditions as homogenous as possible. However, planting pot effects are recognized, especially for the open grown seedlings, but this effect was minimized by the use of the filled berm.

Before planting, each seedling was measured for height and base diameter. Twenty additional seedlings for each species were taken to the laboratory for drying (70°C for 48 hr) to determine total biomass of each seedling. Mean base diameter, height, and total biomass were 3.3 mm, 14.1 cm, and 3.1 g for Pacific silver fir seedlings; 1.6 mm, 9.1 cm, and 0.4 g for western hemlock seedlings; 4.7 mm, 34.4 cm, and 32 g for Douglas-fir seedlings.

Measurements of Light and Soil Substrates

The light conditions of the understory and clearcut plots were measured simultaneously. In each of the understory plots, a sunfleck ceptometer was placed at 60 cm above the ground at plot center. In each of the clearcut plots, three LI-COR 190 SA sensors, each connected to a LI-1000 datalogger, were placed in the plot center. The instruments were calibrated and their clocks were synchronized prior to taking measurements. All instruments were programmed to take one measurement every minute, and to average the measurements every 30 min.

Samples for nutrient determination were air dried to constant mass. Mineral soil samples were passed through a 2 mm sieve and stored for chemical analyses. Forest floor and decaying wood samples were ground with a Wiley mill to pass through a 2 mm sieve, and stored at room temperature for chemical analyses. Soil pH was determined using a pH meter in a 1:1 suspension in water for mineral soil and a 1:5 suspension for forest floor and woody substrate. Total carbon was determined by loss on ignition at 500°C (induction furnace) using a LECO carbon analyzer (Carter 1993). Total N was determined by a Technicon Autoanalyzer following micro-Kjehldal digestion (Carter 1993). Mineralizable N was determined

by an anaerobic incubation procedure (Powers 1980), where the soils were incubated at 30°C for 14 days and released NH_4^+ was determined colorimetrically using a Technicon Autoanalyzer. Available P was determined colorimetrically using the ascorbic acid reductant method on Bray P-1 (dilute acid ammonium fluoride) extract. Extractable Ca, Mg, and K were determined by extraction with Morgan's solution of sodium acetate at pH 4.8 and absorption spectrophotometry with an acetylene-air flame (Price 1978). Extractable S (SO_4-S) was determined using an inductively coupled plasma (ICP) spectrophotometer on a 0.01 M $CaCl_2$ extract (Price 1978).

Measurements of Survival and Growth

Seedling survival surveys were conducted in September 1996 (i.e., after two growing seasons). Any visible damage such as browsing, dieback, foliage chlorosis, pathological symptoms, and other injuries was noted. Three healthy seedlings from each of the three replicated sites, two light conditions, three substrates, and three species were randomly sampled. Only a total of 155 seedlings were sampled since most of the Douglas-fir seedlings in the forest understory were either dead or damaged at the end of the second growing season. Seedling height and basal diameter were measured in the field, after which the seedlings were taken to the laboratory to determine total biomass, which was the oven-dry weight at 70°C for 48 hr.

Statistical Analysis

Survival was calculated as the proportion of surviving seedlings to total planted seedlings. To eliminate factors other than light and soil substrate, seedlings with signs of browsing were not included in the survival calculations. Proportion of survival, weighted by the number of all seedlings within each group, was tested with likelihood ratio (χ^2) tests following Hicks (1993) and Neter et al. (1996). The significance level was set at $P \leq 0.05$.

