Western white pine growth relative to forest openings

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Abstract: In northern Rocky Mountains moist forests, timber harvesting, fire exclusion, and an introduced stem disease have contributed to the decline in western white pine (*Pinus monticola* Dougl. ex D. Don) abundance (from 90% to 10% of the area). Relations between canopy openings (0.1–15 ha) and western white pine growth within different physical settings are identified. Objectives include relating western white pine seedling and sapling growth to canopy opening attributes (defined by fisheye photography), identifying western white pine competitive thresholds (occupancy, competitive advantage, free-to-grow status) in relation to opening size, and relating canopy opening attributes to overstory density descriptors. We sampled 620 western white pine plus competing trees, canopy opening characteristics, landscape position, and overstory density descriptors. Analysis included log-linear and polynomial regression. Visible sky (canopy opening) and tree age were significantly related to growth of selected pines. Radiation explained less variation in growth than canopy opening. Thresholds for western white pine to occupy a site (>23% canopy opening), gain a competitive advantage (>50% canopy opening), and achieve free-to-grow status (>92% canopy opening) over western hemlock were developed. There was a significant although weak ($R^2 < 0.12$) relation between canopy opening and overstory density descriptors.

Résumé : Dans les forêts humides de la partie nord des montagnes Rocheuses, la récolte de bois, l'exclusion du feu et une maladie du tronc introduite ont contribué à diminuer l'abondance du pin blanc de l'Ouest (*Pinus monticola* Douglas ex D. Don) qui est passée de 90 à 10 % de la superficie. Les relations entre les ouvertures dans la canopée (0,1 à 15 ha) et la croissance du pin blanc de l'Ouest dans différents environnements physiques sont identifiées. Les objectifs consistaient à relier la croissance des semis et des jeunes tiges de pin blanc de l'Ouest aux attributs des ouvertures dans la canopée tels que définis par la photographie hémisphérique, à identifier les seuils de compétitivité du pin blanc de l'Ouest (occupation, avantage compétitif, croissance libre non concurrentielle) en relation avec la dimension de l'ouverture, et à relier les attributs des ouvertures dans la canopée aux descripteurs de densité de la strate dominante. Les auteurs ont échantillonné 620 pins blancs de l'Ouest ainsi que les arbres compétiteurs, les caractéristiques des ouvertures dans la canopée, la position dans le paysage et les descripteurs de densité de la strate dominante. La visibilité du ciel (ouverture dans la canopée) et l'âge des arbres étaient significativement reliés à la croissance des pins sélectionnés. Le rayonnement expliquait une moins grande portion de la variation de la croissance que l'ouverture de la canopée. Les seuils pour que le pin blanc de l'Ouest occupe un site (ouverture de la canopée > 23 %), obtienne un avantage compétitif (ouverture de la canopée > 50 %), et atteigne une croissance libre non concurrentielle (ouverture de la canopée > 92 %) avec la pruche de l'Ouest ont été développés. Il y avait une relation significative bien que faible ($R^2 < 0{,}12$) entre l'ouverture de la canopée et les descripteurs de densité de l'étage dominant.

[Traduit par la Rédaction]

Introduction

In the northern Rocky Mountains, timber harvesting, fire exclusion, and white pine blister rust (*Cronartium ribicola* J.C. Fisch.) (introduced stem disease) have all contributed to the decline in western white pine (*Pinus monticola* Dougl. ex D. Don) abundance. Historically (circa 1934), this species occupied 90% of the moist forests (which cover approximately 10.5 million ha) in the northern Rocky Mountains (Fig. 1A). In contrast, this species now (circa 1996) occurs on less than 10% of the area within these extensive and economically important forests (Hann et al. 1997) (Fig. 1B).

Western white pine plays many roles in maintaining the integrity and resiliency of moist forests and is considered a keystone species (Neuenschwander et al. 1999; Fins et al. 2001). It is a long-lived (300–400 years) early- to mid-seral species that is well suited to the northern Rocky Mountain moist forest environment. It has high genetic plasticity (Rehfeldt 1994), grows across a wide range of environmental gradients (elevation 780–1560 m above sea level (a.s.l.) on all aspects) (Graham 1990), sheds snow and ice readily (Minore 1979), and is resistant to many endemic diseases and insects (Harvey 1994). To successfully restore moist forests, an increase in western white pine abundance, both locally and across landscapes, has been suggested (Hann et al. 1997; Neuenschwander et al. 1999; Fins et al. 2001).

Traditionally, the clear-cut silvicultural method was preferred for regenerating and growing western white pine be-

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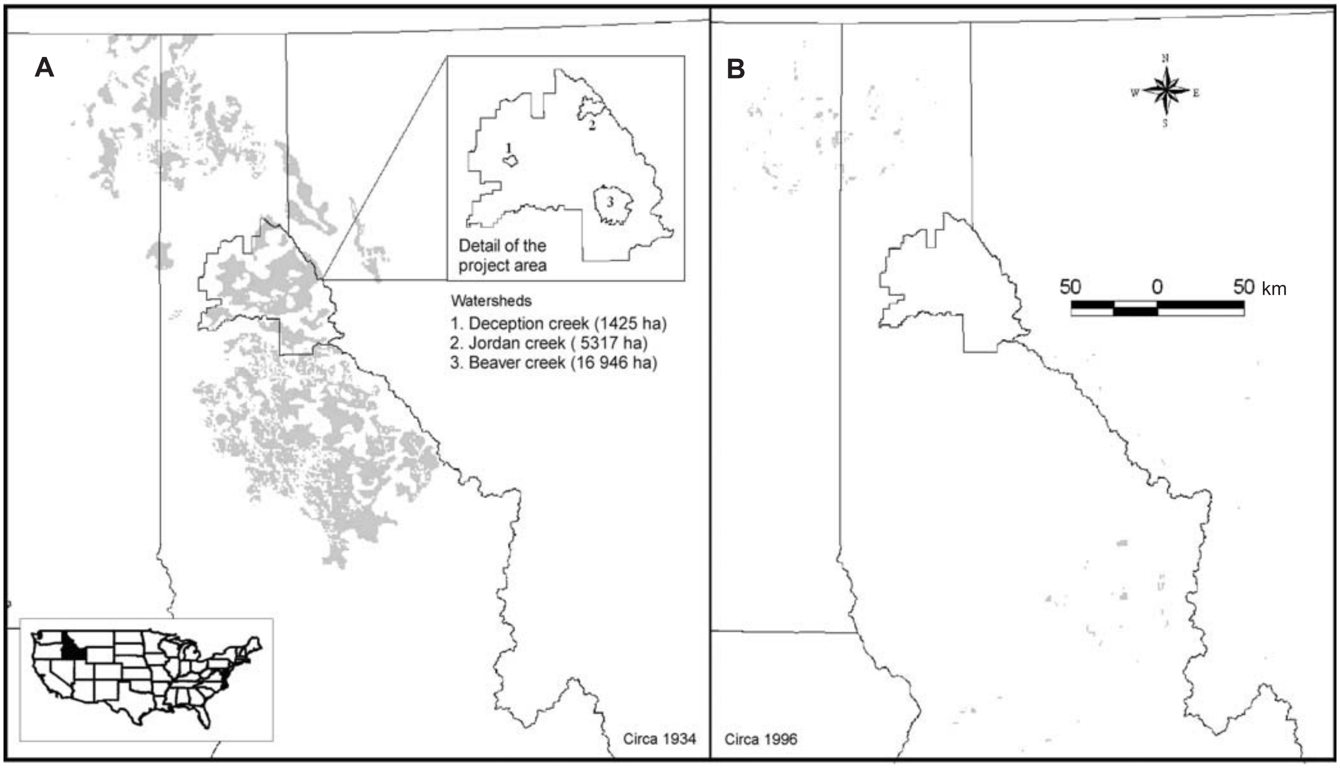
Fig. 1. Circa 1934 (A) and circa 1996 (B) western white pine abundance in the northern Rocky Mountains, United States (Hann et al. 1997). Within the Coeur d'Alene River basin (A), three watersheds (Deception, Jordan, and Beaver Creek) were selected as the study area.



