Acclimation of Natural and Planted Amabilis Fir to Clearcut and Stand Edge Microclimates on a Coastal Montane Reforestation Site
Acclimation of Natural and Planted Amabilis Fir to Clearcut and Stand Edge Microclimates on a Coastal Montane Reforestation Site

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EXECUTIVE SUMMARY

Delayed growth of shade-tolerant conifer regeneration has been widely reported on high-elevation coastal sites following stand removal using traditional clearcutting systems. The acclimation and subsequent growth of natural and artificial regeneration after harvesting is strongly dependent on site microclimatic conditions. Although stand edges and residual overstory trees can have a moderating influence on light and temperature, it is unclear what effect these microclimates have on the acclimation of shade-tolerant montane conifers.

In this study, clearcut and overstory-moderated microclimates were assessed for their influence on the physiological and morphological acclimation of natural and planted amabilis fir regeneration on a coastal montane cutover. Seedling response was monitored on clearcut, outside, and inside stand-edge microclimates. Morphological adjustments to exposure were evident both above and below ground. Both natural and planted stock on the clearcut had needles characteristic of sun foliage, with smaller surface areas relative to their dry weight than seedlings on the inside and outside edge plots. Root systems of advance amabilis fir on the clearcut and outside edge plots were more extensive and fibrous than on the inside edge. In contrast, the confined root plugs and succulent shoots of the nursery stock probably retarded acclimation in the first growing season after planting.

Assimilation of CO\(_2\) on the outside edge and clearcut plots differed only when the shade of the stand eclipsed the outside edge plot, after which light levels dropped well below the saturation point for maximum photosynthesis of amabilis fir. Low understory light intensities on the inside edge plot resulted in marginal CO\(_2\) assimilation rates and suppressed growth of both natural and planted seedlings. In contrast, annual cambial increment of natural regeneration in the outside edge and clearcut plots has increased at a near exponential rate since clearcutting in 1989. Natural and planted seedlings differed in their response to microclimatic conditions on the clearcut and outside edge plots. The relative height growth and annual cambial increment of natural regeneration on the outside edge and clearcut plots was similar despite differences in total hours of direct sunlight, air temperature, and evaporative demand. Although height growth of planted seedlings was greatest in the outside edge plot, shoot and root biomass was much greater on the clearcut plot, suggesting that differences in light environment prompted different strategies for carbon allocation in planted stock.

Planted stock had significantly lower CO\(_2\) assimilation rates than their natural counterparts and were more chlorotic in appearance, possibly a result of nitrogen deficiency. Foliar N concentrations of planted seedlings were well below those found in natural regeneration on both the clearcut and outside edge plots. The confined root plugs of planted stock and their limited egress into the soil may have restricted access to available soil nitrogen, and probably contributed to the low CO\(_2\) assimilation rates and chlorosis observed after planting. Plant water deficits were low to moderate during the study season and did not differ significantly between planted and natural seedlings, suggesting that moisture stress probably did not reduce photosynthesis in the planted seedlings.
ACKNOWLEDGEMENTS

The authors gratefully acknowledge MacMillan Bloedel for their assistance and permission in locating a suitable study site in the Menzies Bay Division of their Vancouver Island operations. Thanks are also due to Jim Arnott for obtaining nursery stock, and to Dr. Pasi Puttonen and Glen Dunsworth for their useful critiques. This study forms part of the Montane Alternative Silvicultural Systems (MASS) project and was funded by the Canada–British Columbia Partnership Agreement on Forest Resource Development (FRDA II).
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1 INTRODUCTION

Increasing dependency on coastal montane forests for timber resources has raised concern about the effect of progressive clearcutting systems adapted from lowland harvesting practices on the regeneration of native shade-tolerant species. Amabilis fir (Abies amabilis [Dougl.] Forbes) is found in the montane Coastal Western Hemlock biogeoclimatic zones of coastal British Columbia (Krajina 1969) in pure stands, or as a co-dominant with western hemlock (Tsuga heterophylla), mountain hemlock (Tsuga mertensiana), or yellow-cedar (Chamaecyparis nootkatensis) in mixed stands. Advance regeneration of this species in the understory is typically profuse, and is a potentially important component of the new stand following harvesting of the overstory.

Amabilis fir is most often established in cool, moist sites, indicating that this species may not readily acclimate to exposed conditions on large clearcuts that offer little protection from extremes in temperature, light intensity, and soil moisture (Koppenaal and Mitchell 1992). The shade-tolerant attributes that allow amabilis fir to survive in a suppressed state in the understory have been associated with prolonged acclimation periods, and with growth delays following clearcutting (Herring and Etheridge 1976; Wagner 1980). In particular, the shade foliar morphology (Tucker et al. 1987) and shallow rooting habit (Herring and Etheridge 1976) of suppressed understory seedlings, and the relatively poor control of amabilis fir over water loss (Livingston and Black 1988), are attributes that may contribute to delayed release.

