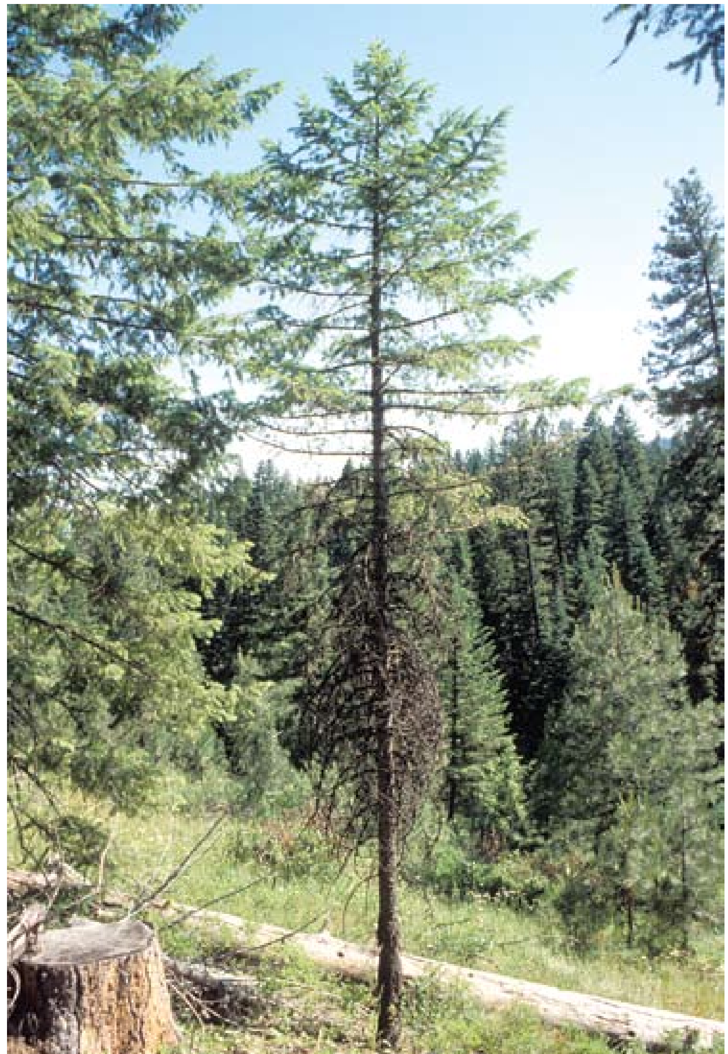
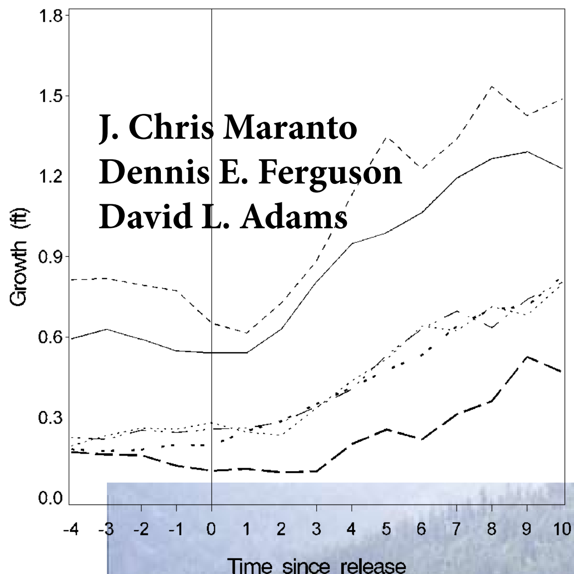
Response of Douglas-fir Advance Regeneration to Overstory Removal





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Abstract

A statistical model is presented that predicts periodic height growth for released *Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco advance regeneration in central Idaho. Individual tree and site variables were used to construct a model that predicts 5-year height growth for years 6 through 10 after release. Habitat type and height growth prior to release were the most important predictors of post-release height growth. Douglas-fir and subalpine fir habitat types had longer adjustment periods compared to grand fir habitat types, and damaged trees did not recover to growth rates as expressed in undamaged trees. Morphological differences between sun- and shade-developed foliage are also important aspects to successful release. Recommendations for releasing Douglas-fir advance regeneration are presented.

Keywords: *Pseudotsuga menziesii*, advance regeneration, release, suppression

Acknowledgments

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Introduction

Advance regeneration results from natural seeding in gaps between overstory trees and by the opportunistic competitive advantage of a species' ability to germinate and subsist in the understory. Many successful understory trees can live for many years and then grow rapidly in height once released. However, foresters have been reluctant to rely on advance regeneration as a component in the next rotation for several reasons. Uncertainty exists between utilizing advance regeneration because of unknown response to release, or replacing advance regeneration with subsequent natural or artificial regeneration. Another concern is the possibility that it may be a dysgenic practice, favoring genetically inferior individuals that can utilize the available growing site between overstory trees but are incapable of growing to site potential after release. Leaving advance regeneration may also accelerate a change in stand composition toward more shade-tolerant species, which may increase the frequency and severity of insect and disease perturbations.

The establishment of advance regeneration has been favored by suppression of wildfires in the western United States. Logging practices also played a significant role by harvesting seral ponderosa pine (*Pinus ponderosa* var. *scopulorum*), which resulted in a species shift to climax Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) and true firs (*Abies* spp.). Long fire-free intervals have allowed stands to become overly dense, resulting in insect and disease problems, as well as catastrophic wildfires (Oliver and others 1994). In central Idaho, Douglas-fir advance regeneration is often responsible for these increased densities. Reducing biomass levels is one way of improving forest health. To reduce forest biomass, managers must know which trees to leave or remove, and the potential growth response of trees following release from overstory competition.

The most important tree response variable to monitor following release is height growth. This is due to competition with shrubs, other tree regeneration, and the presence of large overstory trees. Advance regeneration that responds well to release can mature into crop trees, thus reducing harvest rotation intervals, as well as reducing or eliminating the need to stock the site with subsequent natural or artificial regeneration. This retrospective study is principally centered on tree and site characteristics associated with height growth response of Douglas-fir advance regeneration following overstory removal. Our hypothesis is that pre-release growth and other tree and site variables (for example, habitat type) are significant predictors of post-release height growth.

In an ancillary study, we explored morphology of sun- and shade-developed Douglas-fir needles. Most of the literature covering needle morphology has been directed at characterizing the difference between sun and shade plants, but less to shade-developed foliage suddenly exposed to sunlight. Studies of gymnosperms conducted by Tucker and Emmingham (1977) for residual western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and by Tucker and others (1987) for Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) have shown that differences between sun and shade needles are important in a tree's ability to respond to release.

Tucker and others (1987) found that production of sun foliage preceded any increase in lateral and terminal shoot growth on released Pacific silver fir. They found that foliage damage and leaf abscission were three times higher in the center of a clearcut than along the edge and that maximum height growth did not occur until at least seven growing seasons following release. Additionally, buds that were formed in the shade developed sun-related morphology as long as release occurred before bud burst and needle expansion. This developmental process contrasts with the knowledge of predetermined bud formation in which the previous year's climatic conditions determine height growth in the current year. We believe that a better understanding of the morphological differences in sun- and shade-developed needles will aid foresters in designing an operational framework for releasing advance regeneration.