cause it facilitated blister rust control, was easy to apply at a low cost, and allowed the pine to thrive (Graham et al. 1983). The widespread use of this method helped shape the view that western white pine requires full sunlight to survive and develop, even though Haig et al. (1941) noted that western white pine up to 30 years of age performed better with some canopy protection. Although clearcuts, when applied appropriately, favor western white pine development, their future application will most likely be limited because many forest stakeholders consider clearcuts unsightly, harmful to fish and wildlife habitat, and detrimental to water quality and quantity (Kimmins 1999). Moreover, clearcuts and their associated roads do not necessarily reflect historical disturbances (e.g., residual standing and down biomass is present after windstorms, fire, ice damage) or landscape patterns (landscape patterns are usually not blocked) (Harris 1984; Bliss 2000).

Individually and in combination, group and reserve tree shelterwoods and individual and group selection silvicultural systems can mimic environments created by many fine-scale disturbances (e.g., mixed severity lethal and nonlethal surface fires; endemic insects and diseases; wind and snow). The wide variety of regeneration and stand tending methods inherent in these systems can create a plethora of stand structures and compositions. These silvicultural systems can include small canopy gaps while also maintaining a range of forest cover potentially critical for wildlife and fish. Currently, these systems are often not used in developing vegetative cohorts containing western white pine; however, if the abundance of western white pine is to be increased without exclusively using clearcuts, further knowledge is needed about how vegetation, particularly trees, grow and compete in different environments. In particular, knowledge about how western white pine establishes and develops within a range of canopy opening sizes is needed so that silvicultural methods can be designed to facilitate western white pine development in the face of aggressive competition from the more tolerant grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Minore 1979).

In many forest ecosystems, forest canopy openings are primarily controlled by edaphic or site factors. However, in the moist forests of the northern Rocky Mountain, openings are predominantly created by disturbances, including disease, fire, ice, wind, snow, harvesting, and insects that kill individuals, groups of trees, and even entire stands. These disturbances in turn provide conditions that allow new or residual understory plant communities to develop (e.g., Minckler and Woerhelde 1965; Oliver and Larson 1990). Opening characteristics (size, orientation, location, age, overstory species) shape the operational environment defined by light, heat, moisture, nutrients, root biomass, seed availability, and other biophysical factors (e.g., Spomer 1973; Grubb 1977). These factors in turn influence the composition, regeneration, competition, and growth of trees and other ground-level vegetation (e.g., Canham 1989; Carter and Klinka 1992).

There is a wealth of information on forest canopy gaps and structures. However, most studies in coniferous forests emphasize the vegetative or environmental responses to increases in canopy opening size (e.g., Spies and Franklin 1989; Coates 2000). Although these studies provide valuable information on how vegetation responds to changes in canopy structure, they most often do not provide information on how canopy openings influence the relations among species, when one species has a competitive advantage over another or is free to grow with minimal competition from other plant species; or define the canopy structure or opening size for optimum tree development. By not readily providing this information, these studies have limited benefits in forest management applications.

However, some studies have linked forest canopy structure (opening size) to the growth, density, or regeneration success of seedlings and saplings, making them informative in both ecological and management contexts (Coates 2000; Myers et al. 2000). For example, Coates (2000) quantified conifer seedling growth (5-year height, diameter growth increment, height growth increment) as a function of increasing opening size for several tree species in Canadian moist forests. At approximately 1000 m^2, he observed an asymptote in height and diameter increment and 5-year height for several tree species. Myers et al. (2000) studied the regeneration and development of Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.) seedlings in gaps. Concentrating only on Brazil nut, they found that seedlings could not readily regenerate or survive until canopy gaps were greater than 95 m^2 in size. In both these studies, they identified some thresholds on survival and optimal growth but were unable to (Coates 2000) or did not attempt to identify competitive opening size thresholds that favor one species over another.

To add to our ecological understanding of how western white pine interacts with other tree species and to provide useful information applicable to moist forest management this study had four objectives: (1) to relate western white pine seedling and sapling characteristics to canopy opening attributes (size and light quantity) as defined by fisheye photography; (2) to determine whether relations in tree and canopy opening attributes vary with physical setting (aspect, landscape position); (3) to identify competitive thresholds (occupancy, competitive advantage, free-to-grow status) among western white pine, grand fir, and western hemlock defined by canopy opening attributes; and (4) to relate canopy opening attributes to various overstory and opening size descriptors (e.g., basal area per hectare, tree density, size of opening) often used in stand characterizations.

Materials and methods

Study area

Three watersheds with diverse environments (Deception, 1405 ha; Jordan, 5317 ha; and Beaver, 16 946 ha) were selected within the Coeur d'Alene River basin (Fig. 1A). Young western white pine were growing in these watersheds over a range of forest openings (size, orientation), aspects, and elevations, providing substantial variation useful for understanding western white pine dynamics within canopy openings. All openings supported abundant, extensive white pine forests historically and continue to currently have an abundance of western white pine (Jain et al. 2002).

Sampling design

To ensure that we sampled western white pine growing in a variety of conditions within each watershed, we used a 24-cell sampling matrix representing aspect, elevation, opening size, and location within an opening. Four aspects (northeastern, southeastern, southwestern, and northwestern) and two elevations (<1000 m and >1000 m a.s.l.) were used to ensure data were collected across different topographic settings. Within each aspect and elevation combination, three canopy opening sizes were identified: under canopy (<0.1 ha), small openings (0.1–1 ha), and large openings (1–15 ha). We split each watershed into four sections and used information from vegetation maps, elevation, and aspect to ensure that selected openings were randomly distributed throughout the watersheds and fit within the matrix. Within each opening, we randomly selected two western white pine trees, 0.3–7.0 m in height: one pine near the opening edge, defined as under the drip line of overstory tree crowns (direction of edge randomly selected); and another located in the opening center. This was repeated four times, resulting in our locating 576 trees (192 per watershed). We discovered early in our sampling that we were observing pines growing only in obvious places and that by solely concentrating on these areas we were introducing nonsampling error (bias) into our study (Lohr 1999). To avoid this nonsampling error we subsequently evaluated all possible settings in which western white pine could occur but also conform to our sampling matrix (e.g., very closed canopy conditions, steep southern slopes). If multiple pines were found growing within these unlikely settings, we randomly selected additional trees, resulting in a total of 620 western white pines being sampled (44 additional trees).

