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## Proximity to a Stand Edge Influences Growth of Advance and Planted Pacific Silver Fir Seedlings

### Abstract

Growth and physiology of advance regeneration, present in the understory before harvest, and planted seedlings of Pacific silver fir were compared in three environments created by increasing distance from an edge of a montane clearcut on Vancouver Island, British Columbia, Canada. The objective was to quantify growth limitations and their underlying mechanisms in relation to light and nutrient availability. The site was clearcut in 1989. In 1993, plots were established 5-10 m inside the north-east facing stand edge, and 12-17 m and 60-65 m into the adjoining clearcut. Microclimate data were collected, and biomass allocation, specific leaf area, and net photosynthesis of advance and planted seedlings in the plots were measured in 1993. Height growth and foliar nitrogen concentration of advance and planted seedlings were measured over a 5 yr period.

Light and air temperature increased from the inside edge environment into the clearcut. Soil moisture did not differ greatly among environments. Seedlings of both regeneration types grew tallest in the clearcut, and specific leaf areas were lower in the clearcut. In 1993, root:shoot ratios and rates of net photosynthesis were greater in advance than planted seedlings. Planted seedlings were significantly taller than advance regeneration by 1998, 5 yr after establishment, however, this size difference was due mainly to the larger starting size of planted seedlings. By 1998, foliar nitrogen concentrations did not differ between regeneration types. Foliar nitrogen concentrations were low in all environments, which supports the contention that growth check of Pacific silver fir in montane clearcuts is associated with nitrogen deficiency.

### Introduction

Pacific silver fir (*Abies amabilis*) grows in cool, moist, coastal forests from northern California (41°N) to southwest Alaska (56°N). In the central and southern part of its range, Pacific silver fir is restricted to montane forests above 300 m and 1000 m, but north of 50°N it can be found from sea level to the subalpine zone (~1400 m) (Pojar and MacKinnon 1994). In coastal British Columbia, montane forests containing Pacific silver fir, western hemlock (*Tsuga heterophylla*) and yellow cedar (*Chamaecyparis nootkatensis*) are projected to be the major source of timber for the next 40-60 yr (Canadian Forest Service 1994).

Regeneration requirements of montane forests are significantly different from those of low elevation coastal forests (Klinka et al. 1992). Historically, montane forest regeneration has been slow to establish in clearcuts and has often exhibited growth stagnation (Herring and Etheridge 1976). These problems may relate to a short grow-

ing season, low soil and air temperatures, nutrient deficiency of montane soils, or vegetative competition (Grier et al. 1981, Arnott and Beese 1995, Prescott 1997).

Concerns over ecosystem integrity and diversity, and aesthetic values have resulted in a move away from clearcut systems in coastal montane forests of British Columbia (Arnott and Beese 1997). Few studies have examined regeneration mechanisms under alternative silviculture systems in montane forests, but it is apparent that the increased edge created by partial cutting systems has implications for growth of seedlings. Forest edges, whether created by natural or artificial disturbance, moderate microclimatic extremes and create interactions between light, temperature, moisture, and nutrient availability that can modify seedling growth (Chen and Franklin 1992; Chen et al. 1995; Gray and Spies 1996, 1997; Mitchell 2001). Forest edges, therefore, provide an opportunity to study regeneration responses to gradients of resource availability.

Pacific silver fir is highly shade tolerant, and regenerates abundantly under mature stands (Klinka et al. 1992). Following stand harvest, these

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naturally regenerated seedlings are referred to as advance regeneration. Several studies have examined the response of Pacific silver fir advance regeneration to microclimatic gradients created by forest edges. Leaf morphology and physiology change with gradients of light, temperature, and moisture created by clearcutting (Tucker et al. 1987), and growth of advance regeneration of Pacific silver fir and subalpine fir (*Abies lasiocarpa*) increases with irradiance (Klinka et al. 1992).