Investigative Methods

Growth Response

Stands that were harvested with the overstory removal method were randomly selected from the Salmon, Payette, and Boise National Forests (NF) in central Idaho. Candidate stands must have been harvested at least 10 years prior to sampling, a time period which we considered adequate to allow trees to adjust and attain full height growth potential in the new environment. Potential sample stands had to be larger than 10 acres, had to have been released by a single harvest entry, and could not have been pre-commercially thinned following harvest. Additionally, stands impacted by defoliators were omitted for sampling. Although stands were harvested with the overstory removal method, there were often scattered overstory trees in the stands we sampled. Three growth periods of interest were defined as follows:

1. **Pre-release** growth period (5-year periodic height growth corresponding with year 4 prior to release through release year)
2. **Adjustment** growth period (5-year periodic height growth corresponding with years 1 through 5 after release)
3. **Post-release** growth period (5-year periodic height growth corresponding with years 6 through 10 after release)

We selected 5 years as the period of time assumed necessary for trees to adjust to the new environment, with the post-release period assumed to be when a tree had achieved its full height growth rate for the corresponding site. We used the post-release growth period to calibrate a statistical model that predicts periodic height growth corresponding with the post-release period.

Aerial photographs were obtained for each stand and transect lines connecting easily identifiable landmarks were superimposed within stand boundaries. Transect line distances were divided into equal segments in order to establish a representative distribution of up to 15 sample points across the stand with lines positioned at sufficient distances within each stand so that shading influences from adjacent stands could not have impacted trees along the transect line. At each interval point along the transect, a radius plot equal to 1/2 of the transect interval up to a distance of two chains (132 ft) was imposed. Beginning from the transect azimuth direction, and using the plot radius to circle clockwise, the first tree meeting the sample requirements was selected. If no qualifying tree was present, the field crew continued to subsequent interval points and repeated this procedure.

Sample trees had to be at least 5 years in age and less than 3.0 inches diameter-at-breast-height (dbh) at the time of release. Trees that had been damaged by logging were sampled only if injury occurred to the surface area of the bole. Trees that exhibited frost damage, root and stem rots, defoliation, dwarf mistletoe, broken or forked tops, and extreme stem distortions were not sampled because such trees would not reflect true growth potential. Additional restrictions were imposed to prevent tree selection near roads because openings created by road construction could influence height growth of neighboring trees.

To measure competition and site effects, each sample tree became (1) the center of a variable radius plot to record all trees having a dbh $\geq$ 3.0 inches and (2) the center for a 1/300-acre circular fixed plot to record all trees having a dbh < 3.0 inches. Recorded variables included species and height of other regeneration-size trees on the 1/300-acre plot, pre-harvest basal area (1991 sample data only), residual basal area, slope, aspect, hillslope position (ridge top, upper, mid, lower slope, bench/flat), and topographic horizontal configuration (convex, concave, uniform). The crown of each sample tree was subjectively categorized as to crown class relative to other trees and shrubs. Elevation and geographic location as represented by NF and NF Ranger District (RD) were recorded for the stand. Additionally, the area supporting each sample tree was classified by habitat type (Steele and others 1981). Habitat type is a land classification system based on expected climax vegetation (Daubenmire and Daubenmire 1968) and imparts relative productivity between different types.

Site index was not used in this study because we could not count on locating suitable site trees that had not been suppressed or retarded in height growth for any part of their life. Wykoff and Monserud (1988) showed that a diameter increment model using measured site index performed no better than a model that used habitat type, location, slope, aspect, and elevation to represent site effects.

Each sample tree was cut at ground line and 15 annual height growth increments were measured to the nearest 0.01 foot beginning 5 years before release and extending to 10 years after release. When the growth interval between annual branch whorls could not be accurately determined from examination of the exterior bole, the questionable stem area was cut into sections and split open to expose nodal scarring along the pith column. Techniques of stem dissection are described by Maranto (1993). Nodal scars in Douglas-fir are easily distinguishable and inspection also reveals terminal shoot damage attributed to western spruce budworm (*Choristoneura occidentalis* Freeman), as well as patterns in periodic growth suppression caused by Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough). If these internal characteristics were suspected and found in the segment corresponding to the pre-release period through the post-release period, the tree was not sampled and the survey crew would proceed to the next plot.

Other attributes that were recorded for each sample tree were height at release, total age, release age, and logging damage. Total tree age was determined by measuring annual growth rings at ground line using a 10-power magnifying lens. When growth rings became indiscernible, a disc was brought back to the office and the age determined with a laboratory microscope. Measurements of logging damage were recorded to determine the effect on height growth. The length and circumference of stem scarring was measured for each damaged sample tree. Logging damage was recorded as the percentage of total bole surface area that was scarred. Equations for calculating percent logging damage based on the proportion of scared surface area to total bole surface area are presented in table 1. We assumed that the tree bole had a conical form, which is a reasonable assumption for small trees.

When the harvest date was not known or records did not agree with field observations, callus tissue dating was performed on a sample of trees damaged by logging to ascertain actual harvest year. This required cutting small wedges from tree trunks in the area of scarring and counting the number of growth rings since scarring.

Because of the self-pruning nature of Douglas-fir crowns and the difficulty of reconstructing crowns that were released up to 30 years prior to sampling, we did not attempt to retrospectively establish the live crown ratio at time of release. Tesch and Korpela (1993) discuss the difficulty of determining crown ratio at the time of release in retrospective studies. They found that retrospectively sampled Douglas-fir regeneration had often self-pruned above the total height of the tree at the time of release.

Needle Morphology

Needle samples from four Douglas-fir trees that had developed in shade or full sunlight conditions were obtained from a study stand located on the Payette NF. Sun needles represented current-year foliage from trees that were open-grown. Shade needles represented current-year foliage from suppressed saplings that had a dense overstory of mature Douglas-fir and grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) trees. Microphotographs were developed at the Electron Microscopy Center at Washington State University, Pullman.

Data Analysis

During the first field sample season (1991), the pre-harvest basal area around each sample tree was reconstructed to measure the level of competition before harvest. The location of each sample tree became the center for a variable radius plot to assess overstory competition. Equations developed by Bones (1960) were

Table 1. Equations for calculating percent logging damage based on total bole surface area and scarred surface area.

$$Total_{SA} = \pi \times \left(\frac{Dia_{FF}}{2}\right) \times \sqrt{\left(\frac{Dia_{FF}}{2}\right)^2 + Ht^2}$$

$$Scarring_{SA} = \sum_{i=1} \left[(\pi \times Dia_{ScarHt_i}) \times \frac{Scar_{Width_i}}{\pi \times Dia_{ScarHt_i}} \right] \times Scar_{Length_i}$$

$$LoggingDamage = \frac{Scarring_{SA}}{Total_{SA}} \times 100$$

Where:
$Total_{SA}$ = Total surface area of bole in square inches
$Scarring_{SA}$ =Damaged surface area in square inches
Logging Damage = Percent of bole area affected by scarring
Dia_{FF} = Diameter at forest floor in inches
Ht = Tree height at release in inches
Dia_{ScarHt} = Bole diameter at lowest scar extremity
$Scar_{Width}$ = Scar width in inches
$Scar_{Length}$ = Scar length in inches
i = Measurement for each scar

Table 2. Habitat type groups, frequency of sample trees, and composition.

