BIOPHYSICAL CHARACTERISTICS INFLUENCING GROWTH AND ABUNDANCE OF WESTERN WHITE PINE (*PINUS MONTICOLA*) ACROSS SPATIAL SCALES IN THE COEUR D'ALENE RIVER BASIN, IDAHO

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Major Professor: Penelope Morgan, Ph.D.

AUTHORIZATION TO SUBMIT

DISSERTATION

This dissertation of Theresa Benavidez Jain, submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled "Biophysical Characteristics Influencing Growth and Abundance of Western White Pine (*Pinus monticola*) Across Spatial Scales in the Coeur d' Alene River Basin, Idaho," has been reviewed in final form. Permission, as indicted by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

During the past 50 years the moist forests of northern Idaho changed from being dominated by western white pine (*Pinus monticola*), an early seral species, to ones dominated by late seral species, grand fir (*Abies grandis*) and western hemlock (*Tsuga heterophylla*). Variable fire regimes, successional processes and endemic insects and pathogens worked in concert to produce the stable and resilient forests of the past. This conversion to late seral species would take 200 to 300 years depending on fire regime but because of the destabilizing impacts primarily from white pine blister rust (*Cronartium ribicola*), it took less than 50 years in many places. To reverse these trends and elevate forest stability and resiliency, there is considerable interest in increasing western white pine's abundance.

I conducted three studies in the 350,000 ha, Coeur d'Alene River Basin in northern Idaho. In the first study, I related historical (1930s) western white pine occurrence, abundance, and productivity (outcomes) to a spatial hierarchy defined by weathering, geological feature, and landtype. Using classification and regression trees, I identified the individual and combinations of landtypes and geological features that were related to the outcomes. In the second study, I related western white pine growth to canopy opening (visible sky). In 1999, 620 observations on western white pine seedlings and saplings growing in three watersheds were collected across elevation, aspect, and canopy opening gradients. Using log-linear and logistic regression, I detected positive ($p \leq .05$) relationships between western white pine growth and visible sky. Occupancy (> 25%), competitive advantage (> 50%), and free to grow (> 92%) visible sky thresholds were identified. In the third, study I combined elements from the first two studies to relate western white pine growth to four spatial scales (canopy opening, landtype, geological feature, and weathering).

A log-linear regression model using these spatial scales explained 73% of the variation in western white pine growth. These three studies provided insight into ecosystem function, and the techniques and procedures are useful for future ecological studies. These studies can help inform decisions for increasing the abundance of western white pine in the Coeur d'Alene River Basin.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

In this dissertation I combine knowledge from soil science, gap ecology, species silvics, hierarchy theory, and silviculture to identify biophysical characteristics occurring across multiple spatial scales that influence the growth and historical abundance, presence, absence, and productivity of western white pine (*Pinus monticola*). The study was conducted in the 350,000 ha Coeur d'Alene River Basin in northern Idaho.

The dissertation contains three chapters and three appendices. Chapter 1 includes the introduction, a short literature review, and the research problem. Chapter 2 summarizes the important results from three studies located in the appendices. Chapter 3 discusses and blends the results from the three studies addressing the overall research objective and makes suggestions for future research. Next is the list of references used in the main dissertation. Each of the three appendices contains a complete manuscript (introduction, methods, results, discussion, literature cited) written in the format reflecting a journal where it will be submitted.

CHAPTER 1 - INTRODUCTION

The forests of northern Idaho differ from most other forests of the Interior West. They receive abundant precipitation from moisture-laden air masses originating in the Pacific Ocean, resulting in a modified maritime climate. In addition, deep layers of volcanic ash soils are distributed throughout the region. These conditions create a highly productive and diverse environment favoring many plant and wildlife species providing high economic, social, and ecological values (Baumgartner et al. 1994). During the past 50 years the moist forests of northern Idaho changed from being dominated by early- to mid-seral species including western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), and western white pine (*Pinus monticola*) to ones dominated by late seral species, e.g., grand fir (*Abies grandis*) and western hemlock (*Tsuga heterophylla*) (Hann et al. 1997; Idaho Panhandle National Forests 1998) (Figure 1). Mixed and variable fire regimes, successional processes and endemic insects and pathogens worked in concert to produce the stable and resilient forests of the past. This conversion to late seral species would take 200 to 300 years depending on fire regime, but because of the destabilizing impacts of white pine blister rust (*Cronartium ribicola*), fire exclusion, and aggressive harvesting of the early seral species, it took less than 50 years in many places (Arno 1980; Haig et al. 1941; Harvey et al. 1999; Neuenschwander et al. 1999). Western white pine, which dominated the area early in the 20th century, (Critchfield and Little 1966; Graham 1990; Wellner 1962) now has declined to less than 10% of its former extent (Hann et al. 1997; Idaho Panhandle National Forests 1998) (Figure 1).

