Western white pine development in relation to biophysical characteristics across different spatial scales in the Coeur d'Alene River basin in northern Idaho, U.S.A.

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Abstract: Many studies have assessed tree development beneath canopies in forest ecosystems, but results are seldom placed within the context of broad-scale biophysical factors. Mapped landscape characteristics for three watersheds, located within the Coeur d'Alene River basin in northern Idaho, were integrated to create a spatial hierarchy reflecting biophysical factors that influence western white pine (*Pinus monticola* Dougl. ex D. Don) development under a range of canopy openings. The hierarchy included canopy opening, landtype, geological feature, and weathering. Interactions and individual-scale contributions were identified using stepwise log–linear regression. The resulting models explained 68% of the variation for estimating western white pine basal diameter and 64% for estimating height. Interactions among spatial scales explained up to 13% of this variation and better described vegetation response than any single spatial scale. A hierarchical approach based on biophysical attributes is an excellent method for studying plant and environment interactions.

Résumé : Beaucoup d'études ont évalué le développement des arbres sous couvert dans les écosystèmes forestiers mais les résultats sont rarement placés dans le contexte des facteurs biophysiques à plus large échelle. Les propriétés cartographiées du paysage de trois bassins localisés dans celui de la rivière Cœur d'Alene dans le Nord de l'Idaho ont été intégrées pour créer une hiérarchie spatiale reflétant les facteurs biophysiques qui influencent le développement du pin argenté (*Pinus monticola* Dougl. ex D. Don) dans une gamme d'ouvertures du couvert. La hiérarchie incluait l'ouverture du couvert, le type géomorphologique, la formation géologique et l'altération. Des interactions et des contributions à l'échelle individuelle ont été identifiées à l'aide d'une régression séquentielle logarithmique. Les modèles ainsi obtenus expliquent 68% de la variabilité du diamètre basal du pin argenté et 64% de celle de la hauteur. Les interactions entre les échelles spatiales expliquent jusqu'à 13% de cette variabilité et décrivent les réponses de la végétation mieux qu'aucune échelle spatiale considérée seule. Une approche hiérarchique basée sur les caractéristiques biophysiques constitue une excellente méthode pour étudier les interactions entre les plantes et l'environnement.

[Traduit par la Rédaction]

Introduction

Ecosystem processes (e.g., disturbance, soil development, climate) influence vegetation pattern at multiple spatial scales. For example, growth and abundance of vegetation results from interactions among topography, climate, disturbance, soil processes (e.g., deposition, nutrient cycling), time, and vegetation (both current and historical) (Brady 1974; Jenny 1980; Pickett and White 1985; Crawley 1986; Matérn 1986; Delcourt and Delcourt 1988; Oliver and Larson 1990; Dale 1999). These interactions produce different vegetation patterns that can be viewed over a wide range of spatial and temporal scales (Allen and Starr 1982; O'Neill et al. 1986; Dale 1999). Interstand disturbances (e.g., stand-replacing fires) in a landscape influence vegetation pattern by creating large areas of early seral species with interspersed patches containing mid- to late-seral species (Chandler et al. 1991; Agee 1993; Debano et al. 1998). In contrast, intrastand disturbances (e.g., windthrow, insects, harvesting) create a mosaic of early- to late-seral vegetation depending on the amount of space available for plant establishment and growth (Pickett and White 1985; Canham 1989; Oliver and Larson 1990; Moeur 1997).

Only recently (within the last 20 years) have forest ecologists conducted studies using multiple spatial scales to understand flora and fauna patterns. Hinckley et al. (1998) attempted to understand physiological scaling in trees. They linked three spatial scales (leaf, tree, stand) to estimate carbon fixation using both a bottom-up and top-down approach. The spatial scales they chose, however, were either too fine (individual leaf) or too broad (tree) to effectively understand physiology mechanistically. Song et al. (1997) determined factors influencing canopy structure by first modeling individual three-dimensional trees (fine scale) and then constructing a stand canopy (broad scale) with these trees. From this multiple-scale approach they determined that species

Received 1 May 2001. Accepted 5 February 2002. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 8 June 2002.

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 DOI: 10.1139/X02-032

composition and tree density influenced shape and size of crowns and subsequent patch size. Saab (1999), used three spatial scales: microhabitat (≤0.5 ha of local vegetation characteristics), macrohabitat (0.5–204 ha of cottonwood (*Populus* spp.) forest patch characteristics), and a landscape (310–1440 ha of surrounding vegetation types and land uses) to study patterns of bird distribution and abundance. Her results showed that landscape patterns were most influential in describing the distribution and abundance of most bird species, whereas the other two finer scales were of secondary importance. Cherrill et al. (1995) used a nested hierarchy (land class, land cover type, community, species) to predict plant distributions (presence or absence data) using a series of matrices (probability of occurrence of each community within each land cover type, probability of occurrence of each land cover type within each land class). They found that 59% of the 570 plant species were significantly related ($P \leq 0.05$) to the hierarchy. These four studies used multiple scales, in most cases with significant results, to understand the relations between spatial pattern and structures (landscape features, vegetation characteristics), but they did not always link the spatial scales. Saab's (1999) inferences were only within each spatial scale, Song et al. (1997) and Hinckley et al. (1998) summarized fine-scale data to address broad-scale questions, and Cherrill et al. (1995) linked scales using probabilities of fine-scale information that occurred at the broad spatial scale. None of these studies used samples collected across spatial scales to understand a site-specific response.

Tree regeneration and growth beneath canopies have been studied within many forest ecosystems (Canham 1989; Bradshaw 1992; Carter and Klinka 1992; Runkle 1992; Wilczynski and Pickett 1993; Parsons et al. 1994; Veenendall et al. 1995; Zhang and Zak 1995; Coates and Burton 1997). While these studies contribute to our understanding of processes occurring after fine-scale native disturbances or management activities, results are seldom placed within the context of broad-scale biophysical factors (e.g., erosion, climate, soils). Lertzman et al. (1996) used two spatial scales (forest, gap) to provide context and insight for processes that create gaps over a range of forest developmental stages. Old and mature forests have a greater proportion of gap area than younger forests. Many of the gaps in mature forests were larger than the gaps in old forests, although both had similar proportions of gap area. At the gap scale, Lertzman et al. (1996) hypothesized that damaging winds created large gaps in mature forests, but in old forests, diseases killed individual trees to create small gaps. Brown et al. (1993) showed that total sun per day (a macroclimate factor) had a positive linear relation to the amount of photosynthetically active radiation reaching the center of the gap (1.5 m above forest floor), thereby influencing the microclimate within a gap. Thus, the processes that either create gaps or influence microclimates within gaps operate at more than one spatial scale.

To address complex forest management issues requires a knowledge of how fine-scale disturbances are influenced and constrained by processes and structures occurring at broad scales (Quigley and Arbelbide 1997). Defining and using multiple spatial scales, however, can be challenging. Hierarchy theory can be used to identify relevant spatial scales (Allen and Starr 1982; Klijn 1994). Scales are often nested, and in general, higher levels within the hierarchy have greater spatial extents than lower levels (Delcourt and Delcourt 1988), have slower process rates than lower levels (O'Neill et al. 1986), and contain or constrain processes or patterns occurring at lower levels (Allen and Starr 1982).

Klijn (1994) developed and mapped a spatial hierarchy by combining characteristics defined by different classification systems from Canada, the United States, and Europe. From this combination, he integrated biophysical factors (environmental hazards such as pollution and acidification) occurring within a spatial scale that controlled the spatial pattern of flora and fauna at each level within the hierarchy. Although spatial hierarchical classifications such as potential vegetation type (Daubenmire 1953), ecotypes (Bailey 1995), and geology are readily available, it is unclear the degree to which each of these are related to ecosystem function. As Klijn (1994) suggested, combining these systems into a spatial hierarchy may describe vegetation pattern more effectively than any single variable. Unfortunately, there is usually insufficient funding or time to develop and map such an integrated spatial hierarchy.

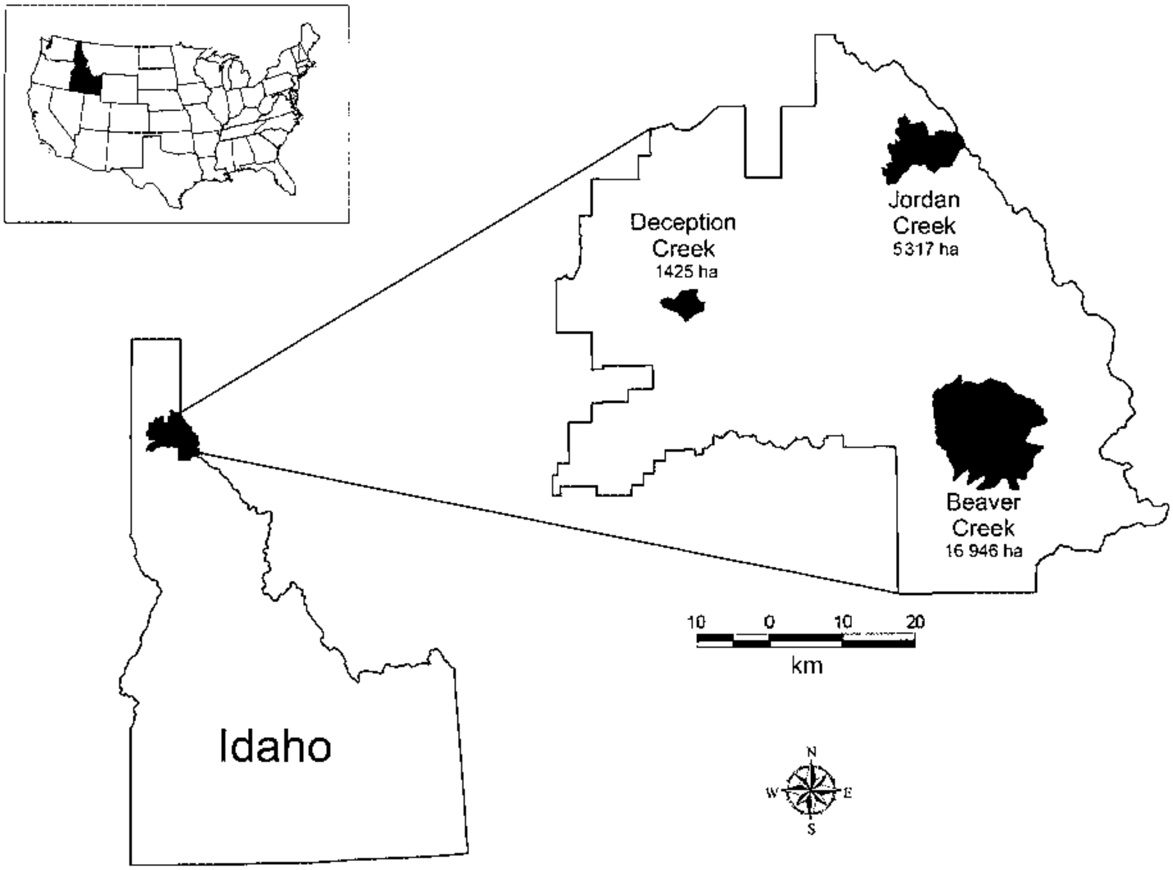
As an alternative, we integrated currently mapped characteristics for a set of watersheds to create a spatial hierarchy reflecting biophysical factors that influence western white pine (*Pinus monticola* Dougl. ex D. Don) development. We expected that predictions of western white pine characteristics would be influenced by canopy opening attributes (Haig et al. 1941). However, we also hypothesized that other spatial scales representing biophysical factors would further improve and refine the predictions. Instead of using one spatial scale representing one set of biophysical properties or grouping fine-scale phenomena to address broad-scale responses, we assessed how biophysical factors operating at multiple spatial scales relate to tree characteristics by sampling across spatial scales. Our objectives were to determine if spatial scales defined on biophysical properties influence western white pine characteristics and to identify significant interactions among the spatial scales. In addition, linked spatial scales and subsequent interactions may be useful in understanding vegetation dynamics and influence site-specific silvicultural decisions.