Group name[a]	Frequency	Comprised of:
PSME/CARU	83	PSME/CARU (77), PSME/CAGE (3), PSME/FEID(3)
PSME/SPBE	34	PSME/SPBE (34)
PSME/PHMA	34	PSME/PHMA (19), PSME/VAGL (8), PSME/ARCO (6), PSME/LIBO (1)
ABGR/ACGL	54	ABGR/ACGL (48), ABGR/VAGL (3), ABGR/SPBE (3)
ABGR/CLUN	21	ABGR/CLUN (20) ABGR/COOC (1)
ABLA/CAGE	11	ABLA/CAGE (9), ABLA/SPBE (2)

[a] Habitat type codes as defined by Steele and others (1981). The taxonomic abbreviations are the scientific names of species representing the climax overstory/understory plant community. Species codes for habitat type abbreviations are as follows:

ABGR	*Abies grandis*	COOC	*Coptis occidentalis*
ABLA	*Abies lasiocarpa*	FEID	*Festuca idahoensis*
ACGL	*Acer glabrum*	LIBO	*Linnaea borealis*
ARCO	*Arnica cordifolia*	PHMA	*Physocarpus malvaceus*
CAGE	*Carex geyeri*	PSME	*Pseudotsuga menziesii*
CARU	*Calamagrostis rubescens*	SPBE	*Spiraea betulifolia*
CLUN	*Clintonia uniflora*	VAGL	*Vaccinium globulare*

used to estimate dbh from stump diameter. Statistical tests were performed on the relationship between post-release height growth of advance regeneration and pre-release stand basal area (n=116). Results followed similar studies (Ferguson and Adams 1980; Helms and Standiford 1985), which demonstrated that the pre-harvest basal area was not a significant predictor of post-release height growth when other variables were included in the regression equation such as 5-year pre-release growth, habitat type, geographic location, elevation, slope, aspect, logging damage, and height at release. Consequently, reconstructing pre-harvest overstory density was discontinued.

Analysis of data after the 1991 field season revealed that the adjustment period was extending beyond 5 years after release for the dry and cold habitat types. Therefore, an additional 5 years of growth increments (years 11 through 15) were recorded on the remainder of sample trees specifically to address the extended adjustment period provided that the stand had been released 15 years prior to sampling. One hundred and eleven (111) trees out of a possible 162 trees in the Douglas-fir and subalpine fir habitat types were sampled in 1992 for the additional 5 years of height growth.

Due to the large number of habitat types existing in the study area and the limited sample representation of minor types, habitat types that had similar ecological characteristics were grouped following guidelines outlined by Steele and others (1981). Table 2 presents habitat type groups and their respective frequency. For the remainder of this document, habitat type refers to the most prevalent habitat type recorded for that group.

The MIXED procedure in SAS (SAS Institute 1996) was used to estimate model coefficients at the $P \leq 0.05$ level of significance. Independent variables were plotted against the post-release growth period and transformations were used to achieve homogeneity of error variance, to achieve normality of error effects, and to obtain additivity of effects (Kirk 1982). Residuals were plotted against predicted values to detect trends in the data that would suggest lack-of-fit. Trees within stands were considered independent samples due to the small sample size, systematic spacing of trees along transect lines, and recording of individual plot and tree attributes.

Results

Growth Response and Post-Release Height Growth Model

During the summers of 1991 and 1992, 237 trees were sampled in 38 stands. An average of 6.2 trees were sampled in each stand (median: 6; minimum: 2; maximum: 15). The dataset includes 136 sample trees from the Salmon NF, 80 sample trees from the Payette NF, and 21 trees from the Boise NF. Table 3 presents simple statistics for continuous variables and table 4 shows the frequency of sample trees by aspect and slope.

By using stem dissection techniques, we were not restricted to sampling stands that were only recently released. For this study, we sampled stands that were released as early as 1962 and as recently as 1977. Table 5 shows sampling frequency by release year.

Table 3. Data summaries for 237 released Douglas-fir advance regeneration.

Variable	Mean	Standard deviation	Range	Unit of measure
Stand elevation	60.3	12.4	40 to 81	100's of ft
Age at release	38.9	23.0	6 to 143	years
Height at release	8.3	6.9	0.5 to 35.9	ft
Other regeneration on fixed plot	1.2	1.8	0 to 12	frequency
Residual basal area	16.1	20.0	0 to 80	ft^2/acre
Logging damage (n=51)	12.1	8.6	2 to 38	percent of total surface area
Annual height increment before (-) and after (+) release:				
-4 years	0.36	0.35	0.02 to 1.75	ft
-3 years	0.37	0.35	0.02 to 1.70	ft
-2 years	0.37	0.34	0.02 to 1.80	ft
-1 year	0.36	0.31	0.02 to 1.80	ft
Release year	0.34	0.29	0.02 to 1.80	ft
+1 year	0.34	0.26	0.02 to 1.55	ft
+2 years	0.39	0.29	0.02 to 1.55	ft
+3 years	0.48	0.36	0.03 to 1.80	ft
+4 years	0.58	0.42	0.04 to 2.10	ft
+5 years	0.66	0.44	0.05 to 2.03	ft
+6 years	0.73	0.45	0.06 to 2.05	ft
+7 years	0.81	0.47	0.07 to 2.15	ft
+8 years	0.85	0.47	0.09 to 2.00	ft
+9 years	0.87	0.46	0.07 to 2.10	ft
+10 years	0.92	0.44	0.09 to 2.25	ft
5-year height growth:				
Pre-release	1.8	1.5	0.1 to 8.8	ft
Years 1 to 5 after release	2.4	1.6	0.3 to 7.6	ft
Years 6 to 10 after release	4.2	2.1	0.4 to 9.7	ft

Table 4. Number of sample trees by aspect and slope.

Aspect		Slope percent	
Group	Frequency	Group	Frequency
North	29	0 to 9	2
Northeast	36	10 to 19	39
East	36	20 to 29	49
Southeast	30	30 to 39	50
South	12	40 to 49	59
Southwest	13	50 to 59	18
West	43	60 to 69	12
Northwest	38	70 to 99	8

Table 5. Frequency of sample trees by release year.

Year of release	Frequency
1962	3
1965	7
1966	14
1967	24
1968	16
1969	5
1970	6
1971	9
1972	48
1973	25
1974	57
1975	14
1976	2
1977	7

Having a broad range of release years helped to average variations in weather.

To explain differences in height growth associated with local environmental conditions and individual tree characteristics, a statistical model was developed that predicts 5-year periodic height growth associated with years 6 through 10 after release. Height growth during this period was assumed to represent a tree having reached full growth rate based on tree and site variables.

Table 6. Coefficients for predicting height growth 6 through 10 years after release. The model form is $\hat{y} = ß_0 + \sum ß_i X_i$, where $\hat{y}$ is predicted height growth and $ß_i$ and X_i take on the values below.

	English $\hat{y}$ in ft			Metric $\hat{y}$ in m	
Variable (X_i)	**Coefficient ($ß_i$)**	**t value**	**Units**	**Coefficient ($ß_i$)**	**Units**
Constant	3.7291	3.69	$ß_0$	1.4138	$ß_0$
Boise NF	-1.6952	-5.36	categorical[a]	-0.5167	categorical[a]
Payette/Salmon NF	0.0	.	categorical	0.0	categorical
PSME/CARU	0.9550	2.33	categorical	0.2911	categorical
PSME/SPBE	1.2240	2.66	categorical	0.3731	categorical
PSME/PHMA	-0.1200	-0.26	categorical	-0.0366	categorical
ABGR/ACGL	1.2524	2.47	categorical	0.3817	categorical
ABGR/CLUN	1.3880	2.47	categorical	0.4231	categorical
ABLA/CAGE	0.0	.	categorical	0.0	categorical
Elevation	-0.0468	-3.94	ft/100	-0.0468	m/100
sqrt(Slope)	2.2905	3.50	percent/100	0.6981	percent/100
cos(Aspect) x sqrt(Slope)	-0.6579	-2.61	aspect in radians	-0.2005	aspect in radians
sin(Aspect) x sqrt(Slope)	-0.2195	-1.21	aspect in radians	-0.0669	aspect in radians
(Basal Area)^2	-0.0002	-2.20	ft^2/acre	-0.0010	m^2/ha
Logging Damage	-0.0477	-3.57	percent	-0.0145	percent
5-year Pre-release Height Growth	0.6024	6.45	ft	0.6024	m
ln(Height at Release)	0.7654	3.36	ft	0.2333	m
Height at Release	-0.1142	-4.06	ft	-0.1142	m
PROC MIXED fit statistics:					
AIC		806.3		268.1	

[a] Categorical variable. X_i = 1 for trees in this category; otherwise X_i = 0.