For growth measures, the experimental design was a split-plot design (Hicks 1993). Light (L) was the main effect (whole-plot) and replicated in three clearcuts and old-growth forest understories. Species (P) and substrate (S) were arranged in a completely randomized layout within each of six whole-plots. The following analysis of variance model was used to detect effects of light, soil substrate, and species on growth parameters:

$$Y_{ijklm} = \mu + R_i + L_j + R \times L_{ij} + S_k + R \times S \times P_{il} + S \times P_{kl} + R \times S \times P_{kl} + L \times S_{ik} + R \times L \times S_{ijk} + L \times P_{jl} + R \times L \times P_{ijl} + L \times S \times P_{jkl} + R \times L \times S \times P_{ijkl} + \varepsilon_{m(ijkl)}$$

where Y_{ijklm} is an observation for a particular dependent variable; μ is the overall mean of the dependent variable; R_i (i = 1, 2, 3) is the site replicates; L_j (j = 1, 2) is the effect of light; $R \times L_{ij}$ is the experimental error of whole-plot to test the effect of light; S_k (k = 1, 2, 3) is the effect of soil substrate; $R \times S_{ik}$ is the error to test the effect of soil substrate; P_l (l = 1, 2, 3) is the effect of tree species; $R \times P_{il}$ is the error to test the effect of species; $S \times P_{kl}$ is the interaction of substrate and species; $R \times S \times P_{ikl}$ is the error to test the interaction of substrate and species; $L \times S_{ik}$ is the interaction of light and substrate; $R \times L \times S_{ijk}$ is the error to test the interaction of light and substrate; $L \times P_{jl}$ is the interaction of light and species; $R \times L \times P_{ijl}$ is the error to test the interaction of light and species; $L \times S \times P_{jkl}$ is the interaction of light, substrate, and species; $R \times L \times S \times P_{ijkl}$ is the error to test the interaction of light, substrate, and species; and $e_{m(ijkl)}$ is the sampling error within treatments and replicates. If differences were significant, Tukey's multiple range test was use to detect for differences between substrates.

Results

On sunny, summer days (30 June to 3 July, 1996), the mean daily photosynthetic photon flux density (PPFD) was 42.3 mol m^{-2} day^{-1} in clearcuts and 1.25 mol m^{-2} day^{-1} in the forest understories (Table 2). The forest understory received only 3% of the PPFD in the clearcuts. Within each of the two light regimes, the differences in light availability among plots were small (Figure 1).

TABLE 2. Light environments for clearcuts and adjacent old-growth forest understories in coastal British Columbia. Measurements were recorded for three consecutive, predominantly sunny days in from June 30 to 2 July 1996. Daily mean photosynthetic photon flux density values are means (±SE) for measurements made between 06:00 and 21:00 local time.

Light descriptor	Clearcut	Understory
Daily total PPFD (mol m^{-2} day^{-1})	42.3 (4.5)	1.25 (0.15)
Daily mean PPFD (mmol m^{-2} s^{-1})	759 (75)	20.2 (4.2)

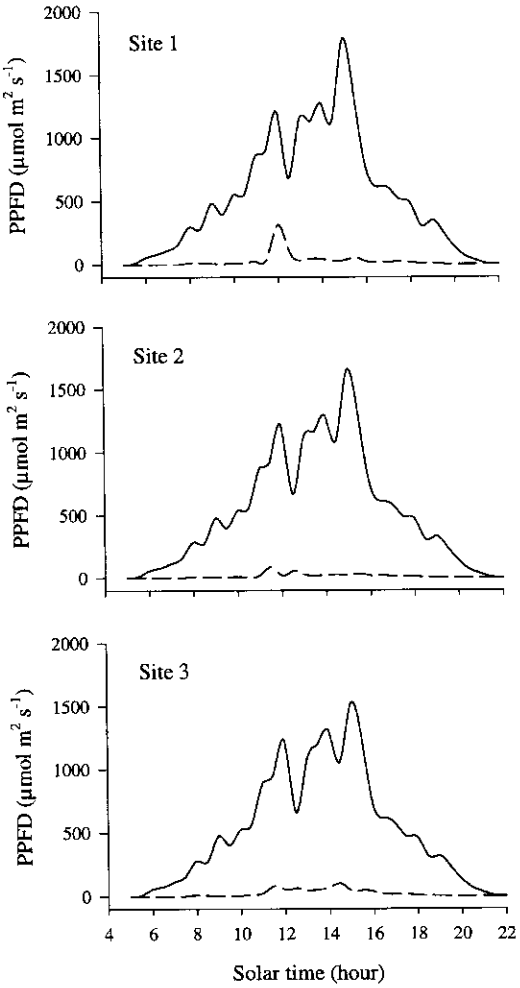

Figure 1. Representative daily light environment pattern for the three study sites. Solid lines represent clearcuts, and dashed lines, understories. Measurements were taken simultaneously on 1 July 1996.