Pacific silver fir advance regeneration is often relied upon to reduce the risks and costs associated with plantation establishment on montane sites in British Columbia. While Pacific silver fir responds to release even after long periods of suppression (Klinka et al. 1992) and advance regeneration may outperform planted stock (Scagel et al. 1989), stocking and performance of advance regeneration is often a concern (Weetman and Vyse 1990, Green and Bernardy 1991). The shade-tolerant attributes that allow survival in the understory may be associated with prolonged acclimation periods and growth delays in advance regeneration following clearcutting (Herring and Etheridge 1976, Wagner 1980). Shade foliage morphology (Tucker et al. 1987) and shallow rooting habit (Herring and Etheridge 1976) may contribute to poor initial performance of advance regeneration. Nursery-grown container seedlings used for regeneration of montane sites differ from advance regeneration because they have higher foliar nitrogen concentrations and lower root:shoot ratios, and may respond differently to resource availability.

While many studies have examined growth of advance regeneration of Pacific silver fir, few have compared the performance of advance and planted seedlings. In this study, growth and physiology of advance regeneration were compared to planted seedlings of Pacific silver fir in three environments created by increasing distance from an edge of a montane clearcut on Vancouver Island. The objective was to quantify growth limitations and their underlying mechanisms in relation to light and nutrient availability.

## Methods

The study site is located on eastern Vancouver Island (46° 55' N, 125° 25' W, 800 m) in the Coastal Western Hemlock (CWH) mm2 biogeoclimatic variant (Meidinger and Pojar 1991). Site aspect

is N20°E on a 4° slope. The soil is a coarse loamy orthic humic podzol with a thick humus layer (14-40 cm). Mean air temperature on the site is 15.0°C in July and -1.0°C in January (Ross Benton, Pacific Forestry Centre, personal communication), and mean annual precipitation is > 1400 mm (Environment Canada, unpublished report, Campbell River Airport). Part of the old-growth stand on the site was clearcut in midsummer, 1989. Western hemlock, mountain hemlock, Pacific silver fir, and yellow cedar were the predominant overstorey species, averaging 28 m in height.

In April 1993, three treatment environments were established: clearcut, 60-65 m from the northeast facing stand edge; outside edge, 12-17 m from the stand edge; and inside edge, 5-10 m inside the stand edge. Three replicate plots, 25 m × 5 m were established with their long axes parallel to the northeast-facing stand edge in each environment. The three replicates in each environment compensated for variation in microtopography across the site.

Within each treatment environment, 50 seedlings of Pacific silver fir advance regeneration < 50 cm in height were randomly selected across all replicates and tagged. An age of 10 ± 2 yr was determined for a sample of six advance seedlings of similar size in each environment which confirmed they were present in the understory prior to harvest. Forty 1-yr-old container seedlings of Pacific silver fir (PSB 313B 1+0) were planted at 1 m × 1 m spacing in each replicate plot.

From 4 June–29 September 1993, air temperature, photosynthetically active radiation (PAR), and soil water potential were measured every 10 min in each environment, an hourly average calculated and recorded with an Omnidata International Easylogger 900. Air temperature was measured at one location in each environment with shaded thermocouples 30 cm above the soil surface. PAR was measured at ground level with four LI-COR 190SA quantum sensors in both the inside and outside edge environments, and two sensors in the clearcut. Soil water potential at -10 cm was measured with soil matric potential blocks at one location in each environment. Over the 5 yr study, the relative ranking of the three treatment environments by temperature, light, and moisture conditions was consistent.

Height of the planted and advance seedlings was measured at the time of establishment in April

1993, and in September 1994 and 1998. In September 1993, six seedlings of both planted and advance regeneration were excavated in each replicate and analyzed for root and shoot dry mass and specific leaf area (SLA = leaf area/leaf dry mass).

Owing to differences in initial size between planted and advance seedlings and among advance seedlings in the three environments (Figure 1), 5 yr height was analyzed using analysis of covariance, with initial height as the covariate. Mortality and browse resulted in uneven sample sizes within regeneration types, and sample sizes differed among replicates for advance seedlings, thus analysis of variance was carried out using a general linear model (SAS Institute Inc. 1988). Means were compared with Tukey's means test. Height relative growth rate (RGR) between 1994 and 1998 was also calculated ( $[\ln(\text{height '98}) - \ln(\text{height '94})]/4 \text{ yr}$ ) to examine growth rates independent of initial seedling size. A 4-yr period was chosen because planted seedlings were considered established after two growing seasons. RGR results were arcsine square root transformed and analyzed by ANOVA (SAS Institute Inc. 1988). The level of significance for all statistical analyses was  $P \leq 0.05$ .