Table 6 presents the form of the model with coefficients in English and metric units. Significant independent site variables include habitat type, geographic location, elevation, residual basal area, and the interaction of slope and aspect, with significant tree variables represented by pre-release growth, height at release, and percent logging damage.

Habitat type is a significant predictor of post-release height growth. Habitat effects are incorporated by estimating independent intercepts for individual habitat type groups (table 2). Figure 1 shows the average growth curve for undamaged released regeneration by habitat type group. The general shape of the curves after release follows a sigmoid pattern. The leveling-off of the curve for the grand fir habitat types is attributed to trees having reached full growth rate, whereas this potential apparently has not been reached on the Douglas-fir and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) habitat types likely due to drier or colder site conditions that both types represent.

Figure 2 shows the 5-year periodic height growth by habitat type group for each of the three growth periods. The relationships displayed generally conform to the relative growth rates one would expect knowing the potential productivity of each habitat type. Except for the subalpine fir habitat group (only 11 trees), each habitat type group shows substantial growth increases during the adjustment period.

Geographic location as represented by NF is significant and likely serves as a surrogate for climatic differences within the study area that are not related to growth differences within a habitat type. Wykoff (1990) used similar geographic groupings to account for variable growth performance within habitat types. Released Douglas-fir grows significantly slower on the Boise NF than on the Payette or Salmon NFs.

Increasing elevation is negatively correlated with post-release height growth. Additionally, the interaction of slope and aspect is a significant predictor of post-release growth when used in the model as proposed by Stage (1976). This transformation indicates that the greatest growth rate occurs in the southwest quadrant at an aspect of 198 degrees. Additionally, released regeneration grows slower as residual stand basal area increases.

Pre-release growth is a strong predictor of post-release growth. Greater height growth prior to release results in greater height growth after release. Figure 3 shows a strong linear relationship between predicted post-release height growth and pre-release height growth.

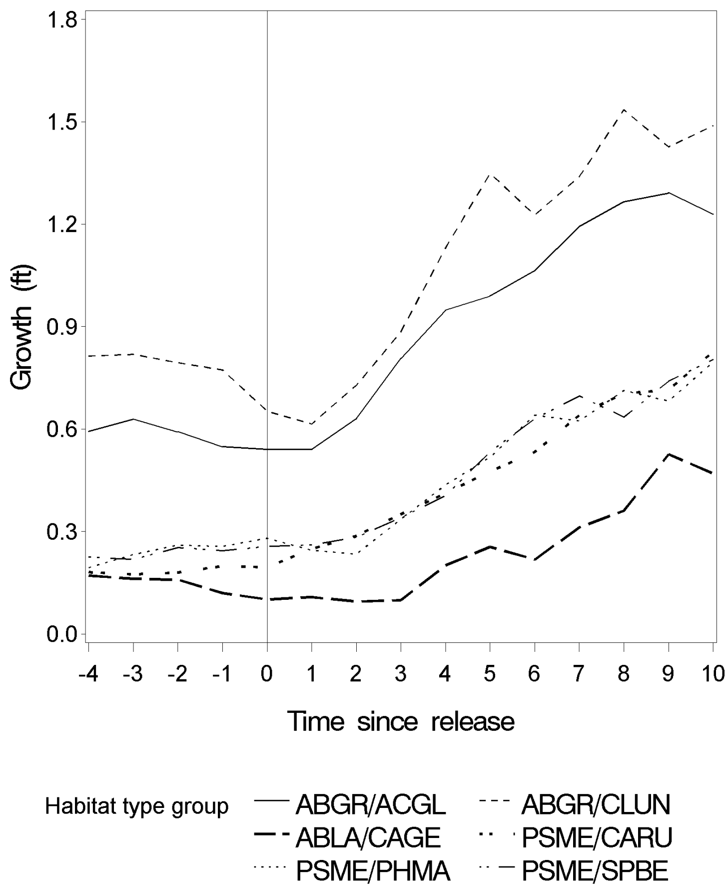

Figure 1. Average annual height growth curves for 186 undamaged trees by habitat type group.

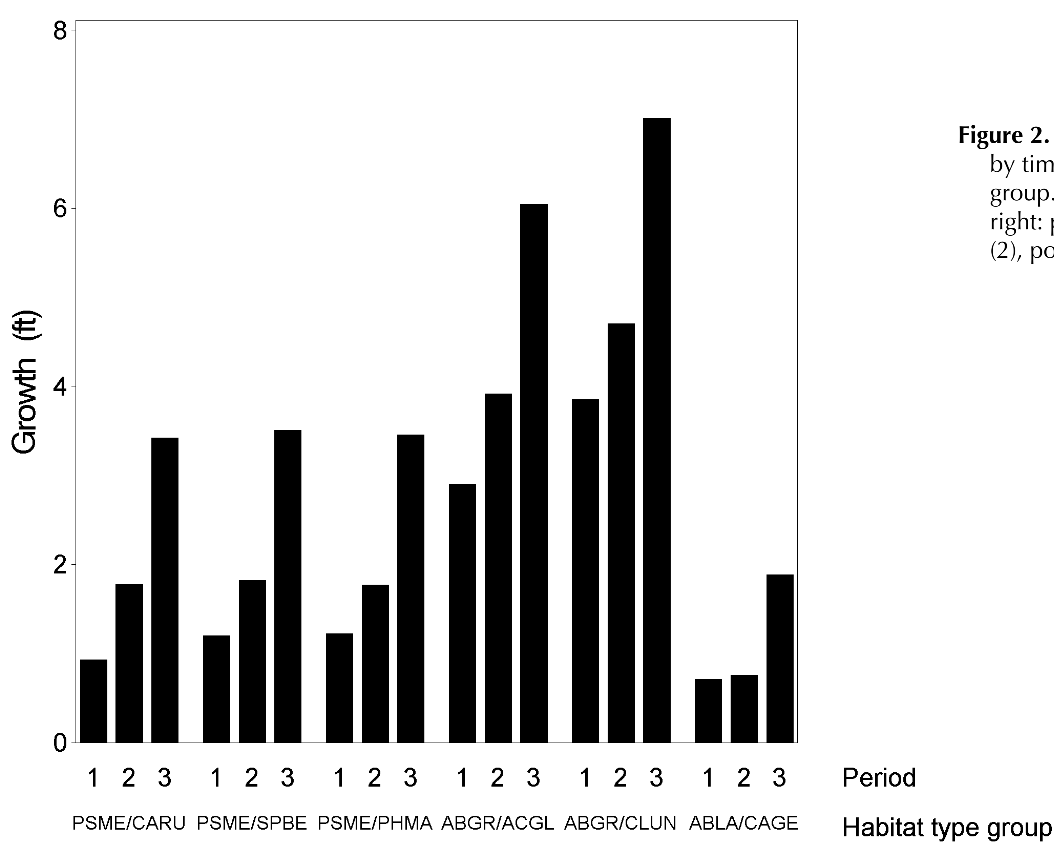

Figure 2. Five-year height growth by time period and habitat type group. Growth period left to right: pre-release (1), adjustment (2), post-release (3).