The objective was to compare the physiological and morphological performance of natural (advance) and planted amabilis fir regeneration in response to a transition in microclimate from the understory of an old-growth montane forest into the stand edge and also into an adjoining clearcut. Microclimates moderated by stand edges and/or residual overstory trees typically associated with patchcut, shelterwood, and other alternative silvicultural systems can strongly influence seedling survival and growth (Seidel and Cooley 1974; Tucker and Emmingham 1977; Wagner 1980). Study plots were situated on the inside (understory) and outside edges of the old-growth hemlock-fir stand, as well as on the clearcut, to assess the influence of overstory-modulated microclimates on the acclimation of shade-tolerant regeneration.

The homogeneity of the 1–0 nursery stock planted in the spring of 1993 contrasted with the diversity in distribution, size, and age typical of advance amabilis fir regeneration (Herring and Etheridge 1976), and provided a more controlled assessment of seedling acclimation to the different site microclimates. Since productivity can differ between natural and planted conifer regeneration on montane sites (Arnott et al. 1995), the performances of advance and planted amabilis fir were compared in light of their inherent differences in root and shoot morphology at the time of planting.

2 SITE DESCRIPTION

The study site is located on eastern Vancouver Island in the CWHmm2 biogeoclimatic zone (49°55'N/125°25'W), within MacMillan Bloedel's Iron River Operation, Menzies Bay Division. It is situated at an elevation of 800 m on a 7% slope, and faces North 20° East. Part of the study site was clearcut in 1989 and fall-planted with yellow-cedar in 1991.

The average air temperature in the area is 16.6°C in July and 0.4°C in January. The mean annual precipitation is 1406.0 mm (Campbell River Airport, Environment Canada). The soil
is a coarse loamy Orthic Humic Podzol with a thick humus layer (14-40 cm), overlying mineral soil with stony glacial deposits and weathered bedrock.

The predominant species in the forest overstory are old-growth western hemlock, mountain hemlock, amabilis fir, and yellow-cedar. The average height of the tree canopy is 27.9 m. Advance regeneration in the clearcut, outside edge, and inside edge plots is primarily amabilis fir, mostly under 30 cm high, with a smaller component of hemlock (Figure 1). Amabilis fir regeneration is much less dense and less evenly distributed in the clearcut than in the forest understory.

The forest understory is composed primarily of Vaccinium ovatifolium, and the ground is densely covered by mosses and patchy herbs. The Vaccinium is still present in the clearcut, but at a lower density, and Epilobium angustifolium and Rubus pedatus occupy most of the herb layer, while the mosses are almost completely absent (Appendix). Vegetation on the outside edge of the forest is transitional between the forest and the clearcut, with more Vaccinium present than in the clearcut.

3 METHODS AND MATERIALS

A transect was run perpendicular to the northeast-facing edge of the old-growth stand. Three plots measuring 75 m long by 5 m wide were established perpendicular to the transect from 5 m within the forest (inside edge plot) to 60 m out into the clearcut (clearcut plot). A plot between the inside edge and clearcut plots was established 12 m outside the stand edge (outside edge plot). The study period was from April 27 to September 29, 1993.

A climate station consisting of an Omnidata Easylogger and associated sensors was installed at the approximate centre of each plot to continuously record several environmental parameters. Air temperature (°C) and relative humidity (%) were monitored at 30 cm above the soil surface. Vapour pressure deficit (kPa) was calculated from relative humidity and air temperature. Maximum and minimum measurements of photosynthetically active radiation (PAR) (µmol·m⁻²·s⁻¹) in both the inside and outside edge plots were obtained from four Li-cor PAR sensors; two PAR sensors were installed in the clearcut. Soil water potential (MPa) at -10 cm was measured with Water-Mark soil moisture sensors. Sierra Misco rain gauges were installed in the clearcut and inside edge plots to measure precipitation. A programming failure caused a period of lost climate data on the clearcut and inside edge plots from July 20 to August 6, 1993.

Natural and advance regeneration should be considered synonymous in this report, since the amount of regeneration that had seeded-in after harvesting was not significant at the time of this study. To reduce confounding effects from the large variation in the size and age of advance regeneration on the study site, only natural seedlings under 30 cm tall were selected (spring 1992) for use in the study. Amabilis fir nursery stock (1-0) was planted on all plots on April 27, 1993. Height was measured in April and September, 1993 on 50 natural and 75 planted seedlings in each plot. To address the possible effect of variation within plots, both natural and planted study trees in each plot were subdivided into three blocks. At the end of the study period, 18 natural and 18 planted seedlings from each plot were excavated for shoot and root dry-weight analysis, as well as for specific leaf area. Samples were oven dried at 80°C, then shoots and roots were weighed. The fresh surface area of 20 current needles from each seedling was measured on a Li-Cor area meter for specific leaf area, then the oven-dry weight was obtained to provide the ratio of surface area to dry weight. A further 18 natural trees from
FIGURE 1. Density and height of natural regeneration.
FIGURE 2. Maximum daily irradiance. Symbols represent mean daily maxima of photosynthetically active radiation (PAR). Clearcut data from July 20–August 06 and August 28–September 08, and inside edge data from July 20–August 06 not available.
each plot were sampled for measurement of growth rings. These samples were sectioned at
the base of the stem with a sliding microtome, and annual rings measured with the aid of a
compound microscope.