Current-year needles were sampled for nitrogen concentration prior to planting in April 1993, in late September 1993 and 1994, and in November 1998. In September 1993, 60 seedlings per environment and regeneration type, 20 per replicate, were sampled and the foliage bulked by replicate and regeneration type. In 1994, 15 seedlings per replicate of each regeneration type were sampled individually. In 1998, five seedlings per replicate of each regeneration type were sampled. Foliage was oven dried at 80°C, ground to pass a 1 mm mesh sieve, and analyzed using the  $\text{H}_2\text{SO}_4$ - $\text{H}_2\text{O}_2$  digestion method and a Technicon autoanalyzer (Parkinson and Allen 1975). Foliar nutrient concentration data were arcsine square root transformed, and analyzed using analysis of variance (SAS Institute Inc. 1988).

Net photosynthesis (Pn) and transpiration (Et) rates were measured with a portable Leaf Chamber Analyser Type LCA-3 on 8 June, 19 July, 12 August, and 8 September 1993. Five or six randomly selected seedlings of each regeneration type in both the clearcut and outside edge environments were measured between 14:00 and 16:00 hr on the first three dates, and between 9:00 and 10:30

hr in September. Six seedlings in the inside edge environment were measured in July and September only. Xylem pressure potential was measured with a Model 3005 Plant Water Status Console immediately following the photosynthetic measurement for each seedling. Data were analyzed by ANOVA (SAS Institute Inc. 1988).

## Results

### Microclimate

The clearcut was exposed to 100% of full sun, and maximum daily PAR ranged between 400 and 2100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . PAR in the outside edge environment averaged  $84 \pm 1.6\%$  of that in the clearcut, and the maximum ranged from 350 to 1950  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . PAR in the inside edge environment averaged  $18 \pm 1.7\%$  of the clearcut, and maximum PAR was below 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on most days.

Mean daily air temperature at 30 cm in the clearcut ranged from 5 to 18°C. Temperatures in the inside and outside edge environments were generally 1-4°C lower than the clearcut. Maximum air temperatures were 30.5°C in the clearcut, and 26.5°C and 21.5°C on the outside and inside edges. Minimum temperatures averaged 0.5-3°C lower in the clearcut and outside edge environments than the inside edge environment. Soil water potentials in the three environments differed by  $\leq 0.005$  MPa until mid-September, when a period of low rainfall resulted in soil water potential dropping to a low of -0.047 MPa in the inside edge and -0.028 MPa in the clearcut. During the September dry period, soil water potential remained at -0.02 MPa in the outside edge environment.

### Survival, Growth, and Morphology

In 1998, 5 yr after establishment, survival of the advance seedlings selected for measurement was 70%, 98%, and 82% in the clearcut, outside edge, and inside edge environments. Five year survival of planted seedlings was 84%, 81%, and 86% on the clearcut, outside edge, and inside edge environments.

Analysis of covariance showed that the covariate, initial seedling height, had a significant ( $P=0.03$ ) effect on 5-yr height. Both environment and regeneration type significantly ( $P<0.001$ ) affected 1998 height, with the tallest seedlings in the clearcut, and the smallest in the inside edge (Figure 1). Planted seedlings were

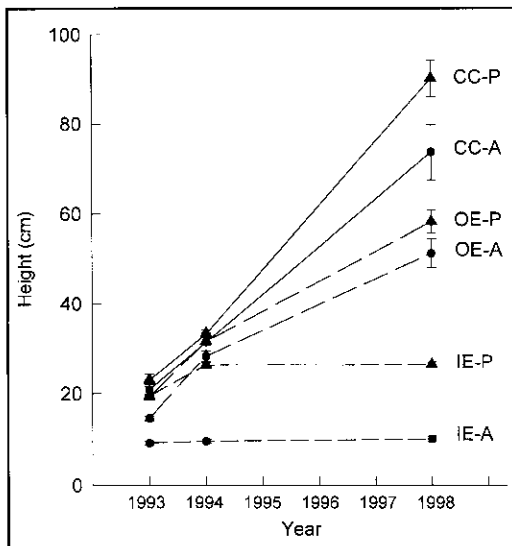


Figure 1. Mean ( $\pm$ S.E.) height of advance (A) and planted (P) regeneration of Pacific silver fir in clearcut (CC), outside edge (OE) and inside edge (IE) environments in year one, two, and five of the study

significantly taller than advance seedlings 5 yr after planting (Figure 1). The effect of replicate within environment was not significant in any of the analyses.