Nutrient properties were significantly different among the three substrates, but did not differ significantly between the clearcut and the understory (Table 3). Both the forest floor and CWD had a significantly lower pH than mineral soil. The forest floor had significantly greater concentrations of all nutrient measures except total C and extractable Mg compared to the woody substrate. The woody substrate had greater concentrations of total C, total N, mineralizable N, extractable P, K, Ca, and Mg than the mineral soil.

The effects of light condition and soil substrate on survival varied among the three species (Figure 2). Except for Pacific silver fir growing in the clearcut, survival of the three species under the two light conditions was not significantly affected by soil substrate. The only exception was the survival of Pacific silver fir, which was significantly lower on woody substrates in the clearcut than under other growing conditions. Light condition affected survival of the three species differently. Douglas-fir survival was significantly higher in the clearcut than in the understory, western hemlock survival was significantly higher in the understory than in the clearcut, and Pacific silver fir survival, except for the CWD substrate in the clearcut, was not significantly different between understory and clearcut.

After two growing seasons, surviving seedlings had significantly different growth rates among growing conditions (Figure 3). Both light and substrate showed significant differences for all measures of seedling growth for all species, and a significant interactive effect between light×species, light×substrate and light×species×substrate was apparent. Although all measures of seedling growth for the three species were sig-

TABLE 3. Mean nutrient properties of the woody substrate, forest floor, and mineral soil (sample size is three for each substrate and light condition). Values with the same superscript letter in the same row are not significantly different.

Nutrient properties	Woody substrate		Forest floor		Mineral soil	
	Clearcut	Understory	Clearcut	Understory	Clearcut	Understory
pH	3.5^{b}	3.4^{b}	3.9^{b}	3.6^{b}	4.6^{a}	4.9^{a}
Total C (%)	50.3^{a}	50.1^{a}	43.5^{a}	46.4^{a}	4.4^{b}	8.1^{b}
Total N (%)	0.22^{b}	0.20^{b}	1.09^{a}	0.94^{a}	0.15^{c}	0.09^{c}
C:N	239^{a,b}	251^{a,b}	40^{b,c}	57^{b,c}	29^{b,c}	124^{b}
Min-N (mg/kg)	55^{b}	48^{b}	344^{a}	309^{a}	24^{c}	11^{c}
Extractable P (mg/kg)	24.2^{b}	14.1^{b}	48.7^{a}	60.3^{a}	5.7^{c}	2.4^{c}
Total SO_4-S (mg/g)	0.30^{b}	0.42^{b}	2.20^{a}	1.62^{a}	0.23^{b}	0.75^{a,b}
Extractable K (mg/kg)	21.3^{b}	30.3^{b}	74.3^{a}	133.3^{a}	11.7^{c}	5.7^{c}
Extractable Ca (mg/kg)	633^{b}	368^{b}	1867^{a}	1023^{a}	70^{c}	37^{c}
Extractable Mg (mg/kg)	133.3^{a}	161.7^{a}	203.3^{a}	211.7^{a}	8.7^{b}	5.3^{b}