Methods

Study area

We selected three watersheds (Jordon, Beaver, Deception) within the 350 000 ha Coeur d'Alene River Basin in northern Idaho in the United States (Fig. 1). The selected watersheds were dominated (90% of the area) by three potential vegetation types, grand fir (*Abies grandis* Dougl. ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don) (Cooper et al. 1991; IPNF 1998), and provided a wide range of canopy openings containing western white pine seedlings and saplings. In addition, the three watersheds contained substantial variation in biophysical characteristics, useful for understanding western white pine development within a spatial hierarchy.

Fig. 1. The Coeur d'Alene River basin in northern Idaho, U.S.A. Three watersheds, Deception Creek, Jordan Creek, and Beaver Creek, were used to relate western white pine seedling and sapling characteristics to multiple spatial scales.



Spatial hierarchy

The hierarchy included four spatial scales (canopy opening, landtype, geological feature, weathering class) that integrate the biophysical factors influencing site-specific vegetation response (Table 1). The broadest scale was weathering, which classifies settings based on the relative extent to which bedrock has weathered compared with its presumed, unweathered state (Schoeneberger et al. 1998; USDA 1999). This scale reflects long-term climate and geologic processes and biophysical factors that operate across several watersheds (≤ 14 029 ha). The second scale was defined using geological features based on parent material (P.D. Derkey, unpublished data;[2] Hosterman 1956; Harrison and Jobin 1963, 1965; Hobbs et al. 1965; Lewis and Derkey 1999; Lewis et al. 1999; Miller et al. 1999; Munts 2000). The classification represents variation in bedrock lithology, sediment bedding characteristics, metamorphic structure layers, and rock size. These characteristics influence surface relief, hydrology, water-holding capacity, nutrition, and soil formation (Godron 1994; Shen et al. 2000). Geological feature reflects biophysical characteristics operating within large watersheds (≤2425 ha) that occur within a particular weathering class. The third spatial scale uses a landtype classification, based upon landform, elevation, potential vegetation, slope gradient and shape, aspect, and microrelief (USDA 1999). This scale represents variation in soil depth as well as topographic features influencing surface climate, potential moisture, and overstory tree composition and structure. Landtype reflects biophysical factors operating within watersheds (≤650 ha) that occur within a geological feature. The fourth spatial scale with the smallest spatial extent was canopy opening. This scale represents variation in microsite temperature, moisture, and light duration and intensity (Canham 1989; Norman and Campbell 1989; Runkle 1992). This scale reflects biophysical factors that vary within stands (≤15 ha) occurring within a particular landtype.

The spatial scales defined by canopy opening, landtype, geological feature, and weathering vary spatially, have different geographic extents, and although the scales were not perfectly nested, reflect the relations among the biophysical characteristics they represent. The processes and structures observable at the broader scales constrain those operating at the finer scales. For example, soil depth (structure) and erosion (process) operating at the landtype scale were constrained by geology and climate operating at the weathering and geological feature scales. Processes (photosynthesis, decomposition) observable at the finer scales (canopy opening and landtype) occur faster (from seconds to years) than those occurring at the weathering and geological feature (centuries to millenniums) scales. In addition to being relatively stable the landtype, geological feature, and weathering scales integrate the soil-forming factors (climate, time, organisms, to-

[2] Derkey, P.D. Unpublished digital data, St. Maries Quadrangle. Available from the U.S. Geological Survey, Spokane, Wash.

Table 1. Spatial hierarchy showing geographic extent and estimated number of classes within each spatial scale within the selected watersheds (Deception, Jordan, and Beaver).

Spatial scale	No. of classes	Geographic extent (ha)	Resolution (cell size, m)	Data source
Canopy opening	620	≤15	1	Field sampling
Landtypes	19–45	≤650	30	IPNF[a]
Geological feature	3–15	≤ 2 425	30	USGS, IGS[b,c]
Weathering class	2–3	≤ 14 029	30	IPNF[a]

[a]Weathering class and landtypes were provided by IPNF (1998).
[b]Geological features were supplied by the U.S. Geological Survey (USGS) and the Idaho Geological Survey (IGS) with the classification based on individual geological reports of the study area and digital data (Hosterman 1956; Harrison and Jobin 1963, 1965; Hobbs et al. 1965; Lewis and Derkey 1999; Lewis et al. 1999; Miller et al. 1999; Munts 2000).
[c]Derkey, P.D., unpublished digital data, St. Maries Quadrangle. Available from the U.S. Geological Survey, Spokane, Wash.

Table 2. For each watershed (Deception, Jordan, and Beaver) a sampling matrix stratified by elevation (two), aspect (four), size of opening (under canopy, small opening, large opening), and location within opening (edge, center) was used for plot location.

		No. of plots with low-elevation openings			No. of plots with high-elevation openings			
Aspect (azimuth, °)	Plot location	Under (<0.1 ha)	Small (<0.5 ha)	Large (>1 ha)	Under (<0.1 ha)	Small (<0.5 ha)	Large (>1 ha)	Total
0–90	Edge	4	4	4	4	4	4	24
	Centre	4	4	4	4	4	4	24
91–180	Edge	4	4	4	4	4	4	24
	Centre	4	4	4	4	4	4	24
181–270	Edge	4	4	4	4	4	4	24
	Centre	4	4	4	4	4	4	24
271–360	Edge	4	4	4	4	4	4	24
	Centre	4	4	4	4	4	4	24
Total		32	32	32	32	32	32	192

pography, initial parent material) that influence vegetation pattern, composition, and canopy opening (Jenny 1980; Aber and Melillo 1991; Sollins 1998).

Sampling design

The finest scale, canopy opening, was sampled using a matrix with four aspect and two elevation classes ensuring a variety of topographic settings were sampled within each watershed. Twenty-four plots were randomly (using random number generator) located within each aspect and elevation class and distributed among three canopy openings (under canopy, small, large) ranging from 0.001 to 15 ha in size (Table 2).

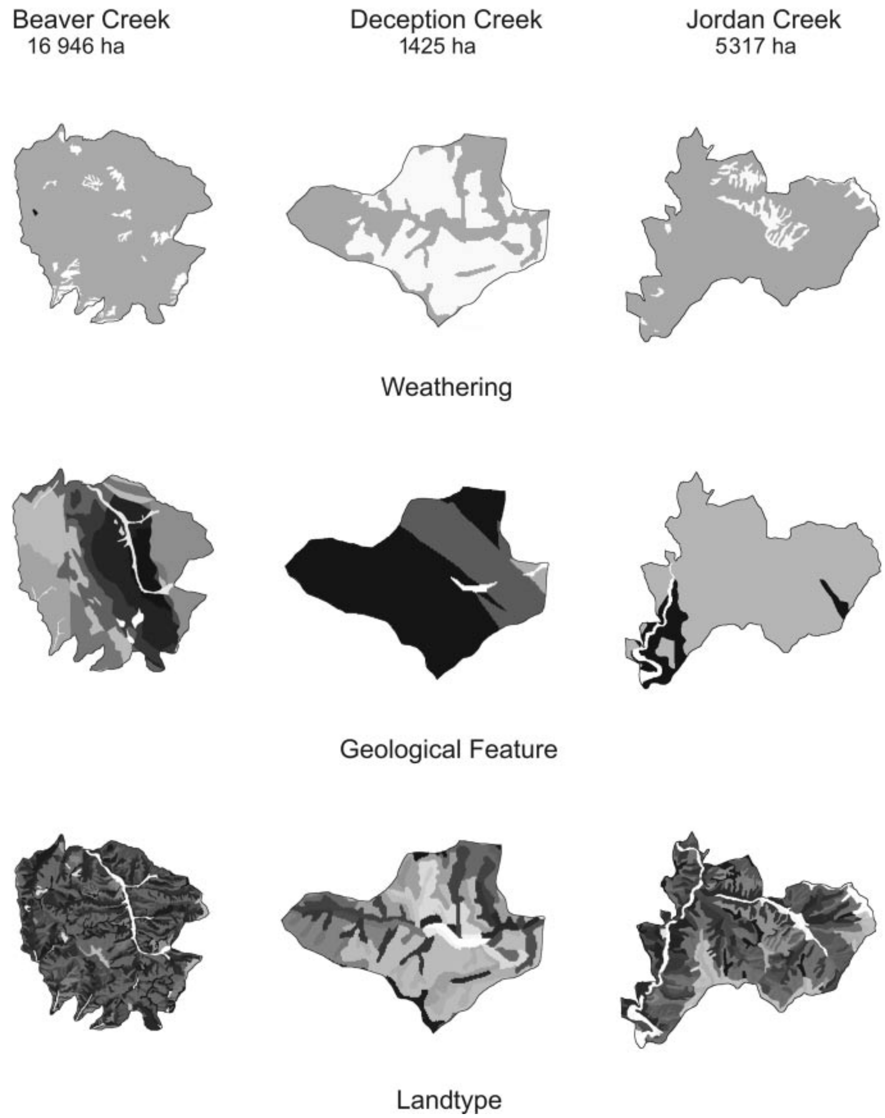
Within each elevation, aspect, and opening class, a plot was randomly selected, near the opening's centre and edge. Within the plot area a western white pine was randomly selected and designated as plot centre. After the 192 cells (within each watershed) of the matrix were filled, additional plots were added to ensure that all possible settings where western white pine could potentially grow were sampled. These areas included closed canopy conditions, steep southerly slopes, and other places tending to disfavor western white pine occupancy. If multiple western white pines occurred in these conditions, plots were randomly selected (centre and (or) edge) and added to the study. A total of 620 plots with pines growing in a variety of canopy openings on a variety of topographic settings were sampled.