Analysis of 4-yr height RGR showed no significant difference between regeneration types, thus the effect of regeneration type on 1998 height was due to differences in initial size. Environment significantly affected height RGR ( $P < 0.001$ ). Height RGR was  $0.16 \pm 0.02$  in the clearcut,  $0.11 \pm 0.01$  in the outside edge, and  $-0.003 \pm 0.05$  in the inside edge environment. The negative RGR in the inside edge environment was due to the die-back of shoot tips in some seedlings.

Analysis of SLA in 1993 showed that planted seedlings altered foliar morphology in response to the different light environments in one growing season. SLA of both regeneration types was greatest in the edge environments and least in the clearcut. SLA of advance seedlings was  $88.5 \pm 2.5 \text{ cm}^2 \text{ g}^{-1}$ ,  $106.4 \pm 4.1 \text{ cm}^2 \text{ g}^{-1}$ , and  $101.2 \pm 4.6 \text{ cm}^2 \text{ g}^{-1}$  in the clearcut, outside, and inside edge environments. SLA of planted seedlings was  $81.8 \pm 9.7 \text{ cm}^2 \text{ g}^{-1}$ ,  $123.7 \pm 7.4 \text{ cm}^2 \text{ g}^{-1}$ , and  $152.7 \pm 9.7 \text{ cm}^2 \text{ g}^{-1}$  in the same environments. Dry needle weight of advance seedlings was greater than

planted seedlings ( $0.54 \pm 0.01 \text{ g}/100 \text{ leaves}$  vs.  $0.35 \pm 0.01 \text{ g}/100 \text{ leaves}$ ). Dry needle weight of both regeneration types was greater in the clearcut than in the outside or inside edge environments ( $0.55 \text{ g}/100 \text{ leaves}$ ,  $0.41 \text{ g}/100 \text{ leaves}$ , and  $0.38 \text{ g}/100 \text{ leaves}$ ).

In 1993, mean root:shoot ratio of advance seedlings was  $0.53 \pm 0.05$ , significantly greater than planted seedlings ( $0.32 \pm 0.01$ ) ( $P < 0.01$ ). Root:shoot ratio of planted seedlings did not differ among environments, and one growing season after planting still reflected conditions in the nursery rather than the planting site. By 1993, advance seedlings in the outside edge and clearcut had three growing seasons to respond to changed conditions created by overstory removal. Root:shoot ratio of advance seedlings differed among environments and was  $0.77 \pm 0.08$  in the inside edge,  $0.43 \pm 0.05$  on the outside edge, and  $0.41 \pm 0.03$  in the clearcut. No further biomass sampling was conducted after 1993 due to the difficulties of seedling excavation.

#### Foliar Nutrients

Prior to planting, foliar nitrogen concentration of five container seedlings averaged  $1.8 \pm 0.09\%$ . We assumed that prior to harvest, foliar nitrogen concentrations of advance regeneration were similar to inside edge seedlings in 1993, about  $0.8\%$ . In September 1993, one growing season after planting and four growing seasons after harvest, foliar nitrogen concentration of current-year needles had declined to less than  $1.2\%$  in all planted seedlings, but was greater than  $1.2\%$  in advance seedlings in the clearcut and outside edge (Figure 2). There was a significant interaction between environment and regeneration type in foliar nitrogen concentration ( $P < 0.05$ ). Foliar nitrogen concentration was greatest in advance seedlings in the high-light clearcut and outside edge environments, while nitrogen concentration in planted seedlings was highest in the inside edge (Figure 2).