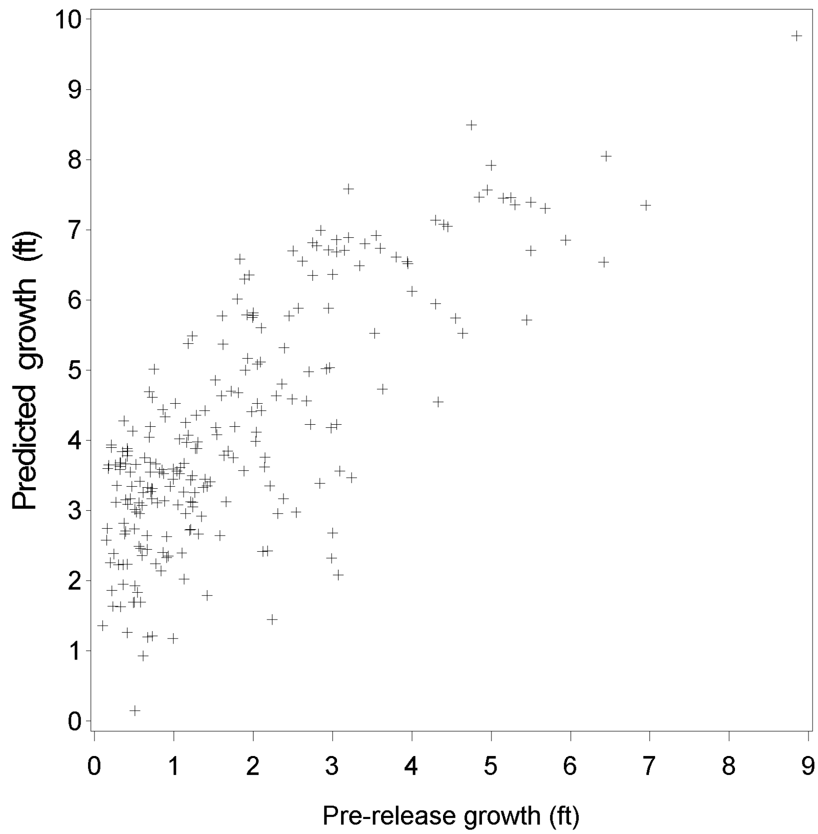

Figure 3. Predicted height growth years 6 through 10 after release versus pre-release height growth.

Table 7. Frequency of sample trees by percent damage in total stem area.

Damage percent	Frequency
0	186
1 to 9	25
10 to 19	16
20 to 29	7
30 to 38	3

Height at release is a significant predictor of post-release height growth. The shorter (≤5 ft at release) and taller (≥20 ft at release) trees do not grow as well as trees between these height classes (Maranto 1993). Age is not a significant variable but is roughly correlated with release heights because taller trees are generally older.

Table 7 presents damage percentages of total stem area by frequency, and figure 4 shows the mean growth of damaged versus undamaged trees. Trees sustaining logging damage are substantially hampered in height growth and do not appear capable of rebounding to the growth rates found in undamaged trees.

Figure 5 shows the average growth curve for undamaged trees by habitat types where the additional 5 years in post-release data were collected (years 11 through 15). These data show that on Douglas-fir habitat types, Douglas-fir advance regeneration may require approximately 10 years to fully adjust to release before full growth potential is expressed and may require an even longer period for Douglas-fir trees on subalpine fir habitat types.

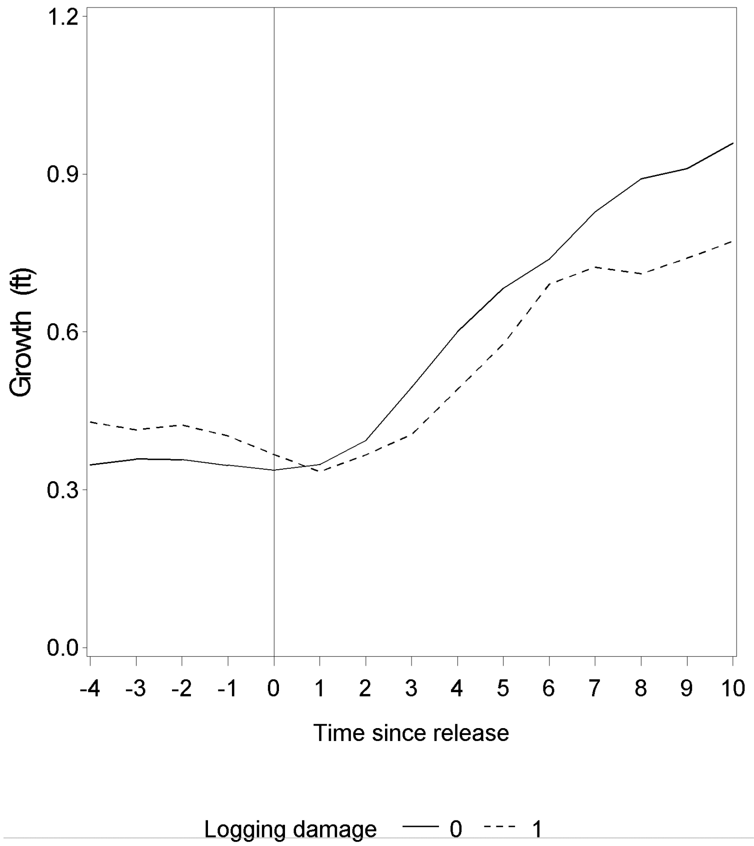

Figure 4. Average annual height growth for damaged (1) and undamaged (0) trees.

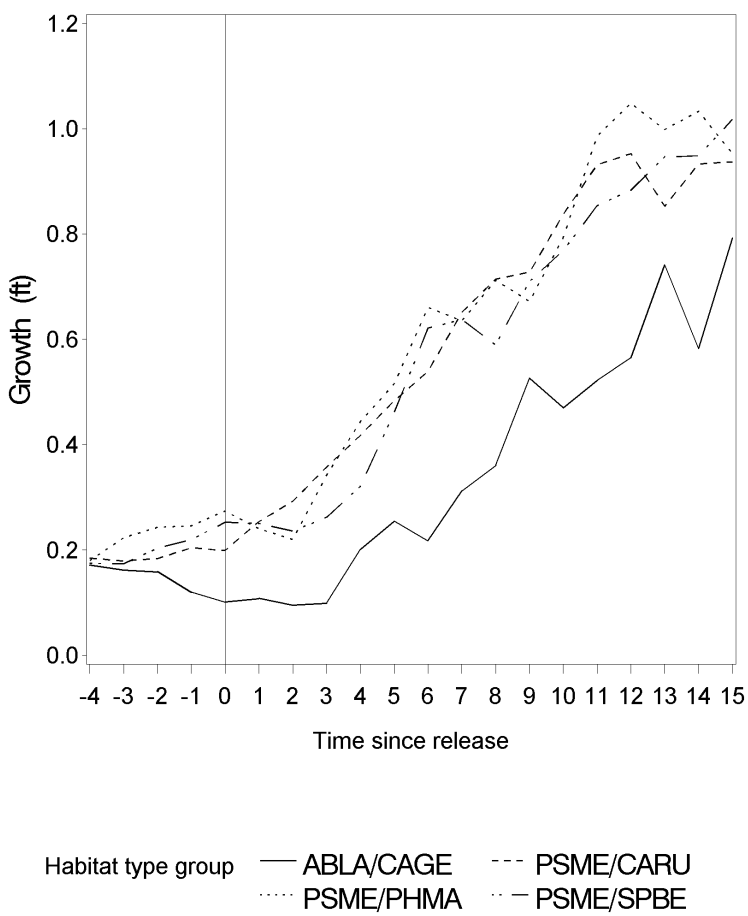

Figure 5. Average annual height growth for 111 undamaged trees on Douglas-fir and subalpine fir habitat types where annual growth was measured an additional 5 years beyond the post-release period of this study.