Digital spatial data containing weathering class, geological feature, and landtype for the three watersheds were obtained from the Idaho Panhandle National Forests, Idaho Geological Survey, and the United States Geological Survey. For each plot the respective weathering class, geological feature, and landtype were extracted using a geographical information system (Fig. 2).

Canopy opening dependent variables

The dependent variables were the characteristics of the randomly selected western white pines. Selected trees ranged from 20 to 700 cm in height, were well established (ages 5–50 years), and free of damage (no blister rust (*Cronartium ribicola* Fisch) stem cankers, no visible branch cankers, no broken tops, no obvious bark or stem damage). Although some sampled pines may have been infected with blister rust (needle spots), their selection did not compromise the data. Blister rust does not impact tree growth until the pine stem is encircled by a canker (Bingham et al. 1973; Hoff and Steinhoff 1980; Hoff 1984). Moreover, most western white pines (62%) regenerating under tree canopies die

Fig. 2. Weathering (3 classes), geological feature (10 classes), and landtype (19 classes) spatial scale patterns for each sampled watershed (Beaver Creek, Deception Creek, Jordan Creek).



before 3 years of age. Western white pines surviving beyond this time have the potential to live and grow for long periods under relatively dense canopies (Haig 1936).

Measurements on the selected western white pine included total height from the root collar to base of terminal bud, total age (2.5 cm above root collar), and stem diameter 2.5 cm above the root collar. From these data, mean annual height increment (cm) was calculated.

Canopy opening independent variables

Independent variables were separated into two classes: understory tree attributes and opening attributes. A circular microsite plot (60-cm radius) quantified and characterized trees surrounding the selected western white pine. Because these plots could contain hundreds of trees, data were separated into two classes: trees with heights less than one-half the height of the selected western white pine and trees with heights greater than one-half the height of the selected western white pine. Trees were tallied by species in 30-cm height classes with one tree randomly selected from each species and height class with the following measurements obtained: total height from root collar to base of terminal bud, total age (2.5 cm above the root collar), and stem diameter 2.5 cm above the root collar. From these measurements, mean annual height increment was calculated.

The second class of data described opening attributes using a vertical fish-eye photograph (Lawton and Putz 1988; Runkle 1992; Coates and Burton 1997; Delta T Devices Ltd. 1997). The camera lens was level with the camera top facing magnetic north and centered over the stump at a height equal to midcrown of the selected western white pine. To maximize light evenness and avoid bright reflections, all photographs were taken on cloudy days, in early morning, or late evening. Using 400 ASA color film, a 17-mm lens provided a 180° view of the overstory canopy.

The vertical fish-eye photographs were developed and placed on compact disks. Using these photographs and digital analysis software (HemiView; Delta T Devices Ltd. 1997), we quantified the overstory attributes. The effect of surface orientation was accounted for by multiplying the cosine of the angle of incidence between the intercepting surface and the sky (Rich 1988, 1989; Delta T Devices Ltd. 1997).

Canopy opening analysis

The variables were placed into three classes to insure the results were both biologically and statistically relevant: (*i*) variables characterizing the selected western white pine (height, basal diameter, mean annual height increment, and age); (*ii*) variables describing the competing trees of the selected western white pine (number of additional western white pine on the microsite plot and their mean annual height increment and mean annual height increment of western hemlock); and (*iii*) variables from the fish-eye photograph (visible sky (%), yearly below-canopy radiation, number of sunflecks, and total sunfleck duration for June 21, 1999).

We conducted exploratory analysis of individual and combinations of independent (visible sky) and dependent variables (height, diameter) to check for outliers and data behavior (dimension and linearity) using histograms (Ott 1984; Kirk 1995; Johnson 1998). Normality was evaluated using univariate and multivariate normal probability plots and histograms (Ott 1984; Kirk 1995; Johnson 1998). Correlations among variables were investigated within each class using scatterplots, correlation coefficients, principal component analysis, and factor analysis. Normal probability plots and histograms were used to determine if the data were normally distributed and to suggest appropriate transformations for use in later analysis. These included transforming the proportion of visible sky using the arcsine of the square root (referred to as visible sky).

Using scatterplots, relations between the dependent western white pine variables (e.g., height, diameter) and the independent variables (e.g., percentage of visible sky, radiation below canopy) were evaluated. According to the scatterplots, all dependent variables, were related to the independent variables. Many of the scatterplots showed a nonlinear relationship between dependent and independent variables. Therefore, in the statistical analysis, log–linear regression ($\ln(y) = x$) was used rather than linear regression.

A stepwise log–linear regression procedure related each of the dependent variables to the independent variables. 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 regressions. This analysis concluded that visible sky and age as a covariate were the two canopy opening variables that best related to western white pine height and basal diameter.

Three western white pine developmental thresholds, occupancy, competitive advantage, and free to grow, were developed using visible sky as the only independent variable. For the occupancy threshold, we estimated the probability of three or more western white pine (including the sample tree) occupying the microsite plot (60-cm radius) as a function of visible sky. This logistic regression was weighted by the number of western white pine occurring on the microsite plot.

For the competitive advantage and free to grow thresholds we used relative mean annual height increment (RELMAI) between the selected western white pine and the tallest western hemlock (RELMAI = western white pine mean annual height increment (MAI) – western hemlock (MAI) occurring on the 60-cm radius plot). A fourth degree polynomial regression relating RELMAI to visible sky was used to identify a response curve (sigmoid). The competitive advantage threshold was defined at the inflection point where RELMAI dramatically increased, and the free to grow threshold was defined at the inflection point where RELMAI stabilized.

Landscape analysis

Exploratory analysis of the landscape attributes was conducted within each spatial scale (Isaaks and Srivastava 1989; Cressie 1993; Kirk 1995). These analyses used box and scatter plots to ensure the date were free from errors and anomalies. Once again normal probability plots were used to determine if the data were normally distributed. Using the canopy opening model (ln height or ln basal diameter = visible sky + age) and a stepwise approach, we identified interactions and individual scale contributions toward describing the variation of the western white pine characteristics. In some cases, the overall model was significant, but an individual spatial scale was not when observing the partial sum of squares.

When both the overall model and main effects were significant ($P \leq 0.05$), hypothesis testing was conducted by evaluating the predicted square errors from the full model versus predicted square errors from the reduced model (Dielman 1996). A significant F statistic, residual error behavior (residual errors were checked for normality and independence) plus an increase in the adjusted R^2 indicated whether the addition of a spatial scale improved the relationship with the western white pine characteristics. This iterative process was conducted until all relevant combinations of the spatial scales were evaluated.

To evaluate whether the spatial hierarchy influenced the two growth thresholds and the occupancy threshold we used the polynomial and logistic equations without spatial scales and determined that a RELMAI of 4.3 cm occurred at the competitive advantage threshold (inflection point where RELMAI dramatically increased), a RELMAI of 7.3 cm occurred at the free to grow threshold (inflection point where RELMAI stabilized), and two western white pine probabilities (0.57 and 0.80) of occupancy. These values were used in the final equations containing the spatial scales and the equations were solved for visible sky indicating how the spatial scales influenced canopy opening thresholds.

Results

Spatial scale distribution

Within the weathering scale, weakly and moderately weathered classes were represented. The highest plot density occurred within the weakly weathered class (519 of 620) and was distributed across the three watersheds (Table 3). Moderately weathered soils primarily occurred in Deception Creek with only two samples occurring in Beaver Creek. Highly weathered soils were rare within the Coeur d'Alene River basin, and none were sampled.

Differences among geological features can be categorized into whether they were unconsolidated (Qa, Qts) or consoli-

Table 3. Number of plots occurring within each weathering, geological feature, and landtype class within each watershed.

Code	Spatial scale	Watershed Deception Creek	Jordan Creek	Beaver Creek	Total
Weathering					
	Weakly weathered	108	221	190	519
	Moderately weathered	99	—	2	101
	Highly weathered	—	—	—	0
Geological feature					
Kms	Monzonite and sysenite	—	—	5	5
Qa	Alluvial deposits; sand and gravel deposits in active channels	—	13	2	15
Qts	Older gravels; gravel, sand, and silt above modern stream channels	—	—	2	2
Ybk	Burke formation; metamorphosed mudstone; siltite/quartzite	7	—	32	39
Ypl	Lower member of Prichard formation; siltite/argillite/agrillitic quartzite	—	—	16	16
Yr	Revett formation; metamorphosed sandstone; quartzite	68	—	12	80
Ysp	Striped Peak formation; quartzite/siltite/argillite	—	206	6	212
Ysr	St. Regis formation; metamorphosed mudstone; siltite/argillite	132	—	16	148
Ywml	Middle and lower Wallace formation; siliciclastics/argillite/carbonate rocks	—	—	54	54
Ywu	Upper Wallace formation; siltite/argillite/dolomitic siliciclastics	—	2	47	49
Landtype					
130	Stream bottoms and meadows	5	14	2	21
131	Toe slopes on benches above stream floodplains	12	15	—	27
133	Alluvial and colluvial fans at base of steep slopes	2	14	2	18
462	North aspects, moderately weathered	46	—	—	46
466	North aspects, weakly weathered	15	38	39	92
477	North aspects, nondissected stream breaklands	6	12	7	25
480	North aspects, dissected stream breaklands	8	35	48	91
490	North aspect ridge tops, moderately weathered	—	50	6	56
491	North aspect ridge tops, weakly weathered	—	—	2	2
467	North aspects, adjacent to stream drainages	21	8	14	43
464	South aspects, moderately weathered	23	—	—	23
470	South aspects, weakly weathered	6	8	23	37
446	South aspects with shallow stream dissections	28	—	2	30
465	South aspects, slope with deep stream dissections	2	—	—	2
478	South aspects, nondissected stream breaklands with rock outcrops and shallow soils	—	2	7	9
483	South aspects, nondissected stream breaklands	6	9	19	34
488	South aspects, dissected stream breaklands with rock outcrops and shallow soils	—	8	2	10
479	South aspects, dissected stream breaklands	27	—	9	36
468	South aspect toe slopes where one to three streams come together	—	8	10	18

dated (all others) (Table 3). The unconsolidated geological features represent the riparian areas adjacent to stream channels (alluvial deposits) and old gravels. Beaver Creek contained both these geological features, Jordon Creek contained most of the observations within the alluvial deposits. Differences among the consolidated geological features were subtle; only varying by weathering state, composition (quantity and rock type), and structure (layering). For example, both the Striped Peak formation (Ysp) and the St. Regis formation (Ysr) contained siltite and argillite, but the Striped Peak formation also contained quartzite, which weathers into a coarse-textured soil, and St. Regis formation also contained metamorphosed mudstone, which weathers into a fine-textured soil. The Striped Peak (Ysp) geological feature

Table 4. Number of plots occurring in the combinations of landtype and geological features.