In 1994, the environment  $\times$  regeneration type interaction was still significant in the analysis of nitrogen concentration of current-year needles ( $P < 0.0001$ ). Foliar nitrogen concentration was greatest in planted seedlings in the clearcut and in advance seedlings in the outside edge, but not significantly different between regeneration types in the inside edge (Figure 2). On average, nitro-

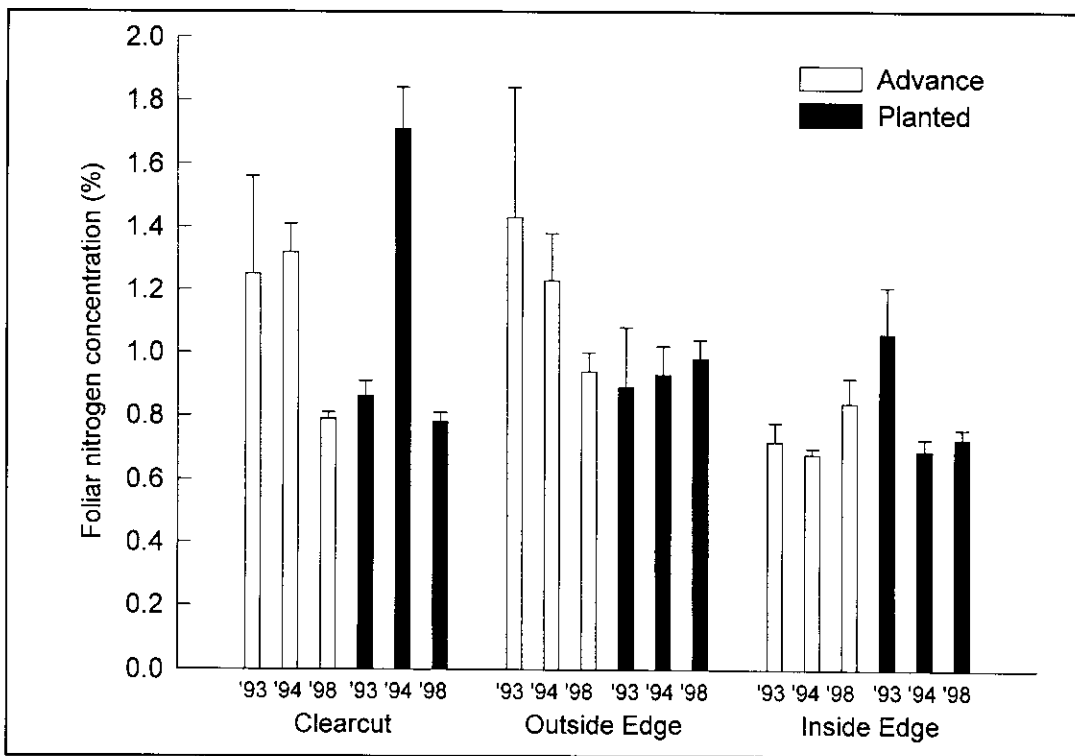


Figure 2. Mean ( $\pm$ S.E.) nitrogen concentration of current-year needles of advance and planted regeneration of Pacific silver fir in three environments in year one, two, and five of the study

gen concentrations were greatest in the clearcut and lowest in the inside edge seedlings.

In 1998, environment was the only significant effect in the analysis of nitrogen concentrations of current-year needles ( $P < 0.005$ ). Nitrogen concentrations were greatest in needles of seedlings from the outside edge, but were not significantly different between the clearcut or inside edge environments (Figure 2).

#### Net Photosynthesis and Water Relations

Over the first growing season Pn and Et of advance regeneration in the clearcut and outside edge environments were consistently higher than those of planted seedlings, except on 8 June which was a cool, overcast day (Table 1). Within each regeneration type, Pn and Et were not significantly different between the clearcut and outside edge environment, except on 8 September when the shade from the stand edge eclipsed the outside edge replicates by the time of measurement (Table 1). On average, however, Pn was greatest in the

clearcut. In the low light environment of the inside edge, Pn was very low in advance seedlings, and negative in planted seedlings (Table 1).

Xylem pressure potentials were not significantly different among environments or regeneration types on two of the four measurement dates (Table 1). On 19 July and 8 September, xylem pressure potentials were significantly lower in the clearcut seedlings compared to the outside edge seedlings ( $P < 0.05$ ). On 8 September, planted seedlings in the outside edge replicates had significantly lower xylem pressure potentials than advance seedlings (Table 1).