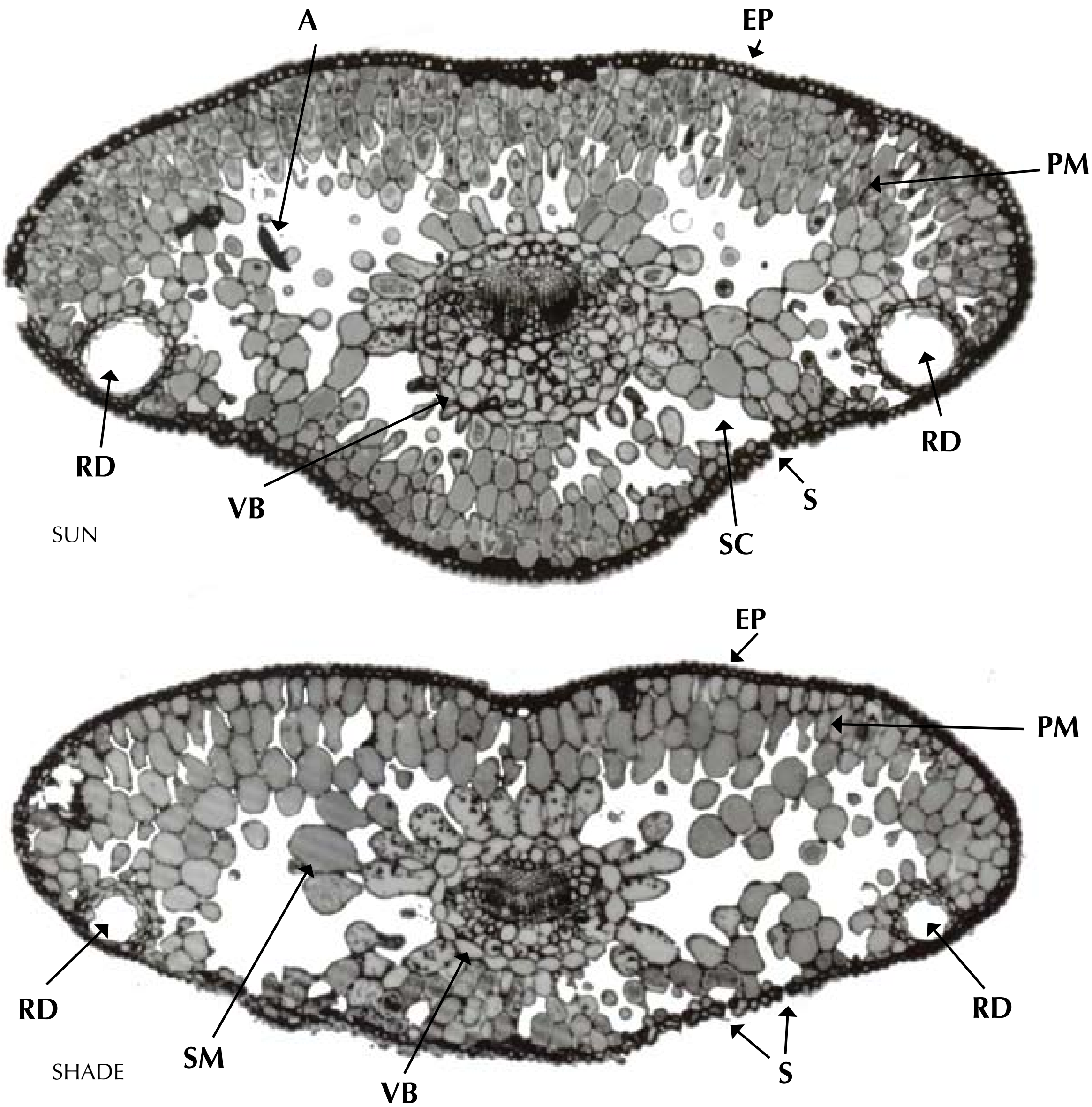

Figure 6. Microphotograph transections of sun-grown (SUN) and shade-grown (SHADE) Douglas-fir needles illustrating the epidermis (EP), palisade mesophyll (PM), spongy mesophyll (SM), vascular bundle (VB), resin ducts (RD), stoma (S), sub-stomatal chamber (SC), and astrosclereid (A).

Needle Morphology

No objective study of Douglas-fir needle morphology is attempted here; however, an introduction to this topic is presented. Figure 6 presents microphotographs characteristic of sun- and shade-grown needles sampled from the study area. These microphotographs illustrate that differences exist between sun- and shade-grown needles, which is consistent with results of other studies (Tucker and Emmingham 1977, Tucker and others 1987). Sun needles are characterized by smaller and denser palisade mesophyll cells composing numerous layers across the upper area of the needle. Additionally, needle thickness is noticeably greater along the vertical plane. In contrast, shade needles have larger but fewer palisade mesophyll cells. Other microphotographs presented in figure 7 show that stomata density is greater for sun needles. The higher stomata density, along with a heavy protective wax layer, aids in reducing evapotranspiration. In contrast, shade needles have fewer stomata and a thinner wax covering.

Discussion and Management Applications

The combination of tree characteristics, site conditions, and degree of physiological shock induced by the sudden change in a tree's environment appears to