	Geological feature										
Landtype	Kms	Qa	Qts	Ybk	Ypl	Yr	Ysp	Ysr	Ywml	Ywu	Total
130	—	2	—	—	—	—	14	5	—	—	21
131	—	7	—	—	—	—	8	12	—	—	27
133	—	6	—	—	—	—	8	2	—	2	18
462	—	—	—	1	—	7	—	38	—	—	46
466	1	—	2	4	11	—	38	17	13	6	92
477	—	—	—	—	—	—	12	6	4	3	25
480	4	—	—	—	—	4	37	10	14	22	91
490	—	—	—	—	—	—	50	—	6	—	56
491	—	—	—	—	—	2	—	—	—	—	2
467	—	—	—	—	2	8	12	21	—	—	43
464	—	—	—	—	—	19	—	4	—	—	23
470	—	—	—	8	2	2	8	10	7	—	37
446	—	—	—	2	—	26	—	2	—	—	30
465	—	—	—	—	—	1	—	1	—	—	2
478	—	—	—	—	—	2	2	—	—	5	9
483	—	—	—	6	—	4	9	2	4	9	34
488	—	—	—	—	—	—	8	2	—	—	10
479	—	—	—	10	1	5	—	16	4	—	36
468	—	—	—	8	—	—	6	—	2	2	18
Total	5	15	2	39	16	80	212	148	54	49	620

Note: Codes and definitions for geological features and landtypes are given in Table 3.

occurred in Jordan Creek, most of the observations of the St. Regis (Ysr) geological feature occurred in Deception Creek, and all the consolidated geological features were represented in Beaver Creek.

A diversity of landtypes occurred in all three watersheds (Table 3). The landtypes (130, 131, 133) describing stream bottoms and alluvial fans occurred in all three watersheds, with most observations occurring in Jordan Creek. Most of the moderately weathered landtypes (462, 464, 490) occurred in Deception and Jordon Creek. In contrast, most of the weakly weathered landtypes (466, 491, 470) occurred in Beaver Creek except for weakly weathered north-facing ridge tops, which occurred in Jordan Creek. Landtypes that contained dissected and nondissected streams (446, 465, 468, 477, 478, 479, 480, 483, 488) were distributed across all three watersheds with Beaver Creek (16 946 ha) containing the highest number followed by Jordan Creek (5317 ha) and Deception Creek (1425 ha), respectively.

The landtypes were distributed among the geological features (Table 4). The alluvial landtypes (130, 131, 133) occurred within the more general alluvial deposit geological feature (Qa). The Striped Peak (Ysp) and St. Regis (Ysr) formations were the most represented geological features and contained the majority of the landtypes. Other geological features that contained a diversity of landtypes included the Burke (Ybk), Revett (Yr), middle and lower Wallace (Ywml), and upper Wallace (Ywu) formations.

Linkages (interactions) among spatial scales

In all cases, when individual spatial scales were added to visible sky and age, they significantly ($P \leq 0.05$) contributed to the positive relationship between western white pine basal diameter and visible sky (Table 5, D1–D4). When geological feature was added to visible sky the adjusted R^2 increased from 0.55 to 0.63, and when landtype was added the adjusted R^2 increased to 0.60. Similar results occurred when spatial scales were added to the equations estimating height (Table 5, H1–H4). For both estimates of basal diameter and height, the best fitting model included a three-way interaction among geological feature, landtype, and visible sky (Table 5, D7 and H7). The western white pine basal diameter model explained 68% of the variation, and for the height, the model explained 64% of the variation.

Geological feature was always significant in the partial sum of squares when estimating both height and basal diameter. Within the geological feature spatial scale, estimated height and diameter of pines growing on the St. Regis formation (Ysr) tended to be larger than the heights and diameters of pines estimated for the other geological features (Tables 6 and 7). Basal diameters of pines growing on Striped Peak (Ysp), middle and lower Wallace (Ywml), and upper Wallace (Ywu) formations were significantly ($P \leq 0.11$) smaller than those estimated for the St. Regis formation (Ysr). Height estimates for pines growing on the upper Wallace (Ywu), middle and lower Wallace (Ywml), and Striped Peak (Ysp) were significantly ($P \leq 0.11$) shorter than those estimated for the St. Regis formation (Ysr).

The landtype spatial scale appeared to play a stronger role in integrating biophysical factors dictating height compared with basal diameter. Western white pines growing on north-facing ridge tops (490) were shorter than pines growing on 14 other landtypes (Table 7). In contrast, pines growing on north-facing ridge tops (490) had smaller basal diameters than pines growing on seven other landtypes (Table 6). Approximately twice as many landtypes were significant for estimating height than for estimating basal diameter.

Results shown in Table 5 (D6, D7, H6, H7) indicate that the site specific response of western white pine growing on these habitats can be linked to the interaction of biophysical properties occurring at multiple spatial scales. Some of these

Table 5. Evaluation of spatial scales in explaining the variation in western white pine basal diameter, height, and relative mean annual height increment in different canopy openings (as defined by visible sky) using full versus reduced model hypothesis testing.

Model No.	Model components	Adjusted R^2	P	Reduced model SSE	Reduced model df	Full model SSE	Full model df	F^b
Ln basal diameter[a]								
D1	Visible sky (S) + age (A)	0.55	0.0001	—	—	138.1	611	—
D2	$S^c + A^c$ + landtype (L)	0.60	0.0001	138.1	611	120.5	594	5.1*
D3	$S^c + A^c$ + geological feature (G)	0.63	0.0001	138.1	611	112.5	602	15.2*
D4	$S^c + A^c$ + weathering (W)	0.57	0.0001	138.1	611	131.5	610	30.6*
D5	$S^c + A^c + W + G + (W \times G)$	0.62	0.0001	—	—	—	—	—
D6a	$S^c + A^c + G + L + (G \times L)$	0.67	0.0001	138.1	611	89.3	541	4.2*
D6b	$S^c + A^c + G^c + L + (G \times L)$	0.67	0.0001	112.5	602	89.3	541	2.3*
D6c	$S^c + A^c + L^c + G + (G \times L)$	0.67	0.0001	120.5	594	89.3	541	3.6*
D7	$S^c + A^c + G^c + L^c + (G^c \times L^c \times S)$	0.68	0.0001	89.3	541	83.2	516	2.9*
Ln height[a]								
H1	S + A	0.53	0.0001	—	—	112.8	616	—
H2	$S^c + A^c + L$	0.58	0.0001	112.8	616	98.9	599	4.9*
H3	$S^c + A^c + G$	0.59	0.0001	112.8	616	95.7	607	12.0*
H4	$S^c + A^c + W$	0.55	0.0001	112.8	616	108.8	615	22.6*
H5	$S^c + A^c + W + G + (W \times G)$	0.60	0.0001	—	—	—	—	—
H6a	$S^c + A^c + G + L + (G \times L)$	0.63	0.0001	112.8	616	79.2	546	3.3*
H6b	$S^c + A^c + G^c + L + (G \times L)$	0.63	0.0001	95.7	607	79.2	546	1.9*
H6c	$S^c + A^c + L^c + G + (G \times L)$	0.63	0.0001	98.9	599	79.2	546	2.6*
H7	$S^c + A^c + G^c + L^c + (G^c \times L^c \times S)$	0.64	0.0001	72.2	521	98.9	599	2.5*
Relative mean annual height increment[a,d]								
R1	S	0.25	0.0001	4140	141	—	—	—
R2	$S^c + L$	0.32	0.0001	4140	141	3382	126	1.9*
R3	$S^c + G$	0.36	0.0001	4140	141	3289	132	3.8*
R4	$S^c + W$	0.25	0.0001	—	—	—	—	—
R5	$S^c + W + G + (W \times G)$	0.36	0.0001	—	—	—	—	—
R6	$S^c + G + L + (G \times L)$	0.36	0.0001	—	—	—	—	—

Note: The adjusted R^2 and P values belong to the full model. All variables are included in the full model. The F value is the result of full versus reduced model test.

[a]For estimating ln basal diameter, N = 613; for estimating ln height, N = 618; and for estimating relative mean annual increment, N = 142.

[b]The F statistic tests the variable addition from the reduced to the full model. *, significant at $P \le 0.05$.

[c]Variables included in the reduced model.

[d]Relative mean annual height increment is the difference between the mean annual increment of western white pine and the mean annual increment of western hemlock.

linkages included the Revett (Yr) formation combined with southern aspects dissected with stream breaklands (479), the upper Wallace (Ywu) formation combined with southern aspects with toe slopes (468), and northern aspects with nondissected stream breaklands (477) (Tables 6 and 7). In addition, many interactions occurred within the St. Regis (Ysr) formation. Conversely, the monzonites (Kms), alluvials (Qa), and old gravels (Qts) did not have any significant interactions (Tables 6 and 7). However, their sample size was rather small, which could explain the lack of interactions (Table 3).

Multiple spatial scales and silvicultural applications

The three developmental thresholds were used to evaluate whether silvicultural practices should be adjusted depending on the landscape setting. The threshold equations indicated there was a 57% probability of western white pine occupying a site when visible sky exceeded 25% and a 80% probability of western white pine occupying the site when visible sky exceeded 45%. Western white pine gains a competitive advantage over western hemlock when visible sky exceeds 55% and is free to grow when visible sky exceeds 92%. However, these results only included the influence of visible sky and only explained 25% of the variation in relative mean annual height increment (Table 5, R1). By adding landtype (adjusted R^2 = 0.32) or geological feature (adjusted R^2 = 0.36) individually to visible sky the amount of variation explained, significantly increased. When landtype and geological feature were both added to the model the relationship was significant ($P \le 0.05$), but according to the full and reduced model comparison, the addition of the two spatial scales did not significantly contribute to the relationship (Table 5, R5 and R6).

Pines growing on alluvials (Qa), old gravels (Qts), and the St. Regis (Ysr) geological features were able to obtain a competitive advantage over western hemlock in relatively

Table 6. The interaction among visible sky (S), geological feature (e.g., Qa, Qts), and landtypes (e.g., 130, 480) for estimating the ln of basal diameter (cm) of western white pine seedlings and saplings.