#### Discussion

Biological responses at forest edges are influenced not only by distance from the edge, but also by edge orientation, patch size and shape, and topographical features, among other variables (Chen and Franklin 1992). We assessed the interactions between climatic factors and seedling growth intensively at one site by studying how the edge

TABLE 1. Mean ( $\pm$  S.E.) rates of net photosynthesis (Pn— $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and transpiration (Et— $\text{mmol m}^{-2} \text{s}^{-1}$ ), and xylem pressure potential ( $\psi$ —MPa) of advance and planted Pacific silver fir seedlings in three environments on four days over the growing season. Means followed by the same superscripted letter are not significantly different within sampling date.

Date	Parameter	Advance			Planted		
		Clearcut	Outside Edge	Inside Edge	Clearcut	Outside Edge	Inside Edge
8 June	Pn (n=5)	3.71 (0.4) <sup>a</sup>	3.29 (0.4) <sup>a</sup>	-	4.56 (0.3) <sup>a</sup>	3.87 (0.2) <sup>a</sup>	-
	Et (n=5)	1.71 (0.1) <sup>b</sup>	1.56 (0.1) <sup>b</sup>	-	2.64 (0.3) <sup>a</sup>	2.27 (0.2) <sup>a</sup>	-
	$\psi$ (n=5)	-0.73 (0.0) <sup>a</sup>	-0.77 (0.1) <sup>a</sup>	-	-0.73 (0.1) <sup>a</sup>	-0.69 (0.1) <sup>a</sup>	-
19 July	Pn (n=6)	2.92 (0.4) <sup>a</sup>	2.71 (0.3) <sup>a</sup>	0.56 (0.3) <sup>a</sup>	1.04 (0.5) <sup>b</sup>	1.03 (0.1) <sup>b</sup>	-2.67 (0.9) <sup>c</sup>
	Et (n=6)	2.61 (0.2) <sup>a</sup>	2.46 (0.2) <sup>a</sup>	0.91 (0.1) <sup>b</sup>	1.05 (0.1) <sup>b</sup>	0.97 (0.0) <sup>b</sup>	1.27 (0.3) <sup>b</sup>
	$\psi$ (n=6)	-1.10 (0.0) <sup>a</sup>	-0.86 (0.1) <sup>b</sup>	-0.83 (n=2)	-1.07 (0.1) <sup>a</sup>	-0.70 (0.1) <sup>c</sup>	-0.77 (n=2)
12 Aug.	Pn (n=5)	4.19 (0.4) <sup>a</sup>	3.15 (0.5) <sup>a</sup>	-	1.82 (0.4) <sup>b</sup>	0.89 (0.4) <sup>b</sup>	-
	Et (n=5)	2.32 (0.2) <sup>a</sup>	1.74 (0.1) <sup>b</sup>	-	1.09 (0.1) <sup>b</sup>	1.43 (0.4) <sup>b</sup>	-
	$\psi$ (n=5)	-1.25 (0.1) <sup>a</sup>	-0.96 (0.1) <sup>a</sup>	-	-1.05 (0.1) <sup>a</sup>	-0.89 (0.1) <sup>a</sup>	-
8 Sept.	Pn (n=6)	3.47 (0.6) <sup>a</sup>	0.60 (0.6) <sup>b</sup>	0.07 (n=2)	2.56 (0.7) <sup>a</sup>	0.63 (0.4) <sup>b</sup>	-0.71 (n=2)
	Et (n=6)	3.57 (0.2) <sup>a</sup>	2.49 (0.2) <sup>b</sup>	0.61 (n=2)	1.77 (0.2) <sup>a</sup>	1.16 (0.2) <sup>c</sup>	0.77 (n=2)
	$\psi$ (n=6)	-1.34 (0.0) <sup>a</sup>	-1.00 (0.1) <sup>b</sup>	-0.81 (n=2)	-1.18 (0.1) <sup>ab</sup>	-0.68 (0.1) <sup>c</sup>	-0.60 (n=2)

environments modified photosynthesis, nitrogen acquisition, and growth processes over 5 yr.