Seedling photosynthesis, transpiration, and xylem water potential were measured four
times between June 8 and September 9, 1993. On these study days, net photosynthesis (A)
(μmol•CO₂•m⁻²•s⁻¹) and transpiration (E) (mmol•H₂O•m⁻²•s⁻¹) were measured with an
ADC LCA-3 gas analyzer. Measurements were made between 2 p.m. and 4 p.m. on five or six
seedlings per plot. On September 9, 1993 these measurements were taken between 9 a.m. and
10:30 a.m. Because photosynthetic rates were consistently near the compensation point on the
inside edge plot (Koppenaal et al. 1995), the above ecophysiological measurements were
concentrated on the clearcut and outside edge

plots. Consequently, ecophysiological measure-
ments on the inside edge plot were measured on only 2 days. Xylem pressure potential (MPa)
was measured in synchrony with photo-
synthetic measurements on five or six seedlings
from each plot, using a pressure chamber
(Ritchie and Hinckley 1975).

Bulked samples of 20 natural and 20
planted seedlings from each of the three blocks
per plot were sent to the Pacific Forestry Centre for determination of foliar N, P, and K.
Total N was determined using a Leco FP128
organic N analyzer. Total P and K were
analyzed by the microwave digestion technique
(Kalra and Maynard 1991). Where appropriate,
data were statistically evaluated by analysis of
variance (SAS Institute, Inc. 1988). The
Student Neuman Kuels mean separation test
was used to identify significant differences
between three or more means.

4 RESULTS AND DISCUSSION

4.1 Microclimate

Maximum photosynthetically active radia-
tion (PAR) in the clearcut ranged between
400 and 2600 μmol•m⁻²•s⁻¹. Maximum daily
PAR in the outside edge plot was generally
150–1000 μmol•m⁻²•s⁻¹ less than in the
clearcut. In contrast, maximum PAR in the
inside stand edge plot was below 300
μmol•m⁻²•s⁻¹ on most days. Higher daily
maximums were largely the result of sunflecks
and brief periods of direct sunlight (Figure 2).
These brief periods aside, PAR levels in the
inside edge plot were far below the light
saturation point for maximum photosynthesis
of amentilis fir¹. While the light environment of the
outside edge plot was under the influence of the
forest edge (northeast facing) throughout
the study period, shade from the stand eclipsed
the outside edge plot earlier in the day as the
season progressed. In July, the outside edge
plot was not shaded by the stand until 2 p.m.,
whereas by September this plot was in shade
by 10 a.m.

¹ A.K. Mitchell, Can. For. Serv., Unpubl. data

Throughout the study, air temperatures at
30 cm were generally highest in the clearcut,
where mean daily temperatures ranged from 5
to 18°C (Figure 3). Mean air temperatures in
the outside edge plot were generally 1 to 4°C
lower than in the clearcut. Mean air
temperatures in the inside edge plot ranged
from 5 to 16°C. The daily range in air
temperature was also greatest in the clearcut,
where temperatures as high as 30.5°C were
recorded. In contrast, daily maximum air
temperatures in the outside and inside stand-
edge plots were 26.5 and 21.5°C, respectively.
Minimum daily temperatures were generally
0.5 to 3°C lower in the clearcut and outside
dge plots than in the inside edge plot. Air
temperatures dipped below 0°C only once
during the study period. For a description of
soil temperatures on this site, see Koppenaal et
al. (1995).

Total precipitation between June 4 and
September 29 was 241 mm, and was enough to
maintain soil water potential at a nearly
constant level until early September (Figure 4).
FIGURE 3. Maximum and minimum daily air temperature. Line thickness increases in order of clearcut<outside edge<inside edge. Symbols represent mean daily temperature. Clearcut and inside edge data from July 20–August 06 not available.
FIGURE 4. Daily precipitation and soil moisture. Bars represent precipitation (data from clearcut plot). Lines represent soil moisture. Clearcut and inside edge data from July 20–August 06 not available.
The only period of low rainfall occurred in September and resulted in higher soil water deficits for that period, particularly in the inside edge plot where soil water potentials reached 0.047 MPa at the end of the study. The overstory demand for soil water in the forest probably accounted for the higher soil water deficits observed in this plot in September. Summer soil water deficits are common within the eastern Vancouver Island rain shadow (Klinka et al. 1979).