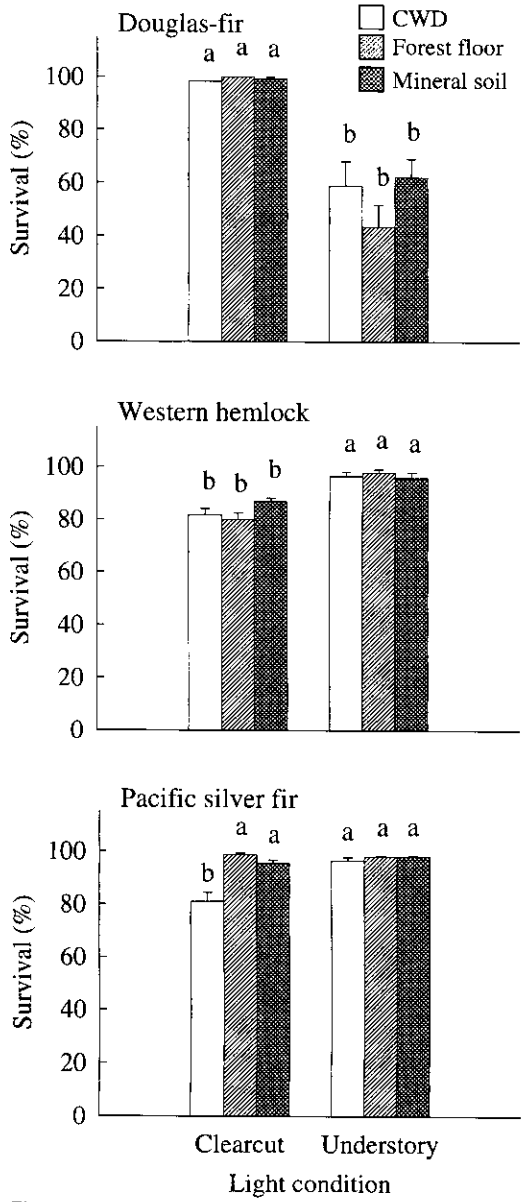

Figure 2. The effect of light condition (understory and clearcut) and soil substrate (woody substrate, non-woody forest floor and mineral soil) on survival at the end of the second growing season. Error bars represent 1 SE. Within each specific graph, values with the same letter are not significantly different.

nificantly larger in the clearcut than the understory, the effect was less pronounced for diameter and height growth of Pacific silver fir. In general, there were consistent significant differences due to substrate for all measures of seedling growth in the clearcut but, with the exception of Pacific silver fir, no significant differences in the understory.

There were different effects of light and substrate between the three species (Figure 3). Douglas-fir seedlings growing in the forest floor substrate were significantly larger for all growth measures than in the woody substrate, but significant differences were not found between the seedlings growing in the forest floor versus the mineral soil substrates. Significant differences in diameter were not detected between the seedlings growing in the woody versus the mineral soil substrates, and significant differences in height were not detected between the seedlings growing on the woody substrate and other substrates in the understory. For the western hemlock seedlings, in the clearcut all measures of growth were significantly larger in the forest floor than either the woody or mineral soil substrates. There were no significant differences between the woody and mineral soil substrates for all measures of growth, and significant differences in height were not detected between seedlings growing in either the woody or mineral soil substrates compared to all the substrates in the understory. Similar to western hemlock, in the clearcut all measures of growth for Pacific silver fir seedlings growing in the forest floor substrate were significantly larger than either the woody or mineral soil substrates. However, the biomass of seedlings growing in the mineral soil substrate was significantly larger than the woody substrate. Both diameter and height of seedlings growing in the woody and mineral soil substrates were not significantly different than seedlings growing in the understory with some exceptions. The response in biomass of Pacific silver fir to both light and substrate showed the most significant differences. There were significant differences between all substrates located in the clearcut, and between the woody and forest floor substrates located in the understory.