A gradient of increasing light and increasing temperature existed from the inside edge environment to the outside edge and clearcut environments. Increased light and temperature can both result in greater rates of net photosynthesis and growth. The estimated light saturation point for Pacific silver fir is as low as  $650 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Mitchell and Arnott 1995) to  $\geq 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Teskey et al. 1984). Under full sun conditions, irradiance in both the clearcut and outside edge environments exceeded these limits, however, average irradiance in the inside edge environment was well below the light saturation point. Seedling growth in the inside edge environment was thus limited by light. We estimated that in the last 3 mo of the growing season the outside edge replicates received ~16% less light than the clearcut replicates due to afternoon shade created by the stand edge. Lower light may have limited net carbon gain by outside edge seedlings.

The optimal temperature for net photosynthesis of Pacific silver fir is  $15 \pm 1.5^\circ\text{C}$  throughout the year, but net photosynthesis is usually within 10% of maximum between  $10^\circ\text{C}$  and  $18^\circ\text{C}$  (Teskey et al. 1984). Mid-summer high temperature compensation points are greater than  $30^\circ\text{C}$  (Teskey et al. 1984). The relatively low optimal temperature for net photosynthesis in Pacific silver fir,

combined with temperatures among the three environments that varied by only a few degrees, indicates that temperature did not limit net photosynthesis in any of the environments.

Soil water deficits were minor, thus we did not consider moisture greatly limiting. The clearcut seedlings had the lowest water potentials on two occasions in late summer (Table 1), and stomatal limitations may have reduced photosynthesis on those days (Livingston and Black 1988). Although soil nutrients were not measured, we believe that higher daytime soil temperatures in the more exposed clearcut and outside edge environments led to greater rates of nitrogen mineralization (Lambers et al. 1998). In a site located 2 km from our study at a similar elevation, Prescott (1997) found *in-situ* rates of net nitrogen mineralization and concentrations of nitrate in forest floor and soil were greatest in a clearcut and least in the forest.

Differences in light availability among environments resulted in advance regeneration and planted trees converging in each environment with respect to physiology (foliar nitrogen concentration) (Figure 2) and relative growth rate. In low light, nutrient limited environments, plants generally have greater root:shoot ratios and decreased concentrations of soluble protein and Rubisco relative to plants in high light environments (Taiz and Zeiger 1998). Thus in the inside edge environment, advance regeneration, acclimated to low

light, maintained root:shoot ratios and foliar nitrogen concentrations while planted seedlings, acclimated to high light, allocated more biomass to roots and less nitrogen to leaves. In the clearcut, planted seedlings tended to stay the same while advance regeneration allocated more biomass to shoots and more nitrogen to leaves. As a result, relative growth rates converged in each environment for advance regeneration and planted trees.

Prior to release in 1989, we believe advance regeneration had high root:shoot ratios similar to the inside edge seedlings in 1993. Tucker et al. (1987) cite several studies of understory Pacific silver fir and grand fir (*Abies grandis*) trees with low root:shoot ratios. The combination of low nutrient availability and low irradiance on our study site, however, would lead to high initial root:shoot ratios. The high root:shoot ratio of inside edge seedlings was also because advance regeneration of Pacific silver fir grows horizontally as the lower stem is buried by organic matter. Guest (2001) excavated 70 advance seedlings of Pacific silver fir and found that seedlings < 50 cm tall had 10-70 cm of buried stem. The buried stems produce adventitious roots, therefore we included them in root biomass. Shoots of advance seedlings in the outside edge and clearcut environments were larger than inside edge seedlings, which reduced the proportional contribution of the buried stem to root:shoot ratios. Acclimation of root:shoot ratio was not observed in planted seedlings, because one growing season was not long enough to change biomass allocation significantly. In a nursery study, no differences were found among root:shoot ratios of 1-yr-old Pacific silver fir PSB 313B container seedlings grown for a second year in high and low light environments (Mitchell and Arnott 1995).

Four growing seasons after harvest, significant differences in leaf morphology were observed in advance regeneration among the three environments, with high SLA in the inside edge. Tucker et al. (1987) suggest that it may take 7 yr for Pacific silver fir to acclimate to overstory removal, therefore advance seedlings had acclimated fully by the end of our study. In seedlings planted in 1993, foliage expanded in the year of planting acclimated rapidly to differences in light among the three environments. Leverenz and Jarvis (1980) found that Sitka spruce (*Picea sitchensis*) could change foliar morphology in the first year if the

tree was exposed to the new light conditions just prior to bud burst.