Parameter	Estimate	SE	*t*	*P* >|*t*|	Parameter	Estimate	SE	*t*	*P* >|*t*|	Parameter	Estimate	SE	*t*	*P* >|*t*|
Intercept*	–1.88	0.32	–5.79	<0.0001	S × Qa × 133	0.75	0.64	1.17	0.24	S × Ysp × 483*	1.03	0.58	1.80	0.07
Visible sky (S)*	0.77	0.45	1.72	0.09	S × Qts × 466	11.53	8.22	1.40	0.16	S × Ysp × 488*	0.53	0.33	1.59	0.11
Kms	–1.39	1.44	–0.96	0.34	S × Ybk × 446	0.41	0.63	0.65	0.52	S × Ysp × 490*	1.47	0.53	2.78	0.01
Qa	–0.49	0.45	–1.08	0.28	S × Ybk × 462	–0.43	0.59	–0.73	0.47	S × Ywml × 466	0.83	0.65	1.28	0.20
Qts	–11.39	8.71	–1.31	0.19	S × Ybk × 466	–0.14	0.57	–0.24	0.81	S × Ywml × 468	1.05	1.00	1.05	0.29
Ybk*	0.70	0.35	1.98	0.05	S × Ybk × 468	0.15	0.63	0.25	0.81	S × Ywml × 470	0.68	0.56	1.22	0.22
Ypl	–0.51	0.68	–0.75	0.46	S × Ybk × 470	–0.29	0.63	–0.45	0.65	S × Ywml × 477	1.06	0.87	1.22	0.22
Yr	0.12	0.30	0.39	0.70	S × Ybk × 479	0.10	0.57	0.18	0.86	S × Ywml × 479	0.90	0.62	1.45	0.15
Ysp*	–0.51	0.21	–2.39	0.02	S × Ybk × 483	–0.56	0.62	–0.90	0.37	S × Ywml × 480	–0.04	0.58	–0.07	0.94
Ywml*	–0.54	0.34	–1.58	0.11	S × Ypl × 466	0.74	0.66	1.13	0.26	S × Ywml × 483*	1.00	0.61	1.65	0.10
Ywu*	–0.69	0.42	–1.64	0.10	S × Ypl × 467	0.99	0.71	1.38	0.17	S × Ywml × 490*	1.70	0.65	2.64	0.01
Ysr	0.00	—	—	—	S × Ypl × 470	0.86	0.71	1.20	0.23	S × Ywu × 133	0.87	0.92	0.94	0.35
130*	1.22	0.42	2.90	0.004	S × Ypl × 479	1.35	1.22	1.10	0.27	S × Ywu × 466	1.02	0.73	1.39	0.16
131*	0.81	0.41	1.99	0.05	S × Yr × 446*	0.82	0.52	1.58	0.11	S × Ywu × 468*	1.25	0.64	1.96	0.05
133*	1.13	0.61	1.85	0.07	S × Yr × 462	0.22	0.55	0.40	0.69	S × Ywu × 477*	1.69	0.81	2.08	0.04
446	0.12	0.46	0.27	0.79	S × Yr × 464	0.73	0.60	1.21	0.23	S × Ywu × 478	–0.46	0.83	–0.56	0.58
462*	0.83	0.38	2.20	0.03	S × Yr × 465	0.93	1.03	0.90	0.37	S × Ywu × 480	0.52	0.63	0.82	0.41
464	0.39	0.53	0.73	0.46	S × Yr × 467	0.51	0.58	0.89	0.38	S × Ywu × 483	0.85	0.86	0.99	0.32
465	0.24	0.56	0.43	0.67	S × Yr × 470	0.12	0.56	0.21	0.83	S × Ysr × 130	–0.10	0.56	–0.18	0.85
466	0.37	0.35	1.07	0.29	S × Yr × 478	–1.37	1.03	–1.33	0.18	S × Ysr × 131	0.52	0.52	1.01	0.31
467	0.29	0.37	0.78	0.44	S × Yr × 479*	1.22	0.66	1.84	0.07	S × Ysr × 133	0.11	0.99	0.11	0.91
468	0.45	0.53	0.85	0.39	S × Yr × 480	–0.33	0.61	–0.55	0.58	S × Ysr × 446	0.80	0.81	0.99	0.32
470	0.55	0.40	1.38	0.17	S × Yr × 483	0.53	0.71	0.74	0.46	S × Ysr × 462	0.60	0.49	1.21	0.23
477	0.44	0.46	0.96	0.34	S × Yr × 490	0.59	0.56	1.05	0.29	S × Ysr × 464	0.21	0.92	0.23	0.82
478	1.76	0.79	2.24	0.03	S × Ysp × 130	–0.04	0.64	–0.07	0.95	S × Ysr × 465	0.00	—	—	—
479	0.22	0.41	0.53	0.60	S × Ysp × 131	0.38	0.58	0.65	0.52	S × Ysr × 466*	0.95	0.48	2.01	0.05
480*	1.00	0.32	3.10	0.002	S × Ysp × 133	–0.22	0.91	–0.24	0.81	S × Ysr × 467*	1.18	0.52	2.28	0.02
483	0.57	0.42	1.35	0.18	S × Ysp × 466	0.86	0.55	1.57	0.12	S × Ysr × 470	0.43	0.51	0.85	0.40
488*	1.16	0.51	2.30	0.02	S × Ysp × 467*	1.01	0.55	1.84	0.07	S × Ysr × 477*	0.92	0.55	1.68	0.09
490	0.00	—	—	—	S × Ysp × 468	0.83	0.72	1.16	0.25	S × Ysr × 479*	1.06	0.55	1.92	0.06
S × Kms × 466	0.32	1.06	0.30	0.77	S × Ysp × 470	0.55	0.59	0.93	0.35	S × Ysr × 480	–0.20	0.47	–0.44	0.66
S × Kms × 480	1.39	1.89	0.73	0.46	S × Ysp × 477	0.83	0.61	1.36	0.17	S × Ysr × 483*	1.14	0.65	1.76	0.08
S × Qa × 130	0.49	0.67	0.73	0.46	S × Ysp × 478	–0.22	0.97	–0.23	0.82	S × Ysr × 488	0.00	—	—	—
S × Qa × 131	0.52	0.64	0.81	0.42	S × Ysp × 480	0.28	0.50	0.56	0.58	Age*	0.07	0.00	21.8	<0.0001

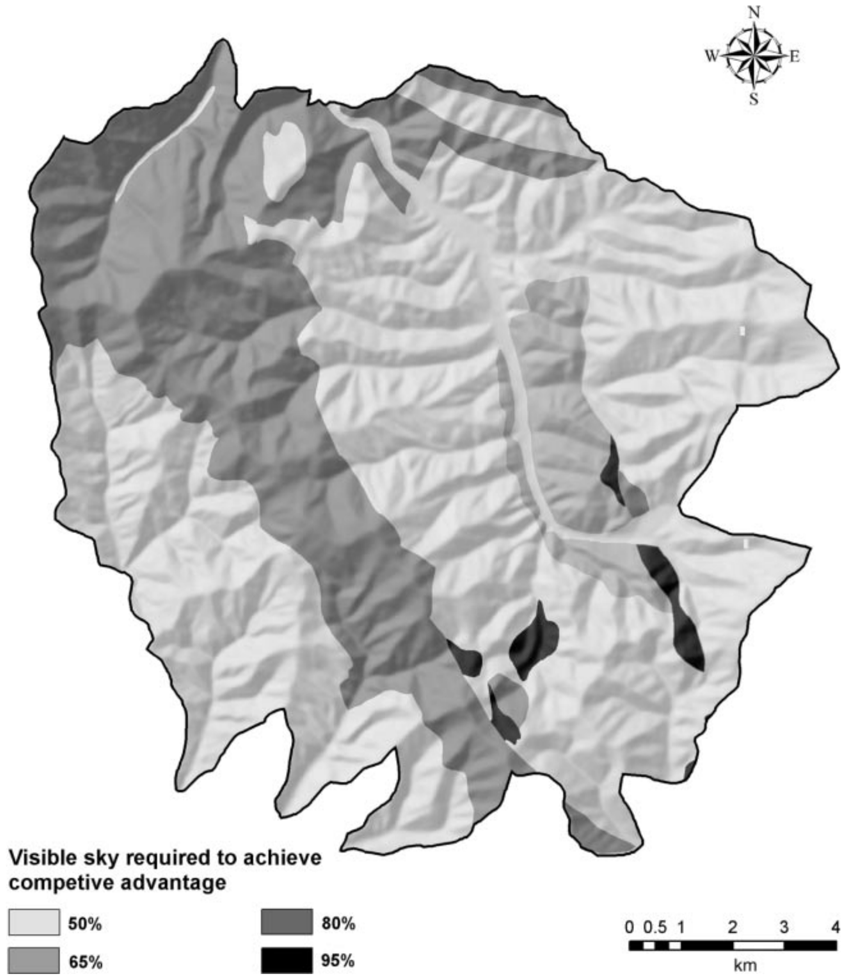
Note: Codes and definitions for geological features and landtypes are given in Table 3.
*Significant variable or interaction ($P \le 0.11$).

Table 7. The interaction among visible sky (S), geological feature (e.g., Qa, Qts), and landtypes (e.g., 130, 480) for estimating ln height (cm) of western white pine seedlings and saplings.