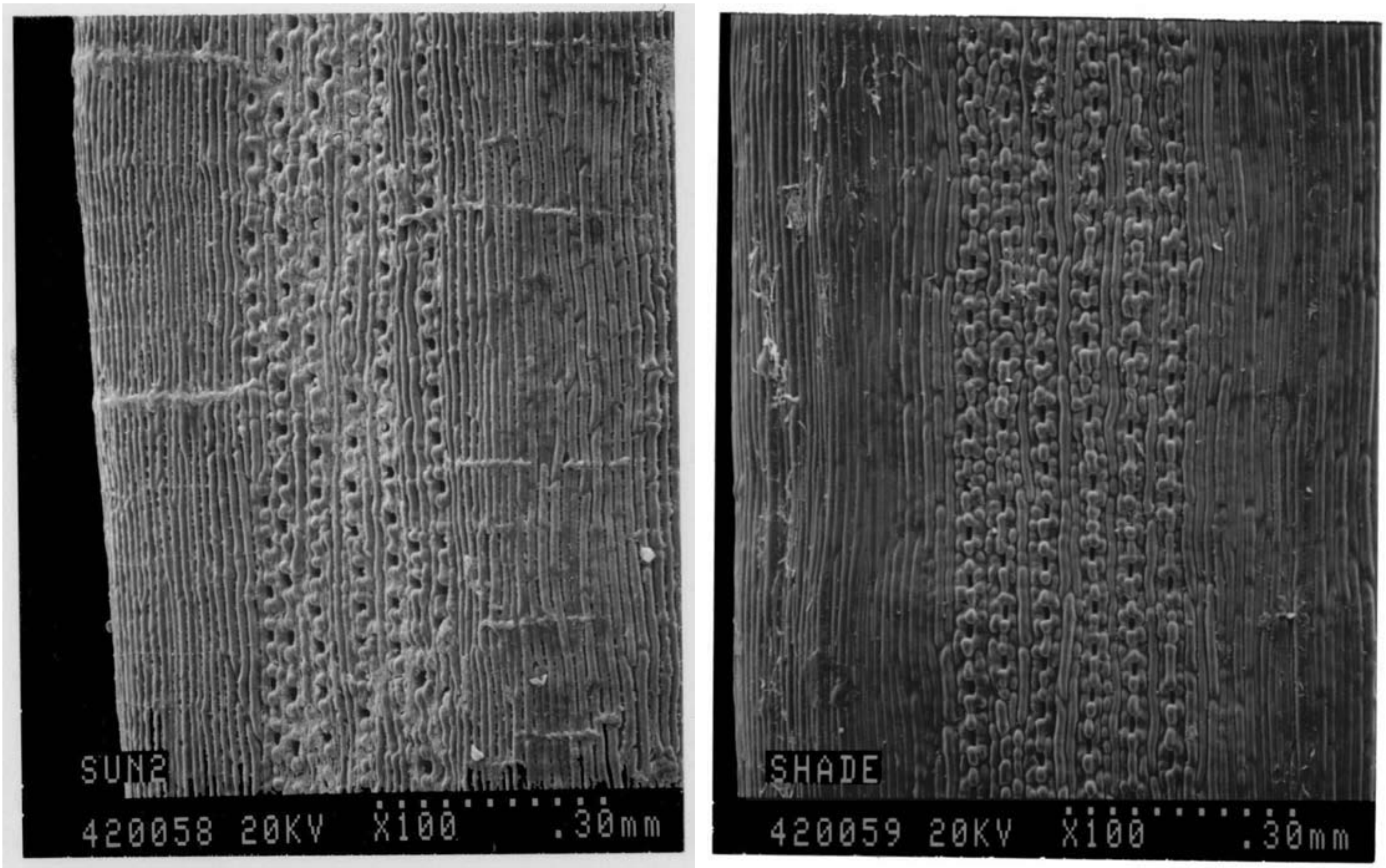

Figure 7. Stomata bands in sun-developed (designated "SUN2") and in shade-developed needles ("SHADE"). Magnification is 100 times, and the point scale at the bottom of the figure represents a distance of 0.30 mm between the first and last points.

be associated with Douglas-fir response to release and the time interval required to reach full growth rate. The statistical model developed in this retrospective study has identified important variables related to the release of Douglas-fir advance regeneration in central Idaho. The study demonstrated that Douglas-fir is a vigorous and adaptable species in response to release. Essentially all sample trees responded to release and grew at rates substantially greater than pre-release growth rates. Relative height growth in the post-release period (years 6 through 10) ranged from 82 to 268 percent more growth than the pre-release period. The mean average across all habitat types for the post-release period was 161 percent.

Habitat type is a good predictor of height growth following release. The cool and moist habitat types produced faster and greater release responses than the warm and dry and the cold and wet habitat types. Grand fir habitat types typify cool and moist environments. In our study, released trees adjusted quickly to the new environment by accelerating in height growth and reaching maximum growth levels more quickly than trees on harsh sites. Responses occurred 2 years following release on grand fir habitat types, whereas response to release on the warm and dry Douglas-fir habitat types was 2 and mostly 3 years and on the wet and cold subalpine fir habitat types, response was observed 4 years following release.

One notable observation concerned the varying adjustment periods observed between habitat type groups. The growth response curve leveled off within the 10-year study period on grand fir habitat types but continued to increase on Douglas-fir and subalpine fir habitat types. The extended growth series collected on the Douglas-fir and subalpine fir habitat types in 1992 (111 out of 162 trees) suggested an adjustment period of approximately 10 years for Douglas-fir habitat types and a period longer than 15 years for subalpine fir habitat types before full growth potential is realized.

The need for a longer adjustment period on harsher sites has also been documented by others investigating response of coastal Douglas-fir (var. *menziesii*) to thinning (Harrington and Reukema 1983) and release (Tesch and Korpela 1993) and for released lodgepole pine (*Pinus contorta* var. *latifolia*) (Murphy and others 1999). This delay is probably due to some needle desiccation caused by increased radiation levels, increased carbohydrate allocation to development of new needles and expansion of rooting systems, carbohydrate allocation within functional needles to produce additional mesophyll cells, and a constrained hydraulic architecture between crown and root networks. Recently, Renninger and others (2007) reported that for Douglas-fir in western Oregon, photosynthetic capacity had initially constrained release until leaf area had sufficiently increased, then, release was limited by imbalances in a tree's hydraulic architecture.

The significance of geographic location, as represented by National Forest, likely accounts for variability in climatic conditions, soils, and other conditions/characteristics that habitat type alone could not fully explain.

The interaction of aspect and slope was modeled as suggested by Stage (1976). Trees on steeper slopes had higher post-release growth rates than trees on more gentle slopes, possibly suggesting association to frost zones and/or insufficient sample representation on excessively steep slopes. The optimum aspect for post-release height growth was 198 degrees, which may seem counter-intuitive. This optimal aspect is perhaps due to the longer growing season relative to northerly aspects. Rehfeldt (1989) demonstrated substantial genetic diversity existing in central Idaho Douglas-fir along elevational and geographic clines where natural selection for cold hardiness was apparent in severe environments and natural selection for high growth potential was demonstrated in mild environments. Ferguson and Carlson (1993) determined an optimum aspect of 223 degrees in developing equations predicting heights of subsequent Douglas-fir regeneration in the northern Rocky Mountains.

Among the tree variables in the model, pre-release height growth was the best predictor of post-release growth. Trees growing better before release grow better after release. Many studies have reported a strong positive correlation between pre-release and post-release height growth (Bassman and others 1992; Ferguson and Adams 1980; Helms and Standiford 1985; Kneeshaw and others 2002; Murphy and others 1999; Seidel 1985; Tesch and Korpela 1993; Tesch and others 1993). Pre-release height growth likely integrates the effects of site conditions and suppression, indicating the degree of suppression. We found that it was not necessary to measure pre-release overstory competition (stand basal area) because the effects of the overstory are reflected in pre-release height growth.

The shortest (≤5 ft) and tallest (≥20 ft) trees at release had lower post-release height growth compared to other trees. Man and Greenway (2004) found the same response existed for released white spruce (*Picea glauca*) regeneration, and Murphy and others (1999) found that taller released lodgepole pine did not grow as well as shorter trees. Kneeshaw and others (2002) reported that height growth shock was greater in larger seedlings for Douglas-fir and lodgepole pine. Ruel and others (2000) discussed the possibility that smaller trees may be less stressed at a given light level than taller trees, so they may be able to respond to release more rapidly.

Twenty-two percent (51 of 237) of the sample trees exhibited logging damage to the bole, but our sample did not include trees with broken tops or disfigured boles. Therefore, on a stand basis, logging damage was higher than 22 percent. Ten years after release, the damaged trees were still not growing as well as the undamaged trees and did not show any indication that they were capable of rebounding to rates demonstrated by undamaged trees. Ferguson and Adams (1980) reported that logging damage decreased growth response of released grand fir regeneration. Murphy and others (1999) reported that logging damage decreased growth of released lodgepole pine regeneration and damaged trees did not recover to grow as rapidly as undamaged trees.