Data collection

Data were collected on (1) the selected western white pine and competing trees that occurred within a 0.6-m radius (microsite plot) of the selected western white pine; (2) canopy opening characteristics as defined by fisheye photography; (3) the landscape position where the selected tree occurred; and (4) overstory and opening size density descriptors. Data collected on each selected western white pine were the following: height, basal diameter (2.5 cm above root collar), last 5-year height growth, crown length, crown ratio, average crown diameter (two widths were taken perpendicular to each other and than averaged), and tree age (ring count at the stem base after it was cut). All pines sampled were at least 4 years old; from this period, seedlings are considered established and able to survive for a long time (Haig et al. 1941). Mean annual height and diameter increment were calculated from height, basal stem diameter, and age. The dominant species occurring on the 0.6-m-radius circular plot were western white pine, grand fir, and western hemlock; however, other species in the plot were also quantified. These competing trees were classified by species in 30-cm height-classes, and the number of trees in each class was recorded. Age and height were determined on one tree randomly selected from each species and height-class. Mean annual increment (MAI) in height was calculated from height and tree age.

Fisheye photography was used to describe the opening characteristics created by overstory tree canopies surrounding the selected western white pine. These photographs were taken at a height equal to that of the mid-crown of the selected western white pine (over the stump) and were used with HemiView software (version 2.1, Delta-T Devices, Ltd., Burwell, Cambs., UK) to quantify the light reaching the selected pine. The values we calculated included the proportion of the sky (referred to as visible sky) that was not obstructed by the overstory trees (Gates 1980; Rich 1989, 1990); the yearly below-canopy radiation (total, diffuse, and direct) ($\text{mol}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) reaching the selected pine (Moon and Spencer 1942; Evans and Coombe 1959; Gates 1980; Pearcy 1989; Rich 1989, 1990); and the number of sunflecks and total sunfleck duration for 21 June 1999 (summer solstice) reaching the selected pine (Pearcy and Yang 1996).

To place the canopy opening and the selected western white pine within the context of the physical setting, we described the proportion of the landscape visible sky, which is the view of the sky from the landscape position without obstructions from adjacent topography or other surface features (Dozier and Frew 1990); the yearly landscape radiation (direct, diffuse, total) reaching the setting; and the slope and aspect of the setting. Yearly landscape radiation is calculated on the basis of the landscape visible sky, the sun position, and the reduction of solar radiation caused by the atmosphere and surface orientation (slope and aspect) (Pearcy 1989; Rich 1989; Fu and Rich 1999). We used a digital elevation model and Solar Analyst software (version 1.0, Helios Environmental Modeling Institute, Lawrence, Kansas) to obtain these landscape radiation estimates.

Overstory descriptors, opening size, and opening orientation were quantified and related to the opening attributes defined by fisheye photography. Overstory descriptors included the density, height, and species of the overstory trees surrounding each sample tree. Overstory trees greater than 15-cm diameter at breast height were quantified by using a probability proportional to tree size plot centered on the selected pine defined by an 8 $\text{m}^2\cdot\text{ha}^{-1}$ angle gauge (basal area factor). Height, species, and diameter were estimated for each overstory tree. From these measurements, basal area per hectare, trees per hectare, and stand density index were calculated and summarized for the overstory characteristics surrounding each selected pine by using the Forest Vegetation Simulator (FVS version 6.21, Forest Service Management Center, Natural Resource Research Center, Fort Collins, Colorado, http://www.fs.fed.us/fmsc/index.php). The direction of the longest axis of the opening defined the opening orientation (Runkle 1992). Length and width of the opening were measured to calculate opening size: area = (pi × length × width)/4 (Runkle 1992).

Analysis

Relating canopy opening characteristics to western white pine

We conducted exploratory analysis of individual and combinations of predictor (visible sky) and response variables (height, diameter, crown ratio) to check for outliers and data behavior (dimension and linearity) (Myers 1990; Johnson 1998). Normality was evaluated by using univariate and multivariate normal probability plots and histograms. Correlations among variables were investigated within each class by using scatter plots, correlation coefficients, principal component analysis, and factor analysis.

Proportion of visible sky was transformed using the arcsine of the square root (referred to as visible sky). We classified opening orientation into four classes (0°–45°, 46°–90°, 91°–135°, and 136°–180°) and aspect into eight classes (0°–45°, 46°–90°, 91°–135°, 136°–180°, 181°–225°, 226°–270°, 271°–315°, and 316°–360°). Three new variables (factor scores) resulted from the factor analysis, each representing a set of correlated variables that occurred among the western white pine descriptors and the microsite and landscape predictor variables. (The ad hoc method used in this analysis was to create a variable by taking the average of the standardized variables that were identified as being correlated in the factor analysis (Johnson 1998).) The western white pine growth factor score contained a linear combination of mean annual diameter increment, 5-year height, and MAI. A microsite factor score contained a linear combination of visible sky, sunfleck duration, and number of sunflecks; and the macrosite factor score contained a linear combination of hours of radiation reaching a landscape position and proportion of visible landscape sky.

Because of the curvilinear nature of the data, log-linear regression ($\ln y = x$) rather than linear regression was used to analyze the data. A step-wise procedure related the predictor variable (x) to each western white pine descriptor variable (y). We added predictor variables individually (to avoid using correlated predictor variables) or in combination (when predictor variables were not correlated) to determine their relationship to the descriptor. The results from the partial sum of squares F tests, adjusted coefficient of determination (adjusted R^2), and behavior of residual errors were used to evaluate the goodness of fit of the models. We used log-linear regression to relate density descriptors (basal area per hectare, stand density index, trees per hectare, size of opening) taken around each selected western white pine to visible sky.

Identifying competitive threshold

For western white pine to occupy a site there has to be seed, and the site needs to favor germination and seedling establishment. Because we measured trees 4 years old or older, we assumed that the trees occurring in the microsite plot were established and occupied that site. However, stochastic events could create conditions favorable for ideal but anomalous seedling germination or mortality. Therefore, we conservatively determined the occupancy thresholds by estimating the probability of three or more western white pines (including the sample tree), grand firs, or western hemlocks occurring alone or in combination on the microsite plot as a function of visible sky. The respective number of western white pine, grand fir, or western hemlock trees occurring on the microsite plot weighted the logistic regressions.