Discussion

Except for Pacific silver fir, substrate did not appear to influence seedling survival after two growing seasons. Seedling growth, however, was substrate dependent in the clearcut but not substrate dependent under shaded conditions. The interaction of light and nutrients was similar for natural

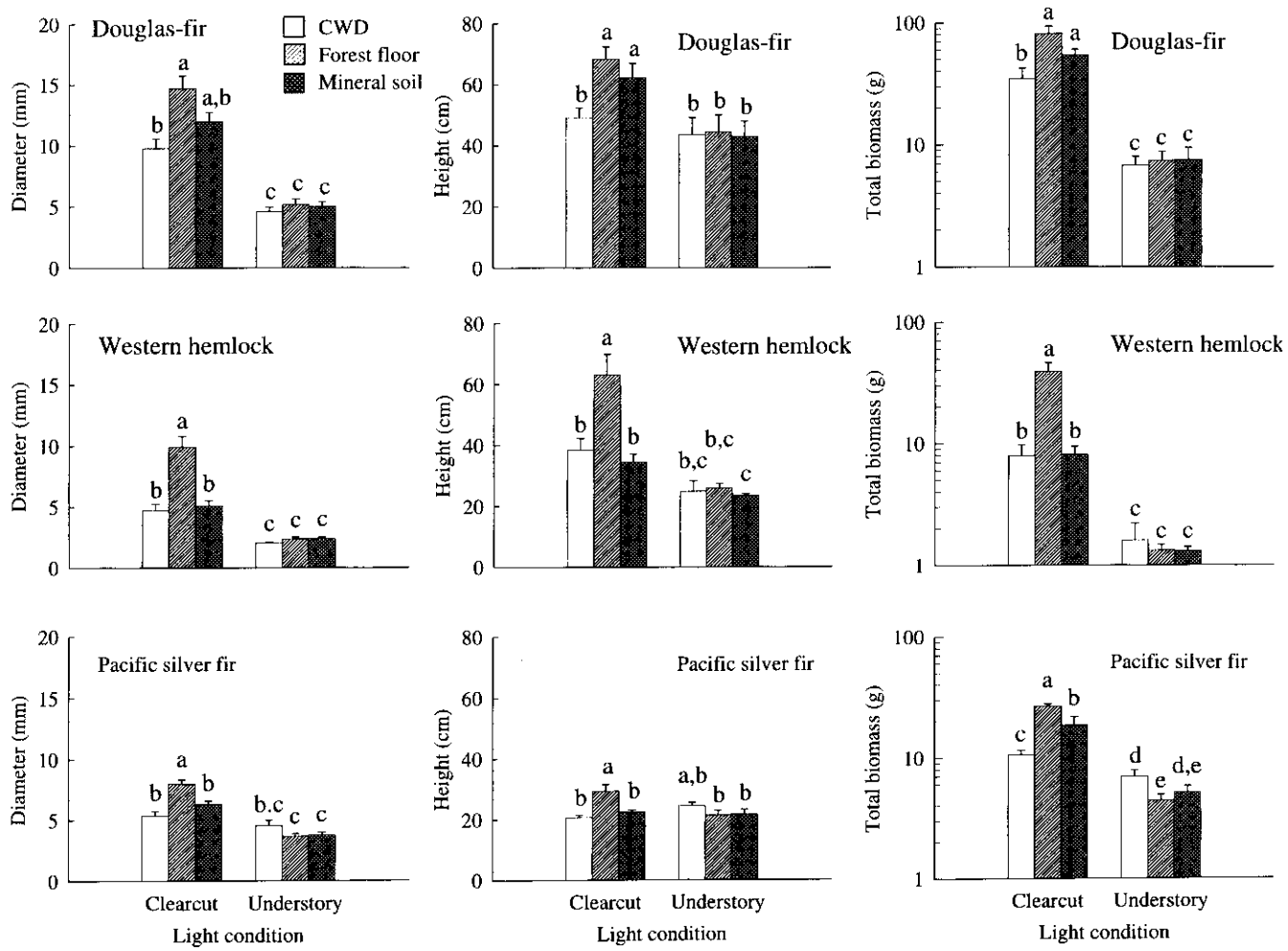

Figure 3. Base diameter, total height, and total biomass of planted seedlings in relation to light condition (understory and clearcut) and soil substrate (woody substrate, non-woody forest floor and mineral soil) at the end of the second growing season. Error bars represent 1 standard error of the mean. Within each specific graph, values with the same letter are not significantly different.