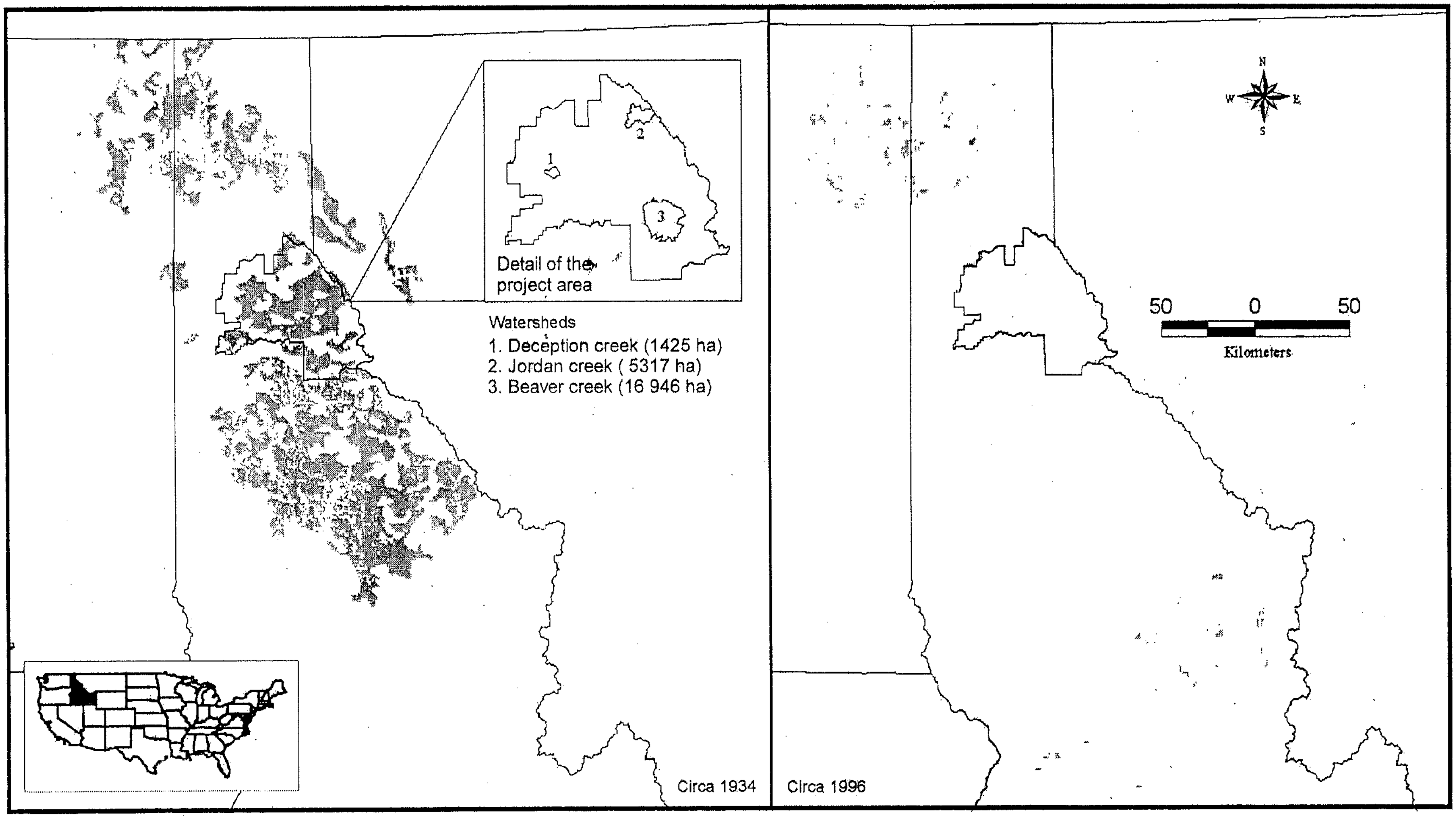

Figure 1. Change in western white pine abundance since 1934 and study area. Change in aerial extent of forests dominated by western white pine (shaded areas) from 1934 (left) to present (right) (Hann et al. 1997). The entire Coeur d'Alene Basin (project area) was used to predict historical western white pine abundance. Three watersheds (Beaver, Deception, Jordan) within the Basin were used to predict current seedling and sapling growth within canopy openings and across multiple spatial scales.

Western white pine is known for its genetic plasticity, its ability to grow across a wide range of environments, its resistant to many endemic diseases and insects, and its long life (200 to 300 years) (Cooper et al. 1991; Daubenmire and Daubenmire 1968; Graham 1990; Haig et al. 1941; Harvey 1994; Larsen et al. 1980; Leiberg 1897; Minore 1979; Rehfeldt 1994). However, the decline in areal extent of forests dominated by western white pine has affected the way these forests function. Lack of this key species has decreased the resiliency (ability to adapt to change) of these forests and increased the risk for catastrophic disturbances. Epidemics of diseases, insects, and severe wildfires can potentially decrease the productivity and subsequent ecological integrity of the forests of northern Idaho (Hann et al. 1997; Harvey et al. 1999; Neuenschwander et al. 1999). Increasing the abundance of western white pine (a major early-seral species in moist forests of northern Idaho) in the northern Rocky Mountains should lead to more stable and sustainable forests (Hann et al. 1997; Harvey et al. 1999; Neuenschwander et al. 1999).

Enhancing western white pine abundance in a few isolated areas would not increase forest resiliency or ecological integrity (Quigley and Arbelbide 1997). Establishing western white pine in every place western white pine can grow would be impractical and economically impossible. A landscape perspective is required to identify locations that favor western white pine occupancy and growth. This requires linking site-specific western white pine responses (growth, abundance, productivity) to the characteristics of large landscapes (1000's of ha).