The competitive advantage and free-to-grow thresholds were defined as western white pine MAI minus grand fir or western hemlock MAI and referred to as relative MAI. This value was predicted as a function of visible sky defined by fisheye photography. The visible sky percentage at which relative MAI became positive was defined as the competitive advantage threshold, and the free-to-grow threshold was defined as the visible sky where relative MAI stabilized. To test this hypothesis, we used a fourth-degree polynomial regression relating relative MAI to visible sky, creating a response curve with inflection points. These inflection points were used to identify competitive advantage and free-to-grow thresholds. To identify the opening size that optimizes

Fig. 2. Regression results showing the relation between the natural logarithms of (A) height and (B) basal diameter of 10-year-old western white pine against visible sky.

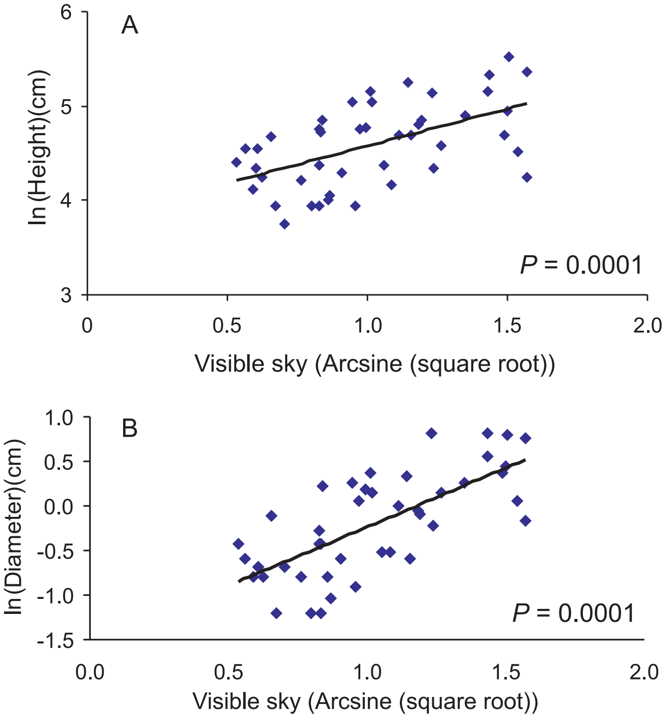
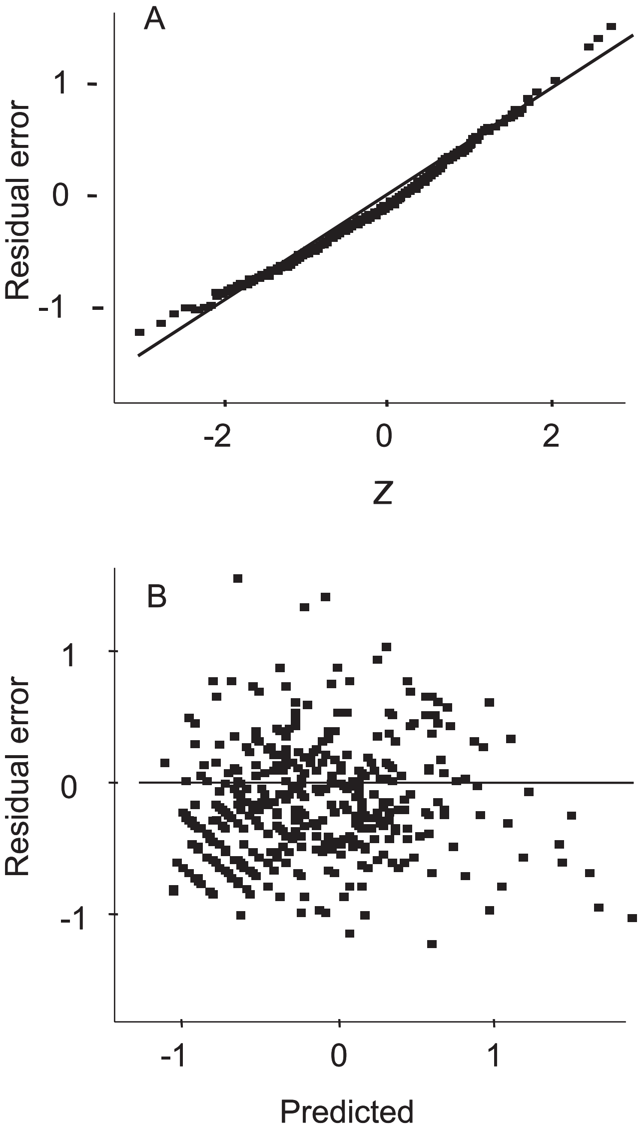


Fig. 3. Regression assumptions of homogeneity of variance and normal distribution of errors were evaluated. Normality was evaluated using a normal probability plot (A); and predicted versus residual errors (B) were used to evaluate homogeneity of variance (Myers 1990). As observed in predicting ln (height), both plots show that residual errors are homogeneous (B) and normally distributed. Similar model behavior occurred when predicting other response variables.



western white pine growth, a second degree polynomial regression was fit that predicted 5-year height and MAI of western white pine as a function of opening size (0.001–15 ha).

Results

By using a simple natural log transformation of basal diameter and height, the regression models successfully found significant relations between western white pine characteristics and canopy opening attributes (Fig. 2). In addition, regression model assumptions were fulfilled as illustrated by residual versus predicted and normal probability plots (Fig. 3). For example, for predicting height as a function of visible sky, normal probability plots (Fig. 3A) and residual errors versus predicted values (Fig. 3B) showed that the errors had a normal distribution and contained a homogeneous variance. These results were easily evaluated and interpreted. Similar model behavior occurred when other response variables were predicted.

As expected, the characteristics of both the selected western white pine and other trees growing within the different sized openings varied extensively (Table 1). The height of selected western white pines ranged from 24 to 637 cm, 5-year height ranged from 6.1 to 307.8 cm, and MAIs were as low as 2.8 cm and as high as 39.6 cm. In addition, western white pine ages were highly variable, ranging from 4 to 50 years. Competing western hemlock tended to have an MAI (10.6 cm) greater than that of western white pine (7.9 cm). There were approximately the same number of grand fir as western white pine seedling and saplings on the microsite plots and about twice as many western hemlock seedlings and saplings (Table 1).

Fisheye photographs captured considerable variation associated with our sampling of different sized openings (Table 2). For example, visible sky ranged from 14% to 100%; and the number of sunflecks for a given day ranged from 1, which occurred in large openings, to as many as 63, which occurred underneath tree canopies. Total sunfleck duration ranged from 2.6 to 15.8 h per day. Selected western white pines were growing on all aspects, and landscape visible sky values ranged from 63% to 96%, with a standard deviation of only 7%. Openings ranged in size from 0.0002 to 15.8 ha, and overstory basal area ranged from 0 to 119 $m^2 \cdot ha^{-1}$ (Table 2).