4.2 Growth and Morphology

The annual cambial increment of natural regeneration, as determined by ring analysis, showed an almost immediate release response to stand removal in both the clearcut and outside edge plots (Figure 5). Since clearcutting in 1989, annual cambial increment increased at a near exponential rate in both plots. Cambial increment 3 years after clearcutting (1992) was more than triple the increment after 1 year (1990), suggesting that acclimation of natural regeneration to overstory removal has probably continued for at least 3 years. These data also suggest that the potential for free growth on this site has not yet been realized. As the advance regeneration becomes fully acclimated to post-harvest site conditions, the rate of diameter growth in the clearcut and outside edge plots should stabilize once an equilibrium is established with the available resources (i.e., light, water, and nutrients). Understory regeneration in the inside edge plot showed no increase in annual cambial increment during this period.

Height growth of natural and planted amabilis fir stock was not comparable the first season after spring planting, since needle primordia of the planted stock were formed in the bud at the nursery the previous fall. However, plot differences in current height increment among planted seedlings was likely related to the study site environment. The relative height-growth rate (April 27–September 9, 1993) of planted seedlings on the outside edge plot was significantly greater than in the clearcut and inside edge plots (Table 1). The mean relative height-growth rate of natural amabilis fir regeneration on the outside edge plot was slightly greater than on the clearcut, although the difference was not significant (Table 1). The height growth of advance regeneration was suppressed on the inside edge plot. The low photosynthetic rates measured in the inside edge plot show that light levels were too low for substantial growth to occur in this understory environment.

Although the relative height growth of planted seedlings was greatest in the outside edge plot, shoot and root dry weight at the end of the season was much greater in seedlings planted on the clearcut (Table 1). The large difference in dry weight between plots suggests that microclimate differences between the clearcut and outside edge plots, particularly in light quantity, prompted different strategies for carbon allocation, at least for planted seedlings. On the clearcut, high light levels over a longer diurnal period may have fueled the production of more shoot biomass and larger root systems, whereas lower levels on the outside edge plot may have favoured vertical growth. Between-plot comparisons of natural regeneration by dry weight were not as meaningful, since the large variation in tree size and age on the study site made completely random selection of samples impractical. Post-harvest cambial expansion and relative height growth of natural regeneration indicates that there has been little difference in biomass accumulation between the clearcut and outside edge plots.

While root:shoot ratios of planted seedlings did not differ between plots, they were significantly lower (p<0.05) than in the natural regeneration. This is especially notable since incomplete root recovery during excavation caused the root weight of natural regeneration to be underestimated. The relatively smaller root systems of planted stock, and the initial confinement of the root plug to a small soil volume, probably contributed to the generally chlorotic and sometimes wilted appearance of planted stock, particularly on the clearcut plot. The larger root:shoot ratios of advance regeneration on the inside edge plot (Table 1) should be interpreted as a measurement artifact, since these plants were much smaller, on average, than their counterparts in the outside edge and clearcut plots, and often displayed severe stem sweep at, and under, the
TABLE 1. Mean (± SE) relative height growth, dry weight, and specific leaf area of natural and planted amabilis fir regeneration

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Natural Clearcut</th>
<th>Natural Outside edge</th>
<th>Natural Inside edge</th>
<th>Planted Clearcut</th>
<th>Planted Outside edge</th>
<th>Planted Inside edge</th>
<th>Natural Sample size/plot</th>
<th>Planted Sample size/plot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative height growth rate (ln x 10⁻⁵)</td>
<td>2.04 (0.20)a</td>
<td>2.36 (0.18)a</td>
<td>0.46 (0.17)b</td>
<td>1.96 (0.12)b</td>
<td>2.98 (0.14)a</td>
<td>2.34 (0.15)b</td>
<td>50</td>
<td>75</td>
</tr>
<tr>
<td>September 1993 height (cm)</td>
<td>21.97 (1.07)a</td>
<td>20.06 (0.70)a</td>
<td>10.35 (0.52)b</td>
<td>29.29 (0.63)a</td>
<td>28.18 (0.57)a</td>
<td>25.77 (0.63)b</td>
<td>50</td>
<td>75</td>
</tr>
<tr>
<td>Shoot dry weight (g)</td>
<td>3.68 (0.43)a</td>
<td>4.36 (0.93)a</td>
<td>1.89 (0.16)b</td>
<td>9.44 (0.80)a</td>
<td>5.75 (0.58)b</td>
<td>5.20 (0.51)b</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>Root dry weight (g)</td>
<td>1.35 (0.14)a</td>
<td>1.64 (0.35)a</td>
<td>1.44 (0.16)a</td>
<td>3.04 (0.22)a</td>
<td>1.76 (0.23)b</td>
<td>1.51 (0.11)b</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>Root:shoot ratio (%)</td>
<td>40.77 (3.29)b</td>
<td>43.07 (4.58)b</td>
<td>76.95 (7.63)a</td>
<td>33.68 (1.94)a</td>
<td>30.50 (2.08)a</td>
<td>31.37 (2.17)a</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>Specific leaf area (cm²/g)</td>
<td>88.54 (2.49)d</td>
<td>106.40 (4.08)c</td>
<td>101.17 (4.03)c</td>
<td>81.84 (4.65)d</td>
<td>123.71 (7.37)b</td>
<td>152.70 (9.68)d</td>
<td>18</td>
<td>18</td>
</tr>
</tbody>
</table>