Foliage and Bud Physiology

This study shows that Douglas-fir is a vigorous and adaptable species once released. Essentially all trees responded to release and grew at rates substantially greater than their pre-release growth rates. This ability to acclimate is perhaps related to the photosynthetic mechanism.

Douglas-fir is considered to have an intermediate shade tolerance, requiring at least 10 to 30 percent of full sunlight irradiance to survive (Spurr and Barnes 1980). Three of the five remaining conifer species occurring in the study area—grand fir, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir—are considered shade-tolerant, with lodgepole pine and ponderosa pine considered very intolerant and intolerant, respectively. Boardman (1977) states that a species' adaptability to a light regime is inherited and results from genetic adaptation to the light environment existing in the native habitat. Additionally, Kozlowski and others (1991) suggest that photoinhibition—injury to the photosynthetic mechanism by bright light—follows a gradient that is a function of a species' shade-tolerance. Therefore, within the tolerance spectrum, species having greater shade-tolerance may have a greater disposition for photoinhibition if a tree growing in the understory is subsequently exposed to full sunlight.

Understory trees typically have flat needle shapes. The flatness of shade needles aids in the capture of sunlight when the tree is suppressed, but potentially exposes the needle to sun scald when the tree is released. The higher density of palisade mesophyll cells found in sun needles protects the chlorophyll from intense radiation (Tucker and Emmingham 1977).

Because of the short growing season in the temperate zone, current-year height growth is generally determined by climatic conditions of the previous year (Kozlowski 1971). Therefore, released regeneration would not be expected to respond in height growth until at least the second year after release. This response lag is illustrated on the characteristically cool and moist grand fir habitat types. Conversely, Douglas-fir trees on Douglas-fir and subalpine fir habitat types that typify harsher environments generally did not show a corresponding response to release until 3 and 4 years after release, respectively.

Managing Release

Since the potential for photoinhibition appears to increase with the degree of a species tolerance to shade, we hypothesize that Douglas-fir resistance to photoinhibition is quite strong, and the results of this study may support this hypothesis. Within any specific habitat type, greater productivity will be found if management decisions focus on seral species. Releasing Douglas-fir on its climax habitat types, especially on the dryer end where it is at its environmental extreme, will result in longer adjustment periods. Cool and moist habitat types provide better microenvironments for release because adequate moisture will help mitigate the harsher environmental conditions created by the overstory removal.

Where managing Douglas-fir advance regeneration, especially on its climax habitat types, several considerations are offered. Unlike buds, tree foliage is not predetermined (Tucker and others 1987). Therefore, implementing a release after crown expansion will subject all current year needles to sunscald because the new foliage will have developed shade characteristics. However, if overstory removal occurs during the dormant season, morphological characteristics in the new foliage can be characterized as sun needles. Having a single-year compliment of sun-developed needles on a shade-developed crown should reduce physiological shock to the tree. Additionally, to decrease potentially adverse impacts, issues of release timing on harsher sites can be mitigated by two-stage harvesting. For example, Tucker and Emmingham (1977) recommend allowing 3 to 5 years for development of sun needles before complete overstory removal.

Other studies, mostly of hemlock and true firs, which have a greater shade tolerance, have found that releasing trees that have a crown ratio of at least 40 to 50 percent resulted in more rapid growth after release (Seidel 1980; Seidel 1985; Helms and Standiford 1985; Oliver 1986). Respective to releasing the more shade-intolerant Douglas-fir, crown ratios of at least 40 percent should be sufficient. Especially important, candidate release trees should have conical crowns, not umbrella-shaped crowns that indicate very slow pre-release height growth (Tucker and others 1987) and extreme competition.

An early indication of response to release is height growth the second year following overstory removal on grand fir habitat types and the third or fourth year on Douglas-fir and subalpine fir habitat types, respectively. Growth displayed during this period reflects the effects of environmental changes induced by overstory removal and the potential to develop into a crop tree.

The Appendix summarizes recommendations for releasing Douglas-fir regeneration. The information can be used by foresters to design inventories, assess post-release growth potential, and implement post-release stand improvement treatments.

Conclusions

This study shows that Douglas-fir can adapt to environmental changes and does not become stagnant by maintaining pre-release growth rates once released. The statistical model is biologically sound, provides high predictive ability, and provides insight for foresters on the important variables related to release of advance regeneration. The rate of growth during the pre-release period is believed to reflect the degree of suppression that is imparted collectively by tree and site conditions. Greater height growth prior to release should result in greater growth after release. Following release, full growth rate is reached within 5 years on grand fir habitat types, extends to 10 years on Douglas-fir habitat types, and extends longer than 15 years on subalpine fir habitat types. Foresters can reduce adverse physiological changes by managing the harvest release window to coincide with tree dormancy or by applying two-stage harvesting. Morphological characteristics are important factors in releasing advance regeneration and an understanding of the photosynthetic mechanism and processes can aid foresters in securing successful release.

The statistical model should give reliable predictions of growth when used within the range of data used in its construction. Professional judgment is important when interpreting predictions and greater attention is warranted when the model is extrapolated outside the calibration data set.

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Appendix: Summary of Recommendations for Releasing Douglas-fir Regeneration

Habitat type:

Habitat type represents the best site variable for predicting the release of Douglas-fir regeneration. Cool and wet environments associated with grand fir habitat types should result in trees reaching full growth rate within 5 years. Longer adjustment periods are associated with dry and hot Douglas-fir habitat types and cold and wet subalpine fir habitat types.

Pre-release growth:

Pre-release height growth is the best tree variable for predicting the release of Douglas-fir regeneration. Annual growth increments indicate the degree of suppression and provide a forecast of future growth that should follow once the overstory is removed. Greater growth prior to release will result in greater growth after release.

Overstory trees:

Two-stage overstory removal can be used to gradually release regeneration, especially on harsh sites or where trees are severely suppressed. Retaining some overstory trees will reduce sunscald on released trees while they develop sun needles; however, retaining overstory trees can reduce height growth after trees have adjusted to release. Because pre-release height growth indicates the degree of suppression, there is no need to record pre-release overstory density.

Damage:

Avoid damaging desirable regeneration during logging. Damaged trees are not expected to have growth rates comparable to undamaged trees.

Crown ratio and shape:

Other research shows the importance of adequate crown ratios for released regeneration. Retaining trees having crown ratios of 40 percent and greater, and no lower than 30 percent is preferable. The degree of suppression can be judged by crown shape. Trees having well-defined conical crowns are more likely to have vigorous growth after overstory removal. Conversely, trees having round or umbrella-shaped crowns are severely suppressed, have a higher probability of mortality following release, and will adjust slowly to release.

Needle morphology:

To help mitigate effects of physiological shock, implement the overstory removal during the dormant season so that shade-developed crowns will develop a current year compliment of sun-developed needles.

Early indicators of response:

The first indicator of response to release will be sunscald and abscission of newly exposed needles. The second indicator will be height increment the second or subsequent year after release. The second year's height growth is the earliest indicator on grand fir habitat types, while 3 or 4 years are needed on Douglas-fir and subalpine fir habitat types.

Adjustment period and subsequent stand improvement treatments:

The adjustment period for released Douglas-fir regeneration to reach full growth rate is approximately 5 years for grand fir habitat types, 10 years for Douglas-fir, and 15 years or more for subalpine fir habitat types. Stand improvement treatments should be delayed until the second half of the adjustment period to give released trees an opportunity to adjust to release. If stands need thinning after release, favor trees having greater post-release height increments and remove trees that have sustained logging damage.

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