Biophysical factors that reflect the variation and interactions among topography, climate (short- and long-term), disturbance (type and extent), soil processes (cycling and formation), time, and vegetation (current and historical) could be used to link a site specific response to the landscape. In addition, these are important biophysical factors that influence vegetation pattern (Delcourt and Delcourt 1988; Jenny 1980; Sollins 1998; White and Pickett 1985). Moreover, some researchers suggest that using multiple spatial scales can identify drivers of ecosystem processes and structures not readily recognizable when observing only one spatial scale (Brown 1995; Delcourt and Delcourt 1988; Poizat and Pont 1996; Turner et al. 1993; Wiens 1989). For example, the drivers of litter decomposition vary by the spatial scale at which they are observed (Meentemeyer 1984). At a fine spatial scale, decomposers and litter composition affect decomposition rates, but at broad scales, climate is the main driver of decomposition. Therefore, to fully understand decomposition requires combining knowledge from both spatial scales.

A similar approach using multiple spatial scales could prove useful in identifying sites for increasing western white pine abundance in northern Idaho. In this dissertation, I describe three studies integrating theories from landscape ecology, soil science, gap ecology, species silvics, hierarchy, and silviculture used to identify a suite of biological and physical characteristics occurring across spatial scales that influence or relate to the growth and abundance of western white pine.

CHAPTER 2 - STUDY SUMMARIES

Study one - Historical vegetation pattern across spatial scales

The following information is covered in more detail in Appendix A, "Characterizing historical (circa 1934) occurrence, abundance, and productivity of western white pine across multiple spatial scales of the Coeur d'Alene River Basin in northern Idaho."