Table 1. Mean, minimum, maximum, and SD of selected characteristics for western white pine and competing trees in the 0.6-m-radius microplot.

Variable	Mean	Minimum	Maximum	SD
Selected western white pine				
Height (cm)	128.1	24.4	637.0	93.4
Basal diameter (cm)	1.0	0.2	5.1	0.8
MAI-height (cm)	11.6	2.8	39.6	5.4
MAI-diameter (mm)	10.0	1.0	30.0	5.0
5-year height increment (cm)	63.5	6.1	307.8	46.4
Age (years)	12.0	4.0	50.0	7.0
Crown ratio (%)	77.0	22.0	100.0	13.0
Crown diameter (cm)	72.8	6.8	276.2	46.9
Competing trees				
White pine	7.9	2.9	17.8	2.9
MAI-height (cm)				
Density (trees·plot^{-1})	4.0	2.0	16.0	3.0
Western hemlock	10.6	4.2	23.2	4.4
MAI-height (cm)				
Density (trees·plot^{-1})	10.0	2.0	53.0	10.0
Grand fir	6.3	2.5	15.6	2.6
MAI-height (cm)				
Density (trees·plot^{-1})	5.0	2.0	26.0	3.0
Other species	7.1	3.9	12.8	2.1
MAI-height (cm)				
Density (trees·plot^{-1})	4.0	2.0	10.0	3.0

Note: MAI, mean annual increment; SD, standard deviation. $N = 620$.

Table 2. Mean, minimum, maximum, and SD of descriptor variables.

Variable	Mean	Minimum	Maximum	SD
Opening characteristics				
Visible sky (%)	62	14	100	22
Total radiation (MJ·m^{-2}·year^{-1})	4340	398	9273	1956
Diffuse radiation (MJ·m^{-2}·year^{-1})	690	174	1083	243
Direct radiation (MJ·m^{-2}·year^{-1})	3650	224	8196	1773
No. of sunflecks daily	16	1	63	11
Sunfleck duration (h·day^{-1})	11.3	2.6	15.8	3.3
Landscape characteristics				
Visible sky (landscape) (%)	77	63	96	7
Direct radiation (Wh·m^{-2}·year^{-1})[a]	4463	3363	5129	424
Diffuse radiation (Wh·m^{-2}·year^{-1})[a]	1420	1042	1683	135
Total radiation (Wh·m^{-2}·year^{-1})[a]	5884	4538	6787	469
Aspect (°)	151.7	0	359	114.7
Stand characteristics				
Basal area (m^2·ha^{-1})	15	0	119	16
No. of trees·ha^{-1}	166	0	1588	226
Stand density index (ha^{-1})	266	0	1607	281
Opening size (ha)	0.7	0.0002	15.8	1.8

Note: SD, standard deviation. $N = 620$.

[a] 1 Wh = 3.6 kJ.

Western white pine characteristics in relation to opening attributes

We related all the predictor variables to the response variables (Tables 3 and 4). In all cases, visible sky was significantly ($P = 0.0001$) related to attributes associated with the selected western white pine (Table 3). Tree age was a significant covariate in many of the relationships, but not when predicting crown ratio ($P = 0.8168$) (Table 3). Visible sky and tree age were most strongly related to tree height (adjusted $R^2 = 0.53$) and basal diameter (adjusted $R^2 = 0.56$) when compared with the other response variables (Table 3). Interestingly, visible sky and tree age were also related (adjusted $R^2 = 0.45$) to the factor score, which proved useful, as it showed that the entire tree responded positively to in-

Table 3. Log-linear regression analysis of response variables.

Response variable	Intercept	Visible sky coefficients	Age coefficients	Model adjusted R^2
Height	3.060	0.827	0.0660	0.53
Basal diameter	–1.379	1.324	0.0650	0.56
Factor score	–2.442	1.664	0.0710	0.45
Crown ratio	0.894	0.207	0.0002	0.12
Crown diameter	2.467	0.904	0.0630	0.49
5-year height	2.797	1.205	—	0.26
Mean annual height increment	1.469	0.826	—	0.25
Mean annual diameter increment	–2.974	1.326	—	0.41

Note: Visible sky was transformed by using the arcsine of the square root. Response variables were transformed by using the natural logarithm. All response variables were significantly related to visible sky ($P = 0.0001$), with overall model $P = 0.0001$. When added to these relationships, age was significant ($P = 0.0001$) except when predicting crown ratio ($P = 0.8168$). The factor score is a linear combination of mean annual basal diameter increment, last 5-year height growth, and mean annual height increment.

Table 4. Variable evaluation for predicting the natural logarithms of western white pine height and basal diameter.

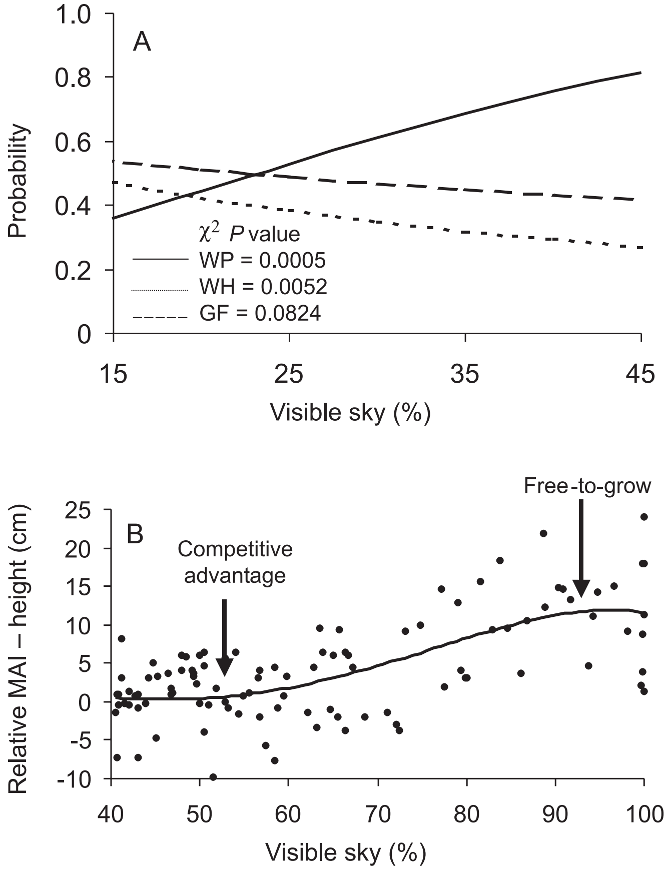
Independent variables	Variable 1 P value	Coefficient	Variable 2 P value	Variable 3 P value	Adjusted R^2
Microsite variables for predicting height					
VS	0.0001	0.8			0.53
Total below-canopy radiation	0.0001	0.00008			0.44
Diffuse below-canopy radiation	0.0001	0.0008			0.48
Direct below-canopy radiation	0.0001	0.00008			0.44
Sunfleck duration	0.0123	0.00001			0.39
Number of sunflecks	0.0001	–0.02			0.50
Microsite factor score[a]	0.0122	0.06			0.40
VS and opening orientation	0.0001	0.83	0.0015		0.54
Landscape variables for predicting height					
VS and total landscape radiation	0.0001	0.8	0.2873		0.53
VS and direct landscape radiation	0.0001	0.8	0.0142		0.53
VS and diffuse landscape radiation	0.0001	0.8	0.3155		0.53
VS and topographic factor score[b]	0.0001	0.008	0.6957		0.53
VS, orientation, and aspect	0.0001	0.84	0.0055	0.0001	0.56
VS and location	0.0001	0.88	0.0001		0.58
Microsite variables for predicting basal diameter					
VS	0.0001	1.3			0.56
Total below-canopy radiation	0.0001	0.0001			0.39
Diffuse below-canopy radiation	0.0001	0.0001			0.45
Direct below-canopy radiation	0.0001	0.0001			0.38
Sunfleck duration	0.0121	0.00002			0.28
Number of sunflecks	0.0001	–0.03			0.47
Microsite factor score	0.0003	0.06			0.30
VS and opening orientation	0.0001	1.31	0.0035		0.57
Landscape variables for predicting basal diameter					
VS and total landscape radiation	0.0001	1.3	0.7139		0.56
VS and direct landscape radiation	0.0001	1.3	0.2981		0.56
VS and diffuse landscape radiation	0.0001	1.3	0.2103		0.56
VS and topographic factor score	0.0001	0.000009	0.7403		0.55
VS, orientation, and aspect	0.0001	1.32	0.0020	0.0002	0.58
VS and location	0.0001	1.39	0.0001		0.63