substrates under natural light conditions used in this study compared to completely controlled nitrogen fertilizer treatments under controlled shaded conditions in greenhouses (Reed et al. 1983, Canham et al. 1996, Walters and Reich 1996), and semi-controlled light-nutrient conditions using natural substrates with shade tents (Minore 1972). In this study in the clearcut, both western hemlock and Pacific silver fir had the largest growth in the nutrient rich non-woody forest floor substrate compared to the woody substrate and mineral soil, which demonstrated a consistency between seedling growth and nutrient availability, at least on a mass basis. Douglas-fir also had the largest growth in the forest floor substrate although not significantly different from the mineral soil. However, under the light limiting conditions of the understory, growth was not substrate dependent.

The results of this study differ from those of Bernsten (1960) for Douglas-fir growing in full light conditions. In this study, contrary to Bernsten (1960), there were significant differences in 2-yr height growth of seedlings between decayed wood and mineral soils. The large variability under field conditions may be the reason for the lack of power in detecting significant differences in Bernsten (1960). However, similar to Kropp (1982) and Christy et al. (1982) this study also did not detect differences in height growth of seedlings growing in CWD compared to seedlings growing in mineral soil.

Once light becomes the limiting factor, substrate appears to have little clear influence on growth for Douglas-fir, western hemlock, and Pacific silver fir seedlings. Under full light conditions substrate appears to have a species specific influence on growth. Douglas-fir, a species most associated with mineral soil substrates (Hermann and Lavender 1990), did not grow as large in woody substrates compared to non-woody forest floor substrates and mineral soil, and grew just as large in either of the latter. Western hemlock, the species most often cited as having an affinity to CWD (Harmon et al. 1986), had the largest growth associated with the non-woody forest floor. Growth on CWD was similar to the mineral soil. Similarly, the growth of Pacific silver fir was the largest on the non-woody forest floor, although not by the same magnitude of difference as western hemlock. Since Pacific silver fir seedlings are noted to have slow early height growth (Crawford and Oliver 1990), presumably with more time and if planting pots were not limiting, the differences in height and diameter would be better expressed.

Some caution is needed when extending the results to formulate management recommendations. One concern is that only one seedlot was used for each of the species for all three replicates. These results depend on each respective seedlot not being a genetically anomalous group having nutrient and moisture uptake properties different from the rest of the population of each respective species. A bigger concern is that pots were used rather than outplanting under non-restricting root conditions. By creating a berm and filling in between the pots, we attempted to minimize any pot effect. Nevertheless, small pot effects must be recognized since root restriction is a limiting factor when using small pots (Will and Teskey 1997, Thomas and Strain 1991). It was evident that many open-grown seedlings, particularly Douglas-fir, had roots circling the base of pots when harvested at the end of second growing season. Finally, although the role of mycorrhizae and CWD is important in the drier climates of the Rocky Mountain Forests (Harvey et al. 1987), we did not purposely inoculate the seedlings with indigenous mycorrhizae. Other than perhaps residual nursery mycorrhizae, a specific mycorrhizal study was beyond the intent of this paper.

This study supports Heilman (1990), who suggests that CWD does not appear to provide any advantage for seedling growth, at least in the wetter climates of south coastal British Columbia where the period of water deficit is much less than the drier forests of the Rocky Mountains. On the other hand, CWD did not appear to be detrimental to seedling survival or growth as suggested for the colder climate of southeastern Alaska (Jurgensen et al. 1990). Greater availability of nutrients and increased growth are associated with the non-woody humus substrate in clearcuts but CWD is not as poor a substrate for seedling growth as implied by its high C:N ratio and low nutrient content.

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