†Different letters indicate significant differences ( p≤0.05) between plots (within stock type) as determined by the Student Newman Kuels mean separation test. Relative height growth and dry weight are not comparable between stock types. Specific leaf area is comparable between stock types as well as between plots.
FIGURE 5. Annual cambial increment of advance amabilis fir before and after clearcutting. Vertical lines represent the standard error of the mean (n=18).
soil surface. Root weight was overestimated, since it was difficult to determine where the effective root system started. Root systems of natural regeneration in the clearcut and outside edge plots were far more extensive and fibrous than those from the inside edge plot. Growth delays of advance amabilis fir following clearcutting have been attributed in part to the shallow, poorly developed root systems of understory regeneration (Kotar 1977; Herring and Etheridge 1976), which must expand before accelerated shoot growth can be supported. Understory advance regeneration in the inside edge plot also displayed a characteristic umbrella-shaped crown, unlike the apically dominant crown structures observed in the clearcut and outside edge plots.

There were also apparent differences in foliar morphology between understory trees growing on the inside edge and those exposed to full sunlight on the clearcut. Both natural and planted stock on the clearcut had thicker needles than their inside and outside edge counterparts (Table 1). This is characteristic of sun foliage, and reflects significantly lower specific leaf areas (the ratio of surface area to dry weight). This sun foliage typically had a double layer of palisade cells, and, presumably, was more resistant to exposure-related desiccation and radiation damage. The specific leaf areas of planted seedlings from the outside edge plot were between those of the clearcut and inside edge plots, indicating that some foliar acclimation had occurred on that plot, presumably in response to increased light. Although the foliage of advance regeneration on the outside edge plot appeared similar to that in the clearcut, specific leaf area measurements were higher. The specific leaf area of advance regeneration in the inside edge plot was also higher than in the clearcut, reflecting thinner shade foliage in the understory. Earlier studies have identified these changes in root and foliar morphology as likely prerequisites for the acclimation of amabilis fir following harvesting (Herring and Etheridge 1976; Tucker et al. 1987).

4.3 Photosynthesis and Water Relations

During the 1993 growing season, net photosynthetic rates of natural regeneration in the clearcut and outside edge plots were consistently higher than those of planted seedlings, except on June 8, which was a cool and overcast day (Table 2). Following this early June measurement, afternoon mean net photosynthetic rates of natural and planted regeneration on the clearcut ranged from 2.9 to 4.2 μmol·m⁻²·s⁻¹ and from 1.0 to 2.6 μmol·m⁻²·s⁻¹, respectively. Pooled afternoon photosynthetic measurements from the clearcut and outside edge plots from July through September show that the net photosynthesis of natural and planted regeneration generally increased curvilinearly with PAR, tapering off to a shallower increase after about 300 μmol·m⁻²·s⁻¹. The magnitude of the response differed most at light intensities over 300 μmol·m⁻²·s⁻¹ CO₂, where assimilation rates of natural regeneration were substantially higher than their planted counterparts (Figure 6). Root and foliar morphological attributes characteristic of the planted stock probably contributed to the low photosynthetic rates and generally chlorotic foliage, although whether either were causal factors is unknown.

Compared to transpiration rates of natural regeneration, which increased linearly with increasing vapour pressure deficit (VPD) (Figure 7), pooled data for July through September show depressed transpiration rates for planted stock from the clearcut and outside edge plots at all encountered VPD levels. Since water deficits of the planted stock were slightly less than those of natural regeneration throughout the growing season (Table 2), it is unlikely that water stress caused the suppressed transpiration rates of the planted seedlings. Increased transpiration of natural regeneration with rising VPD is consistent with the poor control over water loss reported for amabilis fir (Hinkley et al. 1982; Livingston and Black 1988).
TABLE 2. Mean (± SE) afternoon photosynthesis, transpiration, and xylem pressure potential of natural and planted amabilis fir regeneration on 4 days.