Background

In northern Idaho western white pine grows on sites that contain at least 30 cm of volcanic ash soils, receive 65 cm or more of precipitation, and occur between 750 and 1600 m in elevation (Cooper et al. 1991; Graham 1990; Haig et al. 1941). The challenge is, within this large landscape, to locate those areas with the greatest potential for western white pine development. Because western white pine abundance has declined within the last half century from white pine blister rust, aggressive harvesting, and fire exclusion, current vegetation does not accurately reflect settings where western white pine could potentially grow. But information prior to these large changes could be used to evaluate how biophysical factors identifiable at multiple spatial scales relate to historical western white pine abundance, presence, absence, and productivity.

Multiple spatial scales can be used to identify management priorities, provide context for processes occurring at different spatial scales, and to understand population and habitat relations (Cherrill et al. 1995; Poizat and Pont 1996; Quigley and Arbelbide 1997; Wu and Smeins 2000). However, few studies link spatial scales or identify each scale's contribution toward understanding the item of interest (Poizat and Pont 1996). Many studies using multiple spatial scales involve areas with small spatial extents (Hinckley et al. 1998; O'Neill et. al. 1991; Song et al. 1997). Studies with large spatial extents usually concentrate on one spatial scale or use multiple spatial scales only to provide context. Rarely do they attempt to find interactions between spatial scales (Collins and Glen 1991; Flather and Sauer 1996; Gustafson and Gardner 1996). In addition, few spatially oriented studies consider spatial autocorrelation that can bias results. Those that do usually utilize minimal sample sizes (Gotway and Stroup 1997; Gumpertz et al. 2000; Legendre and Fortin 1989; Payn et al. 1999; Rossi et al. 1992). This current study used multiple spatial scales within a large landscape (350,000 ha) to determine if a priori defined spatial scales that are somewhat hierarchically organized can be used to understand historical vegetation relations. This study also determined if links among the spatial scales could describe the broad, mid, and fine spatial scale variation of vegetation occurrence.

Methods

There are a variety of ways to define spatial scales (Cherrill et al.1995; Delcourt and Delcourt 1988; Klijn 1994; O'Neill et al. 1986; Poizat and Pont 1996; Quigley and Arbelbide 1997; Wu and Smeins 2000). For my purposes the spatial scales had to integrate biophysical factors that express vegetation compositions and patterns through time (Delcourt and Delcourt 1988). Conceptually, a spatial hierarchy should have multiple levels that are nested (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; Allen et al. 1984; Delcourt and Delcourt 1988).

After investigating many options (Bailey 1995; Cherrill et al. 1995; Delcourt and Delcourt 1988; Klijn 1994; O'Neill et al.1991; Quigley and Arbelbide 1997; Soil Survey

Staff 1998), I chose to develop a spatial hierarchy using classification systems that represent soil development (Klijn 1994). A hierarchy based on soil development integrates factors such as landform (e.g., aspect, elevations, physiographic position), climate, disturbance, soil nutrition (microbial activity), and past vegetation (Delcourt and Delcourt 1988; Jenny 1980; Sollins 1998) (Appendix A). To capture these factors I used landtypes, geological feature, and weathering data that was available from the U.S. Geological Survey and U.S. Forest Service, Idaho Panhandle National Forests, and placed these spatial scales into a nested hierarchy. Because I wanted to use available data and finish the study within the allotted time, I chose the 350,000 ha Coeur d'Alene River Basin in northern Idaho to conduct the study (Appendix A).

The finest scale, with the smallest geographic extent, was landtype, which identifies settings based on landscape position, elevation, potential vegetation, slope gradient and shape, aspect, and relief. Soil depth and topographic influences on climate were indirectly integrated into this classification. Isolated areas where soil movement has occurred were also recognized at this scale (Table 1, Figure 2C). The geological features scale includes variations in bedrock lithology, sediment bedding characteristics, and metamorphic structure layers. Surface relief, hydrology, water holding capacity, and soil formation features were recognized at this scale with geographic extents ranging to 33,000 ha (Table 1, Figure 2B). The broadest scale in the hierarchy was defined using weathering class, which reflects the relative extent to which bedrock has weathered from its presumed, un-weathered state (Schoeneberger et al. 1998; United States Department of Agriculture 1999).

Three weathering classes occur in the Basin. Soils with no clay development and more than 35% rock content occur in weakly weathered soils, soils with more than 35% rock content and some clay development are classified as moderately weathered, and soils with high amounts of clay and less than 35% rock content are classified as highly weathered (Table 1, Figure 2A).