Parameter	Estimate	SE	*t*	*P* >|*t*|	Parameter	Estimate	SE	*t*	*P* >|*t*|	Parameter	Estimate	SE	*t*	*P* >|*t*|
Intercept*	2.29	0.30	7.73	<0.0001	S × Qa × 133	0.16	0.59	0.27	0.79	S × Ysp × 483	0.59	0.53	1.10	0.27
Visible sky (S)	0.30	0.42	0.71	0.48	S × Qts × 466	10.18	7.62	1.34	0.18	S × Ysp × 488	0.30	0.31	0.96	0.34
Kms	–1.04	1.34	–0.78	0.44	S × Ybk × 446	0.43	0.59	0.74	0.46	S × Ysp × 490*	1.61	0.48	3.32	0.001
Qa	0.24	0.42	0.58	0.56	S × Ybk × 462	0.20	0.55	0.36	0.72	S × Ywml × 466	0.88	0.61	1.45	0.15
Qts	–9.80	8.07	–1.21	0.23	S × Ybk × 466	0.07	0.52	0.14	0.89	S × Ywml × 468	1.24	0.86	1.45	0.15
Ybk	0.31	0.33	0.95	0.34	S × Ybk × 468	0.76	0.58	1.31	0.19	S × Ywml × 470	0.64	0.52	1.23	0.22
Ypl	0.22	0.63	0.35	0.73	S × Ybk × 470	0.09	0.59	0.16	0.88	S × Ywml × 477	0.94	0.80	1.17	0.24
Yr	0.01	0.28	0.04	0.97	S × Ybk × 479	0.39	0.52	0.75	0.46	S × Ywml × 479	0.86	0.57	1.51	0.13
Ysp*	–0.37	0.20	–1.85	0.06	S × Ybk × 483	–0.57	0.57	–0.99	0.32	S × Ywml × 480	–0.02	0.54	–0.03	0.97
Ywml*	–0.54	0.32	–1.71	0.09	S × Ypl × 466	0.28	0.61	0.47	0.64	S × Ywml × 483	0.74	0.56	1.31	0.19
Ywu*	–0.70	0.39	–1.81	0.07	S × Ypl × 467	0.61	0.66	0.93	0.35	S × Ywml × 490*	2.10	0.60	3.53	0.001
Ysr	0.00	—	—	—	S × Ypl × 470	0.16	0.66	0.24	0.81	S × Ywu × 133	1.12	0.85	1.31	0.19
130*	1.26	0.39	3.28	0.001	S × Ypl × 479	0.45	1.13	0.39	0.69	S × Ywu × 466*	1.17	0.68	1.72	0.09
131*	0.90	0.37	2.41	0.02	S × Yr × 446	0.49	0.48	1.03	0.30	S × Ywu × 468*	1.28	0.59	2.16	0.03
133*	1.35	0.57	2.39	0.02	S × Yr × 462	0.46	0.51	0.89	0.37	S × Ywu × 477*	1.78	0.75	2.37	0.02
446*	0.79	0.42	1.85	0.06	S × Yr × 464	0.54	0.53	1.02	0.31	S × Ywu × 478	–0.51	0.77	–0.67	0.50
462*	0.83	0.34	2.40	0.02	S × Yr × 465	0.49	0.96	0.51	0.61	S × Ywu × 480	0.61	0.58	1.05	0.29
464*	0.85	0.47	1.80	0.07	S × Yr × 467	0.65	0.54	1.22	0.22	S × Ywu × 483	0.57	0.79	0.72	0.47
465	0.76	0.52	1.48	0.14	S × Yr × 470	0.19	0.52	0.36	0.72	S × Ysr × 130	0.14	0.52	0.27	0.79
466*	0.59	0.32	1.87	0.06	S × Yr × 478	–1.18	0.95	–1.24	0.22	S × Ysr × 131	0.71	0.48	1.47	0.14
467*	0.63	0.34	1.86	0.06	S × Yr × 479*	1.16	0.61	1.89	0.06	S × Ysr × 133	–0.06	0.92	–0.06	0.95
468	0.32	0.49	0.65	0.51	S × Yr × 480	–0.20	0.56	–0.36	0.72	S × Ysr × 446	0.12	0.75	0.16	0.87
470*	0.91	0.37	2.48	0.01	S × Yr × 483	0.17	0.66	0.26	0.79	S × Ysr × 462*	0.83	0.46	1.83	0.07
477	0.52	0.42	1.25	0.21	S × Yr × 490	0.79	0.52	1.54	0.13	S × Ysr × 464	0.00	0.82	0.00	1.00
478*	2.09	0.73	2.87	0.004	S × Ysp × 130	0.20	0.60	0.33	0.74	S × Ysr × 465	0.00	—	—	—
479	0.45	0.38	1.19	0.23	S × Ysp × 131	0.56	0.54	1.03	0.31	S × Ysr × 466*	0.86	0.44	1.95	0.05
480*	1.31	0.29	4.46	<0.0001	S × Ysp × 133	0.02	0.84	0.02	0.98	S × Ysr × 467*	1.06	0.48	2.21	0.03
483*	1.18	0.39	3.04	0.002	S × Ysp × 466*	0.82	0.51	1.62	0.10	S × Ysr × 470	0.37	0.47	0.78	0.44
488*	1.61	0.47	3.45	0.001	S × Ysp × 467*	0.82	0.51	1.61	0.11	S × Ysr × 477*	0.94	0.51	1.86	0.06
490	0.00	—	—	—	S × Ysp × 468	1.04	0.67	1.57	0.12	S × Ysr × 479*	0.96	0.51	1.87	0.06
S × Kms × 466	0.73	0.98	0.74	0.46	S × Ysp × 470	0.42	0.54	0.76	0.45	S × Ysr × 480	–0.23	0.43	–0.52	0.60
S × Kms × 480	0.91	1.76	0.52	0.61	S × Ysp × 477*	0.98	0.57	1.72	0.09	S × Ysr × 483	0.62	0.60	1.04	0.30
S × Qa × 130	0.12	0.62	0.19	0.85	S × Ysp × 478	–0.47	0.89	–0.53	0.60	S × Ysr × 488	0.00	—	—	—
S × Qa × 131	0.10	0.60	0.16	0.87	S × Ysp × 480	0.15	0.46	0.33	0.74	Age*	0.07	0.00	23.01	<0.0001

Note: Codes and definitions for geological features and landtypes are given in Table 3.
*Significant variable or interaction ($P \leq 0.11$).

Fig. 3. The opening size (defined by percent visible sky) required for western white pine to achieve a competitive advantage over western hemlock in the Beaver Creek watershed. Competitive advantage was achieved with 50% visible sky on the old gravels (Qts), alluvials (Qa), St. Regis (Ysr), middle and lower Wallace (Ywml), and lower Prichard (Ypl) geological features; 65% visible sky on the upper Wallace (Ywu) feature; 80% visible sky on the Revett (Yr) and Burke (Ybk) features; and 95% visible sky on the monzonites (Kms) and Striped Peak (Ypk) features. Definitions for the geological features are given in Table 3.



small canopy openings (50% visible sky) compared with those growing on the Revett (Yr), Burke (Ybk), Monzonites (Kms), and Striped Peak (Ysp) geological features (80–95% visible sky) (Fig. 3). In addition, the occupancy threshold (probability of three or more pines occurring on the 60-cm plot) was related to visible sky, weathering, and geological features (Table 8, O5). This equation showed that western white pine could occupy openings with less visible sky on the Striped Peak (Ysp) formation compared with the amount of visible sky required for pines to occupy settings on the Revett (Yr) and Monzonites (Kms). These results provide information useful for adjusting silvicultural treatments depending on the landscape.

Discussion

Validation of hierarchical concepts

Weathering, geological features, landtypes, and canopy openings may form an imperfect hierarchy, but it appears to be effective in this setting. Theoretically, a spatial hierarchy should have multiple levels that are nested (Allen et al. 1984; O'Neill et al. 1986). Higher levels within the hierarchy should have larger spatial extents and contain or constrain lower levels within the hierarchy (Allen and Starr 1982; Delcourt and Delcourt 1988). Weathering (highest level) did not always have the largest spatial extent. In some cases, lower levels within the hierarchy had different weathering classes (Fig. 2). Also landtypes were not unique to the geological features and landtype boundaries crossed geologic and weathering boundaries. Our intention was not to define the perfect hierarchy but to use available information at multiple spatial scales to reflect variation in topography, soil development, soil movement, and microsite climate. The broader scales (weathering and geological feature) reflect variation in long-term soil development and climate and the finer scales (landtype and canopy opening) reflect variation in microsite climate. This variation directly or indirectly influences light, nutrition, water availability, heat, and other factors that shape the operational environment (interaction of biophysical factors with the plant) that regulates vegetation response (Spomer 1973; Jackson and Spomer 1979). The development of western white pine seedlings and sap-

Table 8. Evaluation of spatial scales in explaining the variation in western white pine occupancy in different canopy openings (defined by visible sky) using logistic regression.

Model No.	Model components	Likelihood ratio *P* value (χ^2 statistic) for occupancy: Overall model	Visible sky	Second variable[a]	Third variable	Fourth variable
O1	Visible sky (S)	0.0005	0.006			
O2	S + weathering (W)	0.0001	0.006	0.0003		
O3	S + geological feature (G)	0.0001	0.008	0.006		
O4	S + landtype (L)	0.0001	0.005	0.140		
O5	S + W + G	0.0001	0.010	0.003	0.05	
O6	S + G + L	0.0001	0.010	0.820	0.56	
O7	S + G + W + (G × W)	0.0001	0.010	0.020	0.06	0.20

Note: Occupancy of a site occurs when three or more western white pines occupy a 60-cm radius plot.
[a]Significance of second (e.g., O2, weathering), third (e.g., O5, geological feature), or fourth (e.g., O7, geological feature × weathering) variable included in the model.

lings were directly or indirectly influenced by the spatial hierarchy: 68% of the variation in western white pine basal diameter and 64% of the variation in height were explained by the spatial hierarchy (Table 5, D7 and H7).

We hypothesized that as progressively broader levels were added to the spatial hierarchy the explanatory power of the models would increase, and the broader levels would explain less height or diameter variation than finer levels. As expected, visible sky had the highest adjusted R^2 when predicting either variable. However, landtype did not always explain the next greatest proportion of the variation in diameter or height. Landtype was significant when added to visible sky and age for estimating both western white pine basal diameter and height; however, it only explained an additional 5% of the variation (Table 5, D2 and H2). In contrast, in both cases an additional 8% of the variation in basal diameter and an additional 6% of the variation in height were explained by geological features (Table 5, D3 and H3). Although there was only a small increase by adding the broader scale (geological features) the model did explain more of the variation in diameter or height than the finer scale (landtype). Reasons for this discrepancy could be caused by either sampling density or spatial scale definition. However, we do not believe sampling density affected the hierarchy, because the standard errors for height and diameter were similar for all landtypes discounting this problem, although there were different sampling densities (two- to five-fold; Table 3) across the 19 landtypes.

Some may argue that potential vegetation type is a more appropriate variable for defining spatial scales than the ones we chose. Potential vegetation type is a classification system that partitions the physical environment through the use of indicator species (Pfister 1989; Fassnatcht and Gower 1998). Ferguson et al. (1986) did not find a significant relationship between western white pine seedling characteristics and potential vegetation type. Moreover, landtypes used in this study (which include landform, slope, aspect, and soils in addition to potential vegetation type) did relate to western white pine basal diameter and height, supporting the use of landtypes rather than potential vegetation types to define spatial scales.