<table>
<thead>
<tr>
<th>Date</th>
<th>Parameter</th>
<th>Natural Clearcut</th>
<th>Natural Outside edge</th>
<th>Natural Inside edge</th>
<th>Planted Clearcut</th>
<th>Planted Outside edge</th>
<th>Planted Inside edge</th>
<th>Sample size</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 8</td>
<td>Net photosynthesis (μmol•m⁻²•s⁻¹)</td>
<td>3.71 (0.41)a</td>
<td>3.29 (0.41)a</td>
<td>–</td>
<td>4.56 (0.27)a</td>
<td>3.87 (0.19)a</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Transpiration (mmol•m⁻²•s⁻¹)</td>
<td>1.71 (0.08)b</td>
<td>1.56 (0.10)b</td>
<td>–</td>
<td>2.64 (0.27)a</td>
<td>2.27 (0.17)a</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Xylem pressure potential (MPa)</td>
<td>0.73 (0.04)a</td>
<td>0.77 (0.08)a</td>
<td>–</td>
<td>0.73 (0.09)a</td>
<td>0.69 (0.08)a</td>
<td>–</td>
<td>6</td>
</tr>
<tr>
<td>July 19</td>
<td>Net photosynthesis (μmol•m⁻²•s⁻¹)</td>
<td>2.92 (0.42)a</td>
<td>2.71 (0.36)a</td>
<td>0.56 (0.27)c</td>
<td>1.04 (0.49)b</td>
<td>1.03 (0.11)b</td>
<td>-2.67 (0.94)c</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Transpiration (mmol•m⁻²•s⁻¹)</td>
<td>2.61 (0.20)a</td>
<td>2.46 (0.22)a</td>
<td>0.91 (0.08)b</td>
<td>1.05 (0.09)b</td>
<td>0.97 (0.03)b</td>
<td>1.27 (0.29)b</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Xylem pressure potential (MPa)</td>
<td>1.10 (0.02)a</td>
<td>0.86 (0.07)b</td>
<td>0.83</td>
<td>1.07 (0.07)a</td>
<td>0.70 (0.06)b</td>
<td>0.77</td>
<td>6 (2)</td>
</tr>
<tr>
<td>August 12</td>
<td>Net photosynthesis (μmol•m⁻²•s⁻¹)</td>
<td>4.19 (0.39)a</td>
<td>3.15 (0.47)a</td>
<td>–</td>
<td>1.82 (0.37)b</td>
<td>0.89 (0.37)b</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Transpiration (mmol•m⁻²•s⁻¹)</td>
<td>2.32 (0.18)a</td>
<td>1.74 (0.06)b</td>
<td>–</td>
<td>1.09 (0.08)b</td>
<td>1.43 (0.42)b</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Xylem pressure potential (MPa)</td>
<td>1.25 (0.11)a</td>
<td>0.96 (0.08)a</td>
<td>–</td>
<td>1.05 (0.07)a</td>
<td>0.89 (0.08)a</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td>September 8</td>
<td>Net photosynthesis (μmol•m⁻²•s⁻¹)</td>
<td>3.47 (0.65)a</td>
<td>0.60 (0.56)b</td>
<td>0.07</td>
<td>2.50 (0.73)a</td>
<td>0.63 (0.38)b</td>
<td>-0.71</td>
<td>6 (2)</td>
</tr>
<tr>
<td></td>
<td>Transpiration (mmol•m⁻²•s⁻¹)</td>
<td>3.57 (0.22)a</td>
<td>2.49 (0.18)b</td>
<td>0.61</td>
<td>1.77 (0.24)c</td>
<td>1.16 (0.18)c</td>
<td>0.77</td>
<td>6 (2)</td>
</tr>
<tr>
<td></td>
<td>Xylem pressure potential (MPa)</td>
<td>1.34 (0.04)a</td>
<td>1.00 (0.11)b</td>
<td>0.81</td>
<td>1.18 (0.08)ab</td>
<td>0.68 (0.05)c</td>
<td>0.60</td>
<td>6 (2)</td>
</tr>
</tbody>
</table>

† Different letters indicate significant differences (p ≤ 0.05) between plots and stock types as determined by the Student Newman Kuels mean separation test. Parenthesis denote sample size on inside edge plot.
FIGURE 6. Photosynthetic response of natural and planted amabilis fir to irradiance (PAR). Symbols represent individual afternoon measurements taken on July 19, August 12 and September 8, 1993. Data presented is from the clearcut and outside edge plots only. Lines represent the upper boundary of data points.
FIGURE 7. Transpiration of natural and planted amabilis fir in response to evaporative demand. Symbols represent individual afternoon measurements taken on July 19, August 12 and September 8, 1993. Data presented is from the clearcut and outside edge plots only. Regression lines for natural and planted fir are $R = 0.70$ and $R = 0.19$, respectively.
Photosynthetic rates of natural and planted stock on the outside edge plot differed significantly from those on the clearcut only when the shade from the stand eclipsed the outside edge plot. This occurred earlier in the day as the season progressed. For example, on the morning of September 9, photosynthetic rates of natural and planted trees on the outside edge plot were a little higher than on the clearcut, but by 10 a.m. the outside edge plot was shaded. Consequently, afternoon photosynthetic rates (measured on September 8) were much lower than on the clearcut (Figure 8). The cumulative effect over the growing season of more hours of direct sunlight in the clearcut was more CO₂ assimilation by planted seedlings, and thus a relative increase (Table 1) at the end of the season in dry weight, but not in height. Light interception by natural and planted regeneration in the understory of the inside edge plot was generally below 200 μmol·m⁻²·s⁻¹, which resulted in marginal rates of photosynthesis that hovered around the compensation point.