Note: VS, visible sky. All models were significant ($P = 0.0001$). We used adjusted R^2, individual variable P values, and coefficient magnitude to evaluate variable effectiveness in predicting height and basal diameter. Tree age was significant ($P = 0.0001$) in all relationships.

[a] Microsite factor score is the linear combination of visible sky, sunfleck duration, and number of sunflecks.

[b] Topographic factor score is the linear combination of hours of radiation reaching a setting and the proportion of visible landscape sky.

Fig. 4. Competitive thresholds when western white pine has an advantage over western hemlock and grand fir. (A) Probability of western white pine (WP), western hemlock (WH), and grand fir (GF) occupying a site as a function of visible sky. Western white pine has a 0.50 probability of occupying a site at >23% visible sky. At <23% visible sky, western hemlock and grand fir have a greater probability of occupying the site. At >45% visible sky, western white pine has a 0.80 probability of occupying the site; in contrast, grand fir has a 0.41 probability and western hemlock a 0.21 probability of occupying the site in the same sized canopy opening. (B) Competitive advantage of western white pine over western hemlock was determined using relative mean annual increment (MAI) in height (western white pine MAI – western hemlock MAI) using a fourth-degree polynomial regression. Competitive advantage when relative MAI becomes positive occurs at approximately 53% visible sky, and free-to-grow status (relative MAI is stabilized) occurs at approximately 92% visible sky.



creases in visible sky. Crown diameter was highly correlated with basal diameter (r = 0.9), facilitating its strong relationship (adjusted R^2 = 0.49) with visible sky and tree age (Table 3). Because of their strong relationship to visible sky, we used height and basal diameter to evaluate other canopy opening variables.

Total, diffuse, and direct radiation occurring below the canopy, along with visible sky and tree age, were significantly (P = 0.0001) related to western white pine height and basal diameter (Table 4). The microsite factor score characterized the environment below the canopy, but it did not prove to be as useful as we had originally hoped. The adjusted R^2 for this factor and tree age for predicting height was only 0.40; for predicting basal diameter, only 0.30. Visible sky was a significant and strong microsite predictor of both height and basal diameter of western white pine. The magnitude of its contribution exceeded that of the other variables, as indicated by the size of its regression coefficient (Table 4).

The number of sunflecks and their duration on 21 June 1999 significantly predicted both height and basal diameter of western white pine (Table 4). In particular, the number of sunflecks was negatively related to both height and basal diameter of the western white pine and had adjusted R^2 values of 0.50 for height and 0.47 for basal diameter. In contrast, sunfleck duration had a positive relationship and explained less of the variation in height (adjusted R^2 = 0.39) and basal diameter (adjusted R^2 = 0.28). We also evaluated the influence of sunfleck duration and number of sunflecks on western hemlock, grand fir, and other western white pine growing in the microsite plot. These results were consistent with those predicting height of the selected western white pine.

In combination with visible sky, the amount of landscape radiation reaching a setting did not add more explained variation to either height or basal diameter of western white pine. The aspect of the setting and the orientation of the opening were significant, but they increased adjusted R^2 by only 0.03 when predicting height and 0.02 when predicting basal diameter when compared with visible sky and age (Table 4).

Western white pine thresholds

We identified competitive thresholds at which western white pine has an advantage over western hemlock and grand fir, its key competitors in establishment and development (Graham 1990). Our results showed there was a 0.57 probability of western white pine occupying a site with at least 23% visible sky (Fig. 4A). Below this visible sky threshold, western hemlock and grand fir have a higher probability of occupying the site than western white pine. At 45% visible sky there was a 0.80 probability of western white pine occupying the site, whereas western hemlock had a 0.28 probability and grand fir a 0.41 probability of occupying the site (Fig. 4A).

Relative MAI of grand fir and western white pine was not significantly related to visible sky (P = 0.3354); however, relative MAI (P = 0.0001) of western hemlock and western white pine was. Western white pine gains a competitive advantage (relative MAI became positive) over western hemlock in canopy openings where visible sky exceeds 50% (Fig. 4B). Western white pine achieves free-to-grow status (relative MAI stabilized) in canopy openings where visible sky exceeds 92% (Fig. 4B). Western white pine MAI and last 5-year height increment are optimized when opening sizes exceed 4 ha (Figs. 5A and 5B).

Visible sky and overstory density descriptors

Our last objective was to relate visible sky to overstory and opening size descriptors, such as basal area per hectare, trees per hectare, and stand density index, even though these stand attributes reflect homogeneous tree spacing. We used these descriptors to characterize the overstory trees for each selected pine to determine whether they could represent val-

Fig. 5. A second-degree polynomial was used to ascertain when western white pine mean annual increment (MAI) in height (A) and 5-year height growth (B) were optimized. In both cases, canopy opening size of approximately 4.0 ha optimized the attributes.