In our study, there were 19 landtypes, adding noise to the western white pine height and basal diameter estimates. Landtypes could be grouped, but as hierarchy theory implies, geological features (a broader spatial scale) should constrain the variation represented in the finer landtype scale. Thus, the geological feature spatial scale, in theory, was grouping landtypes as a function of the biophysical factors operating at this broader spatial scale. A significant interaction among visible sky, geological features, and landtype explained an additional 13% (Table 5, D7) of the variation in western white pine basal diameter and an additional 11% (Table 5, H7) of the variation in height compared with the models containing visible sky and age alone (Table 5, D1 and H6). This indicates that the variation in western white pine tree characteristics was better explained when landtypes were linked to a higher level within the spatial hierarchy. With similar findings, Fassnatcht and Gower (1998) linked forest potential vegetation types to a broader spatial scale defined on soil nutrition and moisture using this procedure. They were better able to detect a significant positive response in leaf area index and forest net primary productivity, relative to using potential vegetation type alone. Our results verified the hierarchical concept that properly defined spatial scales are linked and broader scales constrain or contain finer scales (Allen and Starr 1982; O'Neill et al. 1986; Delcourt and Delcourt 1988).

Scale definition in relation to multiple-scale biophysical factors

In a perfect hierarchy, the finest scale canopy opening should integrate factors that influence the microsite environment created by fine-scale disturbances such as windthrow, insects, wildfires, and harvesting. These disturbances create variation in vegetation depending on the growing space they provide (Pickett and White 1985; Canham 1989; Oliver and Larson 1990; Chandler et al. 1991; Agee 1993; Moeur 1997; Debano et al. 1998). Our finest scale, canopy opening, as measured by percent visible sky, in addition to light, most likely influenced temperature, moisture, and stand dynamics, which subsequently influenced western white pine seedling and sapling growth. Moreover, the greatest portion of the variation in western white pine diameter and height was explained by age and this fine spatial scale (55% of the variation in basal diameter and 53% of the variation in height) (Table 5, D1 and H1). Therefore, it appears that our finest spatial scale defined by visible sky, does a good job of inte-

Fig. 4. The relationship between basal diameter (including standard error bars) of 10-year-old western white pines and canopy opening (defined by visible sky) varies with landtype and geological feature (Table 5, D7). Landtype 467 (north aspects adjacent to streams) and landtype 470 (south aspects) are shown within the St. Regis (Ysr) geological features.

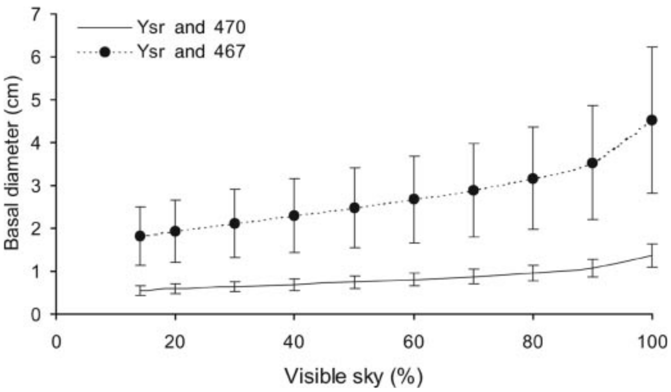
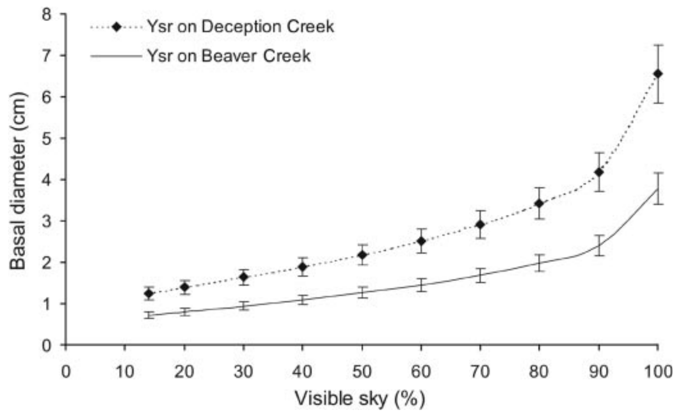


Fig. 5. The relationship between basal diameter (including standard error bars) of 10-year-old western white pine and canopy opening (defined by visible sky) varies within a geological feature between locations. The model, ln(basal diameter) = visible sky + age + location (Beaver Creek, Deception Creek) used only plots occurring on the St. Regis geological feature (Ysr).



grating the operational environment that influences site specific responses.

Visible sky did not, however, reflect differences in the operational environment expressed by geomorphology. An additional spatial scale was needed to account for this mid-level variation. The results from this study showed that western white pine diameter and height were influenced by landform, elevation, aspect, and soils, which were reflected in the landtype spatial scale. For example, the basal diameters of western white pines, growing on settings within landtype 467, were larger than the basal diameters of pines of the same age growing on landtype 470 (Fig. 4). Both of these lands types had abundant water, contained volcanic ash soils, and were located adjacent to streams. Therefore, we believe that the 19 landtypes we used in this study integrated more than just soils and water of the midscale environment and were useful in predicting western white pine tree characterisitics (5% improvement; Table 5).

Geological feature was intended to reflect geological and geomorphological characteristics that change slowly over time (Klijn 1994). This spatial scale was to reflect soil nutrition, water-holding capacity, belowground water flow, and regional climate (Godron 1994; Klijn 1994; Shen et al. 2000). Because the St. Regis formation (Ysr) occurs both in Deception Creek and Beaver Creek, we were able to test this hypothesis. Deception Creek averages 127–135 cm of precipitation annually, and Beaver Creek averages 84–95 cm. We found trees of the same age growing on the St. Regis formation in Beaver Creek had significantly smaller diameters than those growing on the same formation in Deception Creek (Fig. 5). Because the watersheds were located in different areas within the Coeur d'Alene River basin, a spatial scale defined by geological features can also represent a different moisture regime (Fig. 1).

Applying a spatial hierarchy

In this study, the spatial scales do not represent the classification system (e.g., landtype) or named variable (e.g., Striped Peak) alone, but they incorporate climate, soil formation, disturbance, and other biophysical factors operating within each spatial scale. Hierarchies defined this way provide more insight into the processes and structures occurring in the scales than do hierarchies defined geographically (e.g., stand, subwatershed, river basin, region) or politically (e.g., counties, provinces). Geographical and political hierarchies do not reflect the biophysical factors occurring within and among the delineated areas that influence vegetation development (Jackson and Spomer 1979; Crawley 1986; Pfister 1989; Aber and Melillo 1991; Cooper et al. 1991). From this perspective, inferences made using a spatial hierarchy based on biophysical factors are more robust, because they directly or indirectly identify environments unique to a specific geographical area.

We identified the contribution each spatial scale made toward explaining the variation in western white pine tree characteristics. More importantly, we determined that linkages among spatial scales better described vegetation response than any single scale. These results compliment the extensive site-specific knowledge about western white pine regeneration and development (Haig et al. 1941; Minore 1979; Ferguson et al. 1986; Graham 1990), and this knowledge from the hierarchy could be used to design and apply silvicultural treatments. For example, western white pine gained a competitive advantage over western hemlock in smaller openings (50% visible sky) when growing on the St. Regis (Ysr) formation, alluvials (Qa), and old gravels (Qts) compared with western white pines growing on the Striped Peak formation (90% visible sky). Silvicultural treatments can be adjusted to reflect the variation in biophysical factors represented by the spatial hierarchy, thus linking site-specific vegetation responses to the landscape (Fig. 3).

The example used to show how geological features integrated midscale biophysical factors, also shows how the scales reflect "place". Western white pines (same age) growing in Deception Creek, on the St. Regis formation, had larger basal diameters than pines growing on the St. Regis formation in Beaver Creek (Ysr) (Fig. 5). Deception Creek receives more moisture and has more developed soils than Beaver Creek, resulting in larger western white pines. Because of the spatial variation in this study, we would not assume that western white pines growing on the St. Regis formation in other geographic areas would behave as they did in Deception Creek, because the results are tied to the location where they occur. This concept of "place" is inherent to all spatial hierarchies and not only to those defined by soil forming processes.

Limitations

As with all studies, this one has some limitations. Because the sampling densities varied among the categories within each spatial scale, we had an unbalanced experimental design, making this study more exploratory rather than confirmatory. True replication would be impossible, since the objective of this study was never intended to eliminate sources of variation due to place but to indirectly integrate these sources of variation making it difficult to infer cause and effect. There are several ways to define a hierarchy (e.g., geography, climate, disturbance); therefore, we cannot say our hierarchy was the most effective. Our choice was limited by available data and by the requirement of defining a hierarchy on factors related to soil development. The explanatory power of the hierarchy was significant but not remarkable, and although it was imperfect, it nevertheless was useful. This study did not quantify or relate specific biophysical factors to the spatial scales, but future studies could be conducted to accomplish this task. Although there were limitations of our study, we related the landscape spatial scales to a site-specific response. Moreover, the interactions among the spatial scales provided evidence that the spatial scales were linked, thus indicating that multiple spatial scales describe vegetation response better than a single scale.

Summary

This study provides new information that may be useful to other endeavors that consider using multiple spatial scales to explain ecological phenomena. We defined our spatial scales integrating short- and long-term climate, geomorphic processes (e.g., soil creep, deposition, erosion), soil weathering, bedrock, and topographic and physiographic features that influence individual plants to entire forests. This approach of defining scales using biophysical factors would have applicability to ecological questions that have both spatial and operational dimensions. Moreover, when biophysically defined scales are linked they provide insight on ecosystem structures, processes, and functions.

Acknowledgments

We thank the USDA Forest Service, Rocky Mountain Research Station for funding our research. Gerald Neihoff from the Idaho Panhandle National Forests; Dr. Mike Zientek, Dr. Tom Frost, and Pam Derkey from the United States Geological Survey; and Dr. Reed Lewis from the Idaho Geological Survey provided invaluable help in acquiring the landtype and geological information used in the study. A special thanks to Jeff Evans for managing data and providing critical evaluation of the work, Jamie Baker for manuscript processing, and to the manuscript reviewers.

References

Aber, J.D., and Melillo, J.M. 1991. Terrestrial ecosystems. Sanders College Publishing, Philadelphia, Pa.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Allen, T.F., and Starr, T.B. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Ill.

Allen, T.F., O'Neill, R.V., and Hoekstra, T.W. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA For. Serv. Gen. Tech. Rep. RM-110.

Bailey, R.G. 1995. Description of the ecoregions of the United States. U.S. Dep. Agric. Misc. Publ. 1391.

Bingham, R.T., Hoff, R.J., and McDonald, G.I. 1973. Breeding blister rust resistant western white pine VI. First results from field testing of resistant planting stock. USDA For. Ser. Res. Note INT-179.