Over the course of the growing season, the lowest level of plant water deficit on the study site was -1.4 MPa—well above the critical turgor loss point for natural amabilis fir of -2.2 MPa, determined earlier by pressure volume analysis (Koppenaal et al. 1995). Xylem pressure potentials of natural and planted regeneration were comparable, and were lowest in September when soil moisture deficits were highest (Table 2). Afternoon xylem pressure potentials of both natural and planted trees were lower in the clearcut than in the outside edge plot from July to September. Mean afternoon xylem pressure potentials ranged from -1.1 to -1.3 MPa and from -0.7 to -1.0 MPa in the clearcut and outside edge plots, respectively. Lower xylem water potentials in the clearcut probably reflect longer periods of high evaporative demand and slightly higher soil water deficits on this plot, compared to the outside edge plot. Xylem pressure potentials of natural and planted seedlings in the inside edge plot (measured on only 2 days) were similar to those on the outside edge plot.

Foliar nitrogen (N) concentrations of natural regeneration were significantly (p<0.05) higher than in planted seedlings growing on the clearcut (1.25% vs. 0.86%) and outside edge (1.43% vs. 0.89%) plots (Table 3). The foliar N concentrations in planted stock were at levels considered deficient for true fir (Powers 1983), and were comparable to levels found in amabilis fir from other sites in British Columbia and Washington (Beaton et al. 1965; Radwan et al. 1989). Plug root systems confined to a small soil volume, and poor root-soil contact of the newly planted seedlings, may have limited the uptake of available N in the planted stock, and may account in part for their chlorotic appearance. Differences in foliar N concentrations of planted seedlings between plots were not significant (p< 0.05). Concentrations of N in natural regeneration on the inside edge plot (0.72%) were very low compared to those on the other plots. This suggests that greater N availability on the clearcut, possibly in response to higher soil temperatures and increased mineralization. Foliar concentrations of phosphorus and potassium varied between plots, but were at or above critical levels for true fir (Powers 1983).
FIGURE 8. Influence of (A) photosynthetically active radiation (PAR) and (B) vapour pressure deficit (VPD) on (C), photosynthesis ($A_{net}$) and (D) xylem pressure potential ($\psi_x$) in natural and planted amabilis fir on September 8 and 9, 1993. Symbols represent means and standard error (vertical lines) of 6 trees. No seedling measurements were taken on the inside edge plot on September 9.
TABLE 3. Mean (± SE) bulked† foliar N, P, and K concentrations of natural and planted amabilis fir regeneration

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Clearcut</th>
<th>Outside edge</th>
<th>Inside edge</th>
<th>Clearcut</th>
<th>Outside edge</th>
<th>Inside edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (%)</td>
<td>1.25 (0.31)a‡</td>
<td>1.43 (0.41)a</td>
<td>0.72 (0.06)c</td>
<td>0.86 (0.05)bc</td>
<td>0.89 (0.19)bc</td>
<td>1.06 (0.15)ab</td>
</tr>
<tr>
<td>P (%)</td>
<td>0.19 (0.02)ab</td>
<td>0.24 (0.02)a</td>
<td>0.19 (0.03)ab</td>
<td>0.15 (0.03)b</td>
<td>0.18 (0.03)ab</td>
<td>0.20 (0.02)ab</td>
</tr>
<tr>
<td>K (%)</td>
<td>1.03 (0.06)ab</td>
<td>0.97 (0.06)b</td>
<td>0.54 (0.07)c</td>
<td>1.08 (0.02)a</td>
<td>1.00 (0.05)ab</td>
<td>1.13 (0.05)a</td>
</tr>
</tbody>
</table>

† Bulked samples were derived from 20 seedlings from each of three blocks per plot.
‡ Different letters indicate significant differences (p ≤ 0.05) between plots and stock types as determined by the Student Newman Kuels mean separation test.