In the first growing season after planting, foliar nitrogen concentrations in planted seedlings in all environments declined from their pre-planting condition. In 1993, nitrogen concentrations in planted seedlings were highest in the inside edge environment (Figure 2) because shoot expansion was limited. Low nitrogen concentrations in planted seedlings in the high light environments was supported by their chlorotic appearance, but chlorosis may have been due to photooxidation. Foliage of newly planted seedlings may suffer damage from ultra-violet light at high elevation (Tucker et al. 1987). In the second growing season, foliar nitrogen concentrations of planted seedlings in the clearcut increased, but those in the outside and inside edge did not increase (Figure 2). We surmise that seedlings planted in the clearcut experienced rapid root growth, allowing increased nitrogen uptake. Shoot growth may not have increased proportionally, allowing accumulation of nitrogen. Five years after planting, foliar nitrogen concentrations were greatest in seedlings in the outside edge, and lower in clearcut and inside edge seedlings (Figure 2). Although foliar nitrogen concentration was low in clearcut seedlings, leaf weight and shoot size were greater in these plants (Figure 1), thus total nitrogen content was greater.

Three and four growing seasons after overstory removal, advance seedlings in the clearcut and outside edge environments had higher foliar nitrogen concentrations than inside edge seedlings (Figure 2). Greater foliar nitrogen in warmer environments is explained by the expected increased rates of nitrogen mineralization. By 1998, patterns of foliar nitrogen concentration in advance seedlings in the three environments were similar to planted seedlings, and foliar nitrogen in the higher light environments had declined due to growth dilution.

By 1998, foliar nitrogen concentrations were not significantly different between planted and advance seedlings, but were significantly below the 1.15% critical nitrogen concentration defined by Powers (1983) in all environments. In the clearcut and inside edge environments, foliar nitrogen concentrations were also below the average of 0.93% nitrogen for 26 to 37-yr-old trees sampled in 19 stands in western Washington

(Radwan et al. 1989). Although Radwan et al. (1989) suggest that Pacific silver fir may have a high nitrogen utilization efficiency, the low foliar nitrogen concentrations measured on our sites likely limited growth, supporting the contention that growth check observed in natural and planted Pacific silver fir saplings growing in montane clearcuts is associated with nitrogen deficiency (Husted 1982, Arnott and Beese 1995).

Despite apparent nitrogen limitation, growth rates of both planted and advance seedlings were greatest in the clearcut, followed by outside and then inside edge environments. RGR of the two regeneration types were not significantly different, and the pairs of height growth curves for each environment diverged only slightly (Figure 1). Although height of planted seedlings was greater than advance seedlings in all environments, this effect was due to differences in initial size. Other studies examining the response of naturally regenerated Pacific silver fir seedlings and saplings to irradiance or exposure by overstory removal demonstrate that both establishment (Gray and Spies 1996, 1997) and growth (Tucker et al. 1987, Klinka et al. 1992, Gray and Spies 1996) are greater with increased light. While Pacific silver fir is shade tolerant (Teskey et al. 1984, Mitchell and Arnott 1995) and survives suppressed in the understorey for long periods of time (Klinka et al. 1992), when released by overstory removal Pacific silver fir increases height increment by the

third growing season (Herring and Etheridge 1976, Tucker et al. 1987).

The effect of a clearcut on the edge environment of a forest has been documented (Chen and Franklin 1992), and we have confirmed that the edge effect of a forest also extends into the cut block. With increasing use of silvicultural systems that create more edge, the proportion of tree seedlings influenced by forest edge will increase. In this study, the growth of Pacific silver fir seedlings 12-17 m from the edge was reduced relative to those 60-65 m from the forest edge. Growth was reduced in both advance regeneration and planted trees. Growth limitations were, in part, due to reduced light, and possibly to reduced nitrogen availability. Shade-induced growth limitations would increase under nutrient stress. Further study is required to document the depth of edge influence for a wider variety of sites and edge aspects.

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