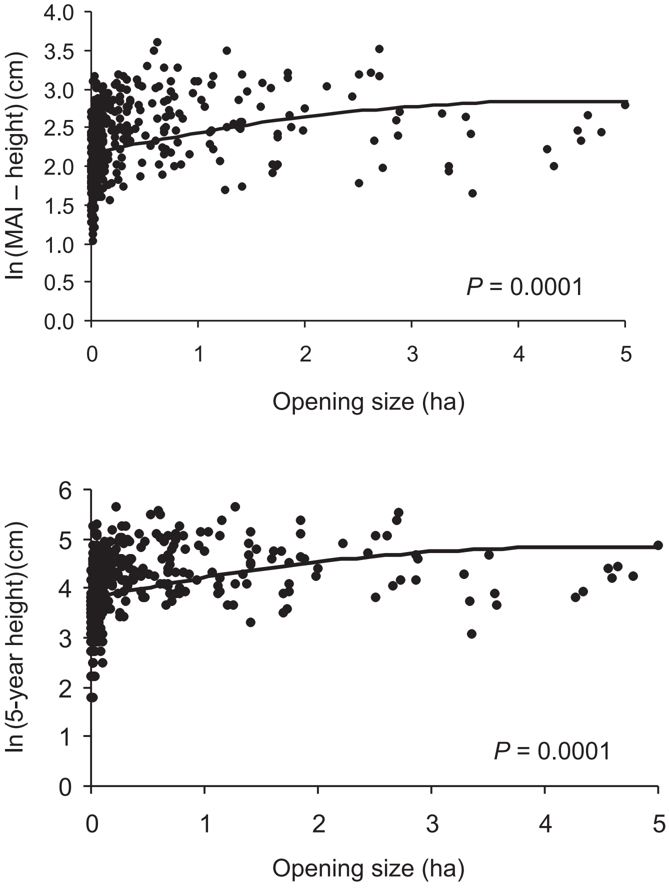
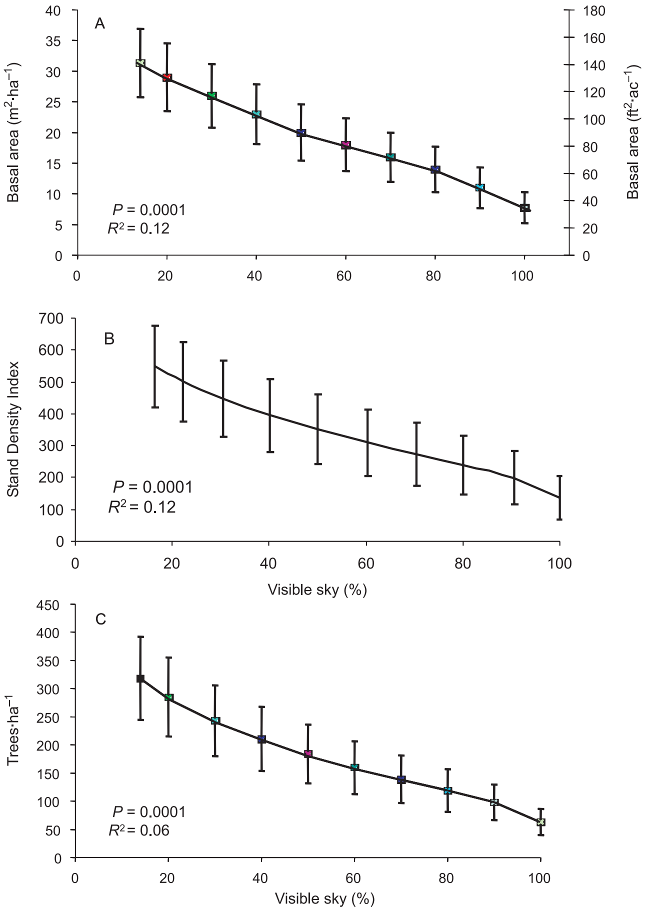


Fig. 6. Relation between percentage visible sky and three stand descriptors: basal area (A), stand density index (B), and trees per hectare (C). In all cases, these relationships were significant (P = 0.0001); however, there was considerable variation around the mean. For example, when visible sky is related with stand density index (B), adjusted $R^2 = 0.12$. Similarly, basal area (adjusted R^2 = 0.12) and trees per hectare (adjusted R^2 = 0.06) had low R^2 values.



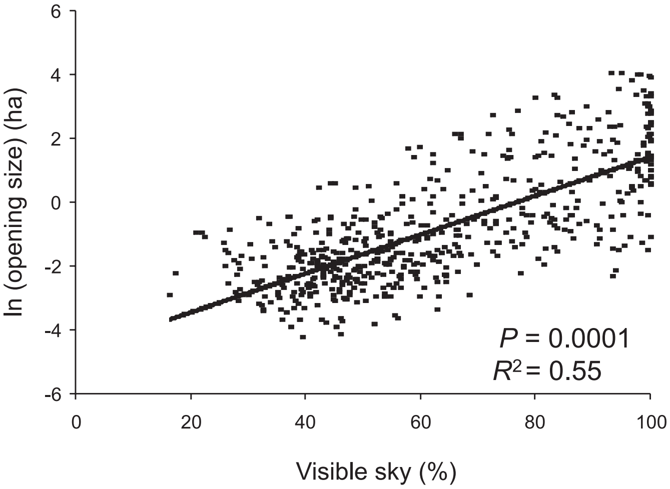
ues determined by the fisheye photographs. In all cases, there was a significant ($P = 0.0001$) relation between visible sky estimated from the fisheye photograph and basal area per hectare, stand density index, trees per hectare, and opening size (Figs. 6 and 7). For example, sites with 20% visible sky contained 30 m^2·ha^{-1}, $s_{\bar{x}}$ = 5 m^2·ha^{-1} of basal area. Sites with 10 m^2·ha^{-1}, $s_{\bar{x}}$ = 5 m^2·ha^{-1} of basal area had 90%–100% visible sky (Fig. 6A). Similar results occurred for stand density index and trees per hectacre (Figs. 6B and 6C). However, adjusted R^2 values were only 0.12, 0.12, and 0.06 in basal area per hectare, stand density index, and trees per hectare, respectively, when related to visible sky (Fig. 6). In contrast, the adjusted R^2 was 0.55 when opening size was related to visible sky (Fig. 7).

Discussion

In northern Rocky Mountain moist forests, canopy openings influence not only light but soil moisture, soil surface temperatures, evaporation rates, humidity, and all other parts of the environment affecting vegetation germination, establishment, and development (Jemison 1934; Haig et al. 1941). In our study, we showed that below-canopy radiation, although significant ($P = 0.0001$), explained a smaller proportion of the variation in western white pine height (adjusted $R^2 = 0.44$) and basal diameter (adjusted $R^2 = 0.39$) than did visible sky (Table 2). This does not imply that light below the canopy is not important, but rather that a combination of soil moisture, nutrients, heat, and other environmental components influenced by forest canopies also influences tree development (Spomer 1973; Brown 1993). For example, Brown (1993) found that maximum air temperature (R^2 = 0.84) and daily duration of temperatures greater than 24 °C ($R^2 = 0.70$) was significantly related to increasing size of canopy opening as well as photosynthetically active radiation ($R^2 = 0.86$).