5 CONCLUSIONS

Other studies of advance amabilis fir regeneration following clearcutting, on a variety of coastal sites in southwestern British Columbia and in Washington State, found delays in height and diameter growth of 1–5 years (Herring and Etheridge 1976; Wagner 1980). While a release response of advance amabilis fir was evident on the clearcut and outside edge plots at this site just one year after clearcutting in 1989, the increase in cambial growth since has been nearly exponential, indicating continuing acclimation to overstory removal. Initiation of free growth of suppressed amabilis fir has been linked with a shift to sun foliage, apical dominance (Tucker et al. 1987), and root expansion (Herring and Etheridge 1976; Kotar 1977)—morphological attributes that were evident in released advance regeneration, but contrasted with the more succulent shoots and confined root plugs of the nursery stock at the time of planting.

Advance regeneration and newly planted stock responded differently to post-harvest microclimates on the clearcut and outside edge plots, probably because of differences in shoot morphology and root development. Similar relative height growth and annual cambial increment of natural regeneration in the clearcut and outside edge plots indicates that, so far, the release response has not differed between these two plots, despite differences in total hours of direct sunlight, air temperature, and evaporative demand. Greater shoot and root biomass of planted seedlings growing on the clearcut was probably the cumulative effect of more hours of direct sunlight, which fueled higher rates of photosynthesis over a longer period of time. In contrast, the influence of shade from the stand on the microclimate of the outside edge plot increasingly restricted photosynthesis of amabilis fir on that plot as the growing season progressed. Microclimate differences between the clearcut and outside edge plots, particularly in the quantity of photosynthetically active radiation, prompted different strategies for carbon allocation in planted stock. This is reflected in the greater relative height growth, but smaller biomass, of seedlings on the outside edge plot.

Higher rates of CO₂ assimilation in natural regeneration were likely related to adjustments in foliar and root morphology. Chlorosis and lower photosynthetic rates in the planted seedlings on the clearcut and outside edge plots probably resulted from nitrogen deficiency. Deficient foliar nitrogen concentrations in
planted stock may also account for their chlorotic appearance, and suggest that the confined soil volume occupied by root plugs and their limited egress into the soil probably limited access to available nitrogen. Low to moderate plant water deficits throughout the season indicate that water stress was not limiting the photosynthesis of planted stock. Low understory light was responsible for the marginal photosynthetic rates and suppressed height growth of both natural and planted trees in the inside edge plot.

On exposed clearcut sites, the potential benefit of long periods at maximum photosynthetic rates must be balanced against the risk of prolonged exposure to drought, elevated temperatures and high irradiance, which can result in desiccation, solarization, and excessive evaporative demand in shade-tolerant regeneration. While an open light environment was the most important factor in the release of advance regeneration 4 years after clearcutting, the morphological attributes of the newly planted nursery stock were not well adapted to open site conditions, and probably retarded acclimation in the first growing season. Given the low drought tolerance of amabilis fir, the risk of more severe injury to nursery stock or unacclimated natural regeneration under less favourable soil moisture conditions cannot be discounted. While critical plant water stress was not observed at the study site, seasonal water deficits occur in this area (Klinka et al. 1979). The stand edge had a moderating effect on light and temperature in the outside edge plot, providing a less stressful microclimate for shade-tolerant regeneration. Presumably, this would be beneficial during periods of drought and high temperatures.
REFERENCES


## APPENDIX

Site vegetation description

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean percent cover</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inside edge</td>
</tr>
<tr>
<td><strong>Overstorey</strong></td>
<td></td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em></td>
<td>37</td>
</tr>
<tr>
<td><em>Tsuga mertensiana</em></td>
<td>13</td>
</tr>
<tr>
<td><em>Abies amabilis</em></td>
<td>8</td>
</tr>
<tr>
<td><em>Chamaecyparis nootkatensis</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Pinus strobus</em></td>
<td>2</td>
</tr>
<tr>
<td><strong>Shrub Layer</strong></td>
<td></td>
</tr>
<tr>
<td><em>Vaccinium ovalifolium</em></td>
<td>47</td>
</tr>
<tr>
<td><strong>Herb Layer</strong></td>
<td></td>
</tr>
<tr>
<td><em>Cornus canadensis</em></td>
<td>2.6</td>
</tr>
<tr>
<td><em>Clintonia uniflora</em></td>
<td>0.4</td>
</tr>
<tr>
<td><em>Streptopus roseus</em></td>
<td>–</td>
</tr>
<tr>
<td><em>Blechnum spicant</em></td>
<td>6</td>
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<tr>
<td><em>Linnaea borealis</em></td>
<td>0.2</td>
</tr>
<tr>
<td><em>Rubus pedatus</em></td>
<td>–</td>
</tr>
<tr>
<td><em>Epilobium angustifolium</em></td>
<td>–</td>
</tr>
<tr>
<td><strong>Tree seedlings</strong></td>
<td></td>
</tr>
<tr>
<td><em>Abies amabilis</em></td>
<td>1.2</td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em></td>
<td>0.4</td>
</tr>
<tr>
<td><strong>Mosses</strong></td>
<td>77.0</td>
</tr>
</tbody>
</table>

Values are the mean of five sample plots (3x3m).