Bradshaw, F.J. 1992. Quantifying edge effect and patch size for multiple-use silviculture: a discussion paper. For. Ecol. Manage. **48**: 249–264.

Brady, N.C. 1974. The nature and properties of soils. Macmillan Publishing Co., Inc., New York.

Brown, A., Birks, H.J., and Thompson, D.B. 1993. A new biogeographical classification of the Scottish uplands II. Vegetation–environment relationships. J. Ecol. **81**: 231–251.

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. Ecology, **70**: 548–550.

Carter, R.E., and Klinka, K. 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. For. Ecol. Manage. **55**: 87–105.

Chandler, C., Cheney, P., Thomas, P., Trabaud, L., and Williams, D. 1991. Fire in forestry: forest fire behavior and effects. Krieger Publishing Co., Malabar, Fla.

Cherrill, A.J., McClean, C., Watson, P., Tucker, K., Rushton, S.P., and Sanderson, R. 1995. Predicting the distributions of plant species at the regional scale: a hierarchical matrix model. Landsc. Ecol. **10**: 197–207.

Coates, K.D., and Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manage. **99**: 337–354.

Cooper, S.V., Neiman, K.E., and Roberts, D.W. 1991. Forest habitat types of northern Idaho: a second approximation. USDA For. Serv. Gen. Tech. Rep. INT-236.

Crawley, M.J. 1986. The structure of plant communities. *In* Plant ecology. *Edited by* M.J. Crawley. Blackwell Scientific Publications, London. pp. 1–50.

Cressie, N.A. 1993. Statistics for spatial data. John Wiley & Sons, Inc., New York.

Dale, M.R.T. 1999. Spatial pattern analysis in plant ecology. Cambridge University Press, Cambridge, Mass.

Daubenmire, R. 1953. Classification of the conifer forests of eastern Washington and northern Idaho. Northwest Sci. **27**: 17–24.

Debano, L.F., Neary, D.G., and Ffolliott, P.F. 1998. Fire's effects on ecosystems. John Wiley & Sons, Inc., New York.

Delcourt, H.R., and Delcourt, P.A. 1988. Quaternary landscape ecology: relevant scales in space and time. Landsc. Ecol. **2**: 23–44.

Delta-T Devices Ltd. 1997. HemiView. Delta-T Devices Ltd., Burell, Cambridge, U.K.

Dielman, T.E. 1996. Applied regression analysis for business and economics. Wadsworth Publishing Co., Belmont, Calif.

Fassnatcht, K.S., and Gower, S.T. 1998. Comparison of soil and vegetation characteristics of six upland forest habitat types in north central Wisconsin. North. J. Appl. For. **15**: 69–76.

Ferguson, D.E., Boyd, R.J., and Stage, A.R. 1986. Predicting regeneration in the grand fir – cedar – hemlock ecosystem of the northern Rocky Mountains. For. Sci. Monogr. 26. **32**: 1–41.

Godron, M. 1994. The natural hierarchy of ecological systems. *In* Ecosystem classification for environmental management. *Edited by* F. Klijn. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 69–83.

Graham, R.T. 1990. Silvics of western white pine. *In* Silvics of North America. Vol. 1. Conifers. *Technical coordinators*: R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 385–394.

Haig, I.T. 1936. Factors controlling initial establishment of western white pine and associated species. Yale Univ. Sch. For. Bull. 41.

Haig, I.T., Davis, K.P., and Weidman, R.H. 1941. Natural regeneration in the western white pine type. U.S. Dep. Agric. Tech. Bull. 767.

Harrison, J.E., and Jobin, D.A. 1963. Geology of the Clark Fork quadrangle, Idaho–Montana. U.S. Geol. Surv. Bull. 1141-k.

Harrison, J.E., and Jobin, D.A. 1965. Geologic quadrangle map: geologic map of the Packsaddle Mountain quadrangle, Idaho. U.S. Geological Survey, Washington, D.C.

Hinckley, T.M., Sprugel, D.G., Brooks, J.R., Brown, K.J., Martin, T.A., Roberts, D.A., Schaap, R.W., and Wang, D. 1998. Scaling and integration in trees. *In* Ecological scale: theory and applications. *Edited by* D.L. Peterson and T.V. Parker. Columbia University Press, New York. pp. 309–337.

Hobbs, W.S., Griggs, A.B., Wallace, R.E., and Campbell, A.B. 1965. Geology of the Coeur d'Alene district, Shoshone County, Idaho. U.S. Geol. Surv. Prof. Pap. 478.

Hoff, R.J. 1984. Resistance to *Cronartium ribicola* in *Pinus monticola*: higher survival of infected trees. USDA For. Ser. Res. Note INT-343.

Hoff, R.J., and Steinhoff, R.J. 1980. Comparative growth rates of western white pine varieties resistant to blister rust. USDA For. Ser. Res. Note INT-290.

Hosterman, J.W. 1956. Geology of the Murray area, Shoshone County, Idaho. U.S. Geol. Surv. Bull. 1027-P.

Idaho Panhandle National Forests (IPNF). 1998. Toward an ecosystem approach: an assessment of the Coeur d'Alene River Basin: summary. USDA For. Serv. Ecosyst. Pap. 4.

Isaaks, E.H., and Srivastava, M.R. 1989. An introduction to applied geostatistics. Oxford University Press, Oxford, N.Y.

Jackson, P.A., and Spomer, G.G. 1979. Biophysical adaptions of four western conifers to habitat water conditions. Bot. Gaz. **140**: 428–432.

Jenny, H. 1980. The soil resource: origin and behavior. Springer-Verlag, New York.

Johnson, D.E. 1998. Applied multivariate methods for data analysis. Brooks/Cole Publishing, Pacific Grove, Calif.

Kirk, R.E. 1995. Experimental design procedures for the behavioral sciences. Brooks/Cole Publishing, Pacific Grove, Calif.

Klijn, F. 1994. Spatially nested ecosystems: guidelines for classification from a hierarchical perspective. *In* Ecosystem classification for environmental management. *Edited by* F. Klijn. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 85–116.

Lawton, R.O., and Putz, R.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology, **69**: 764–777.

Lertzman, K.P., Sutherland, G.D., Inselberg, A., and Saunders, S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology, **77**: 1254–1270.

Lewis, R.S., and Derkey, P.D. 1999. Digital geologic map of the Thompson Falls 1 : 100 000 quadrangle, Idaho. U.S. Geological Survey, Spokane, Wash. Open-File Rep. 99-438.

Lewis, R.S., Burmester, R.F., and McFadden, M.D. 1999. Digital geologic map of the Wallace 1 : 100 000 quadrangle, Idaho. U.S. Geological Survey, Spokane, Wash. Open-File Rep. 99-390.

Matérn, B. 1986. Spatial variation. 2nd ed. Springer-Verlag, New York.

Miller, R.S., Burmester, R.F., McFadden, M.D., Derkey, P.D., and Oblad, J.R. 1999. Digital geologic map of the Sandpoint 1- by 2-degree quadrangle, Washington, Idaho, and Montana. U.S. Geological Survey, Spokane, Wash. Open-File Rep. 99-144.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species — a literature review. USDA For. Ser. Gen. Tech. Rep. PNW-87.

Moeur, M. 1997. Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla*/*Thuja plicata* forests. For. Ecol. Manage. **94**: 175–186.

Munts, S.R. 2000. Digital geologic map of Coeur d' Alene 1 : 100 000 quadrangle, Idaho and Montana. U.S. Geological Survey, Spokane, Wash. Open-File Rep. 00-135.

Norman, J.M., and Campbell, G.S. 1989. Canopy structure. *In* Plant physiological ecology: field methods and instrumentation. *Edited by* R.W. Percy, J. Ehlerginger, H.A. Mooney, and P.W. Rundel. Chapman & Hall, London. pp. 301–326.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., and Allen, T.F. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, N.J.

Oliver, C.D., and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill Inc., New York.

Ott, L. 1984. An introduction to statistical methods and data analysis. Prindle, Weber & Schmidt Publishers, Boston, Mass.

Parsons, W.F.J., Knight, D.H., and Miller, S.L. 1994. Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different size. Ecol. Appl. **4**: 354–362.

Pfister, R.D. 1989. Basic concepts of using vegetation to build a site classification system. *In* Proceedings — Land Classifications Based on Vegetation: Applications for Resource Management. *Edited by* D.E. Ferguson, P. Morgan, and F.D. Johnson. USDA For. Serv. Gen. Tech. Rep. INT-257.

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbances and patch dynamics. Academic Press, Inc., New York.

Rich, P.M. 1988. Video image analysis of hemispherical canopy photography. *In* First Special Workshop on Videography — American Society for Photogrammetry and Remote Sensing. *Edited by* P.W. Mausel. American Society for Photogrammetry and Remote Sensing, Bethesda, Md. pp. 84–95.

Rich, P.M. 1989. A manual for analysis of hemispherical canopy photography. Los Alamos Library, Los Alamos, N.M.

Quigley, T.M., and Arbelbide, S.J. 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. USDA For. Serv. Gen. Tech. Rep. PNW-405.

Runkle, J.R. 1992. Guidelines and sample protocol for sampling forest gaps. USDA For. Serv. Gen. Tech. Rep. PNW-283.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchal analysis. Ecol. Appl. **9**: 135–151.

Schoeneberger, P.J., Wysocki, D.A., Benham, E.C., and Broderson, W.D. 1998. Field book for describing and sampling soils, version 1.1 ed. USDA Natural Resources Conservation Service, National Soil Survey Center, Lincoln, Nebr.

Shen, G., Moore, J.A., and Hatch, C.R. 2000. The effect of habitat type and rock type on individual tree basal area growth response to nitrogen fertilization. Can. J. For. Res. **30**: 613–623.

Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? Ecology, **79**: 23–30.

Song, B., Chen, J., Desanker, P.D., Reed, D.D., Bradshaw, G.A., and Franklin, J.F. 1997. Modeling canopy structure and heterogeneity across scales: from crowns to canopy. For. Ecol. Manage. **96**: 217–229.

Spomer, G.G. 1973. The concepts of "interaction" and "operational environment" in environmental analysis. Ecology, **54**: 200–204.

U.S. Department of Agriculture (USDA). 1999. Soil taxonomy: a basic system classification for making and interpreting soil surveys. U.S. Dep. Agric. Agric. Handb. 436.

Veenendall, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K., and Mullins, C.E. 1995. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. J. Ecol. **83**: 83–90.

Wilczynski, C.J., and Pickett, S.T.A. 1993. Fine root biomass within experimental canopy gaps evidence for a below-ground gap. J. Veg. Sci. **4**: 571–574.

Zhang, Q., and Zak, J.C. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest. Ecology, **76**: 2196–2204.