Canopy characteristics regulate both the amount of light striking the forest floor and light periodicity. The light filtered through canopies is diffuse light, with intense sunfleck periodicity of seconds to hours. These light dynamics can be critical to the structure and composition of ground level vegetation (Chazdon 1988; Evans et al. 1988). Two photosynthetic processes influence a plant's response to sunflecks. First, when photosynthesis is induced, there is a slow increase in CO_2 fixation, which can be interrupted when the sunfleck disappears. Second, light fluctuations, inherent to short and

Fig. 7. An illustration of the significant ($P = 0.0001$) relation between visible sky and opening size. In this relationship, the adjusted R^2 of 0.55 explained the variation.



numerous sunflecks, produce a short-term photosynthetic response (Chazdon 1988; Evans et al. 1988). These irregularities in photosynthesis caused by sunflecks could be partially responsible for our finding that trees responded negatively to increases in sunfleck number (Table 4). Most likely, a few long-duration sunflecks would provide better growing conditions than numerous short-duration sunflecks.

We have shown that site-specific light, along with other aspects of the operational environment, highly influences the development of western white pine. There is also strong evidence that landscape radiation is an important driver of vegetation composition over both time and space (Garnier and Ohmura 1970; Pope and Lloyd 1974). We surmised that opening location (e.g., ridge top, valley bottom), characterized by landscape radiation, would most likely affect how canopy gaps influence vegetation development. Surprisingly, combining direct, diffuse, or total landscape radiation with visible sky did not result in better estimates of western white pine height or basal diameter than using only visible sky and age (Table 4). The amount of radiation (intensity and duration) reaching a landscape position is highly variable and depends on the number of cloudy days, the sun's solar position, daily solar angle, sky brightness, and canopy opening in relation to the solar disk (Anderson 1970; Hutchison et al. 1980). Because of these irregularities, our data may reflect potential rather than actual landscape radiation. Moreover, our landscape radiation values had minimal variation, which limits our ability to detect the effects of landscape radiation on western white pine development (Table 2).

If western white pine is once again going to become a significant component of moist forests, it must become established before, or simultaneously with, its major competitors, western hemlock and grand fir. Once grand fir or western hemlock occupies a site, it is highly unlikely that western white pine can become established. Both grand fir and western hemlock have the ability to become established in gaps with <23% visible sky and thus inhibit western white pine regeneration (Fig. 4A). Further disturbances that increase opening size release this advanced regeneration, disallowing new seedlings to establish (Ferguson et al. 1986).

Western white pine developmental thresholds based on visible sky (Fig. 4) were a unique way of characterizing vegetation response as a function of canopy opening. Relations between canopy opening and photosynthesis (Canham 1989), gap-forming processes across landscapes (Bradshaw 1992), and growth relations as a function of increasing opening size (Coates 2000) have been described. Developmental thresholds provide information on the interaction among different species as opening size increases. By using polynomial regression we were able to provide an unbiased estimate of opening size thresholds that relate to growth of different species. Coates (2000) was unable to identify these types of thresholds. Our results show that grand fir and western white pine develop similarly under the same conditions, since we were unable to determine a threshold for a competitive advantage (visible sky) of western white pine over grand fir. In contrast, we were able to show that western white pine does have a competitive advantage over western hemlock when canopy openings defined by visible sky exceed 50% (Fig. 4B). These findings suggest that if western white pine becomes established in small openings, additional disturbances are needed to remove forest canopy to achieve 50% visible sky; and more canopy needs to be removed if the pine is going to achieve free-to-grow status (92% visible sky) (Fig. 4B).

In this study we used growth to illustrate this interaction. However, other techniques, such as identifying the variation in physiological response among different plant species or identifying how different fine-scale disturbances achieve these thresholds, may provide more ecological understanding. The techniques we used to identify the thresholds could be used in other ecosystems and for other species. Because canopy openings and the disturbances that create them are so influential in determining vegetation establishment and development (Norman and Campbell 1989), it may be an ideal means for investigating vegetation dynamics among species, sites, and ecosystems over both time and space.

A disadvantage of defining forest structures using visible sky is that overstory descriptors were poorly related to this characteristic. We found a weak relationship between visible sky and basal area per hectare, stand density index, and trees per hectare. In contrast, Mitchell and Popovich (1997), using a spherical densiometer, found basal area per hectare strongly related ($R^2 = 0.84$) to visible sky in pure ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands. Most likely, the difference between their findings and ours could be attributed to differences between the canopy characteristics occurring in single species and those occurring in mixed species stands (Moeur 1997). Opening size was a better descriptor of visible sky than the other overstory descriptors (adjusted R^2 of 0.55 versus 0.06–0.12). Although there is considerable variation in the relation between visible sky and overstory descriptors, our results suggest that competitive advantage and free-to-grow status can be accomplished with residual basal areas of $<15\ \mathrm{m^2 \cdot ha^{-1}}$ (Figs. 6 and 7). Western white pines occurring in openings this size or greater will most likely develop and hold a dominant position in the overstory.

The presence of a negative relationship between pine characteristics and the number of sunflecks suggests that regularly spaced canopies in the overstory do not favor western white pine development. Regularly spaced and close tree crowns (>50 trees·ha^{-1}) uniformly intercept light that would have reached the forest floor, thus increasing the number of sunflecks and decreasing their duration. In contrast, grouped or clumped trees create irregular canopy openings, thereby decreasing the number of sunflecks and increasing their duration, which favors western white pine development.

Conclusion

Using knowledge gained from this study to restore western white pine forests in the northern Rocky Mountains will be challenging but not impossible. Growth will be sacrificed when western white pines occur in openings of <4–5 ha (Figs. 5), but the species can persist in smaller openings. This is important, given the current reservations about using clearcuts in forest management (Bliss 2000). A range of canopy opening sizes can be created through silvicultural treatments or native disturbances. If seed is available and a canopy opening producing 25%–45% visible sky exists, there is a 0.55–0.80 probability that western white pine could develop (Fig. 4A), and, most likely, planted pines would survive. However, to ensure that pines growing under these conditions obtain a competitive advantage and achieve free-to-grow status, further canopy reductions through overstory removal and (or) other cultural activities (e.g., weeding, cleaning) would be required. Depending on the setting, this window of opportunity may be 10 years or less (Fig. 4B). To ensure successful western white pine restoration, such treatments should occur within 30 years of tree establishment, as stand composition and future dynamics are largely determined during this period (Graham et al. 1983).

This study disclosed relations among canopy opening characteristics and western white pine attributes and how physical settings affected these relationships. We also investigated how radiation (diffuse, direct, landscape) was related to growth. Although important, light described less of the variation than visible sky (measure of canopy opening). We conclude from these results that visible sky probably expresses the integration of several factors related to tree growth (temperature, light, moisture), rather than radiation alone. We determined that sunfleck dynamics might be more of a driving force in controlling western white pine development than the amount of radiation reaching trees below the canopy.

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