Table 1. Soil hierarchy showing geographic extent and estimated soil development time sequence (Harrison and Jobin 1963; Hobbs et al. 1965; Hosterman 1956; United States Department of Agriculture 1999). Table includes the defined spatial scale and estimated number of classes in the Coeur d'Alene River Basin.

Spatial scale	No. of classes	Geographic extent	Soil development time sequence
Weathering	3	5 to 212,000 ha	current to 600 million years
Geological feature	33	5 to 33,000 ha	current to 600 million years
Landtype	106	2 to 2,400 ha	current to 13 million years

The 1934 forest survey information was used because it provided spatially explicit information on where western white pine occurred before white pine blister rust, fire exclusion, and harvesting caused significant changes in western white pine abundance. The survey covered all ownerships with each stand (> 16 ha) delineated in the field on 9,000 ha topographic maps. Composition, abundance, and productivity (site index) were detailed for each stand (Figure 2D) (Appendix A).

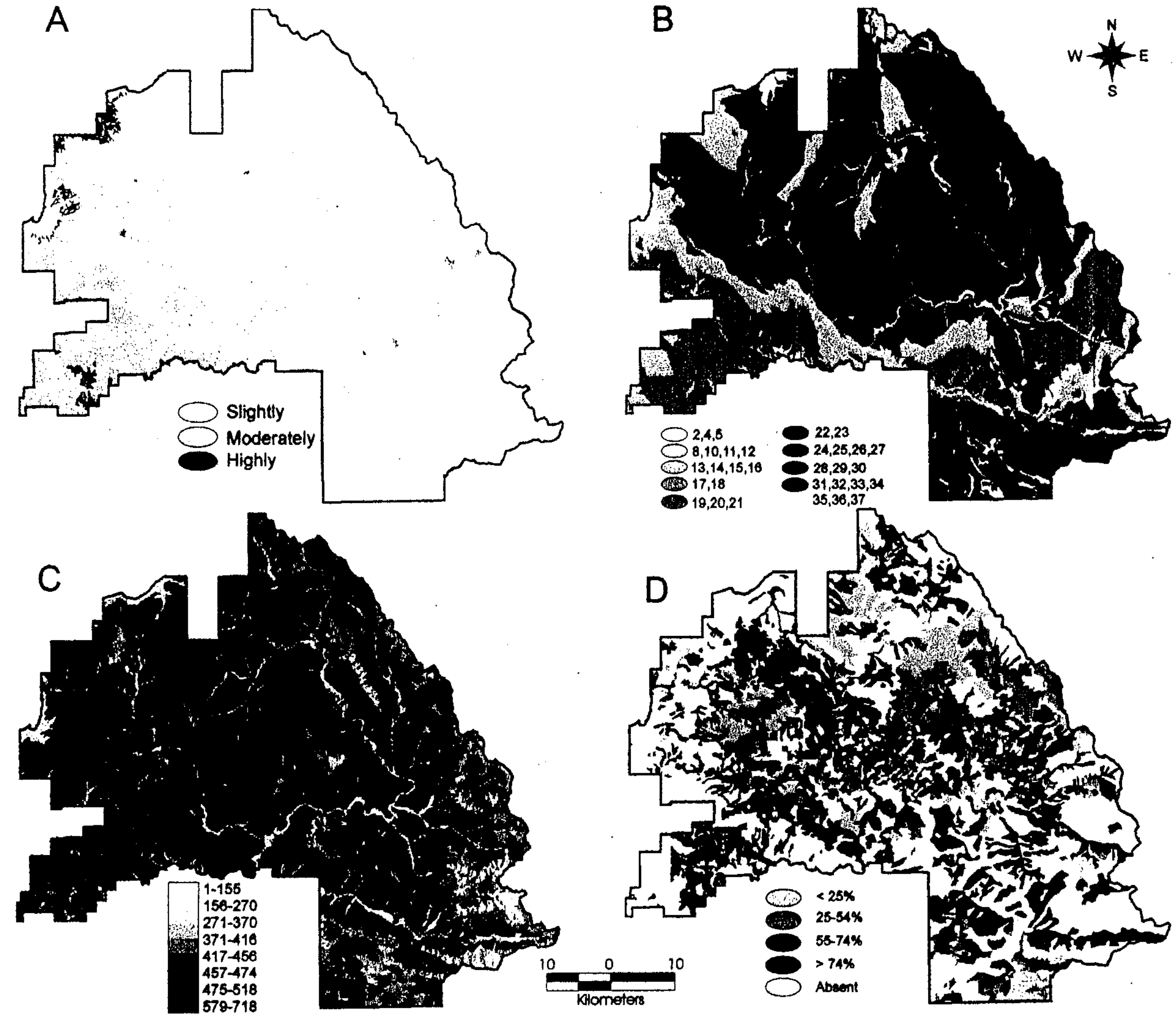

Figure 2. Illustration of spatial scales by broad categories: (A) weathering (three classes), (B) geological feature (33 classes in nine series), (C) landtypes (106 classes in eight series), and (D) circa 1934 western white pine abundance (four stocking classes). Refer to Tables 2 and 3 Appendix A for geological feature and landtype labels, and associated definitions.

To conduct the analysis I needed a sampling and analytical technique that would link spatial scales, handle large amounts of data, address or avoid spatial autocorrelation, analyze categorical variables and their interactions, and provide interpretable results. Because I had spatial data, I used a triangular spatial sampling design that was suggested by McBratney et al. (1981) and Yfantis et al. (1987). A geographic information system (GIS) was used to create the spatial data using a custom sampling method. This method allowed geographic coordinates, a sampling density, and a sampling design to be designated. A flat file was created and Arc/Info extracted the sample points (ESRI 1998).

For the statistical analysis, my investigation included geostatistical methods, marginal logistic regression models with spatial autocorrelation, and spatial analysis using generalized linear models (Cressie 1993; Goovaerts 1997; Gotway and Stroup 1997; Gumpertz et al. 2000; Isaaks and Srivastava 1989). Because the dependent variables (outcomes) were ordinal and not continuous, logistic regression is the more applicable technique. However, the data contained both many categories within each spatial scale and numerous interactions (over 1000) among the spatial scales. The coefficients produced by regression would be difficult to interpret, even if the algorithms accounted for the spatial autocorrelation. Geostatistical methods are not well suited for analyzing categorical data with over 1000 unique combinations. Classification and regression tree (CART) analysis technique was selected because it favored many of the components I wanted to test in the analysis (Breiman et al. 1984; Steinberg and Colla 1995). CART works best with large amounts of data where "different relationships between variables occur in different areas within the measurement space" (Breiman et al. 1984, p.7). It builds classification trees and it inherently tends to nest data when it creates branches within the tree. Thus it provided a way to identify which spatial scale was used to create a particular branch. The analysis inherently links spatial scales and identifies which combinations of spatial scale categories result in a particular class. Because CART is nonparametric, I avoided many parametric issues (e.g., normality) surrounding parametric methods (Appendix A).

I used one data set (classifier) to develop the relations and one data set (test) that reflected the frequency of categories within the spatial scale to evaluate the relations. This way I avoided spatial autocorrelation issues. The chi-square statistic was used to test goodness-of-fit (Ott 1984). The three spatial scales (landtype, geological features, weathering) were related to the historical presence, absence, abundance, and productivity (outcomes) of historical western white pine. A non-significant ($p \geq 0.05$) chi-square goodness-of-fit showed that the classifier data and the test data were similar (Appendix A).

Results and Discussion

The spatial hierarchy I chose was somewhat nested but far from perfect. Ideally, all weathering classes should contain all geological features, and all landtypes should be present within each of the geological features. These inconsistencies created classification trees with a considerable amount of noise (Figure 3). For example, for classifying western white pine presence the proportion correctly classified by the trees ranged from 0.16 to 0.77 depending on the spatial scale (Figure 3, terminal node 11 and 14). Also because of these inconsistencies I was unable to verify if all landtypes behaved similarly within a geological feature. If I would have ensured a fully nested hierarchy, the classifications and chi-square statistics may have improved. But in the real world, ecosystems are not organized perfectly, and inconsistencies among spatial scales add complexity toward explaining how ecosystems

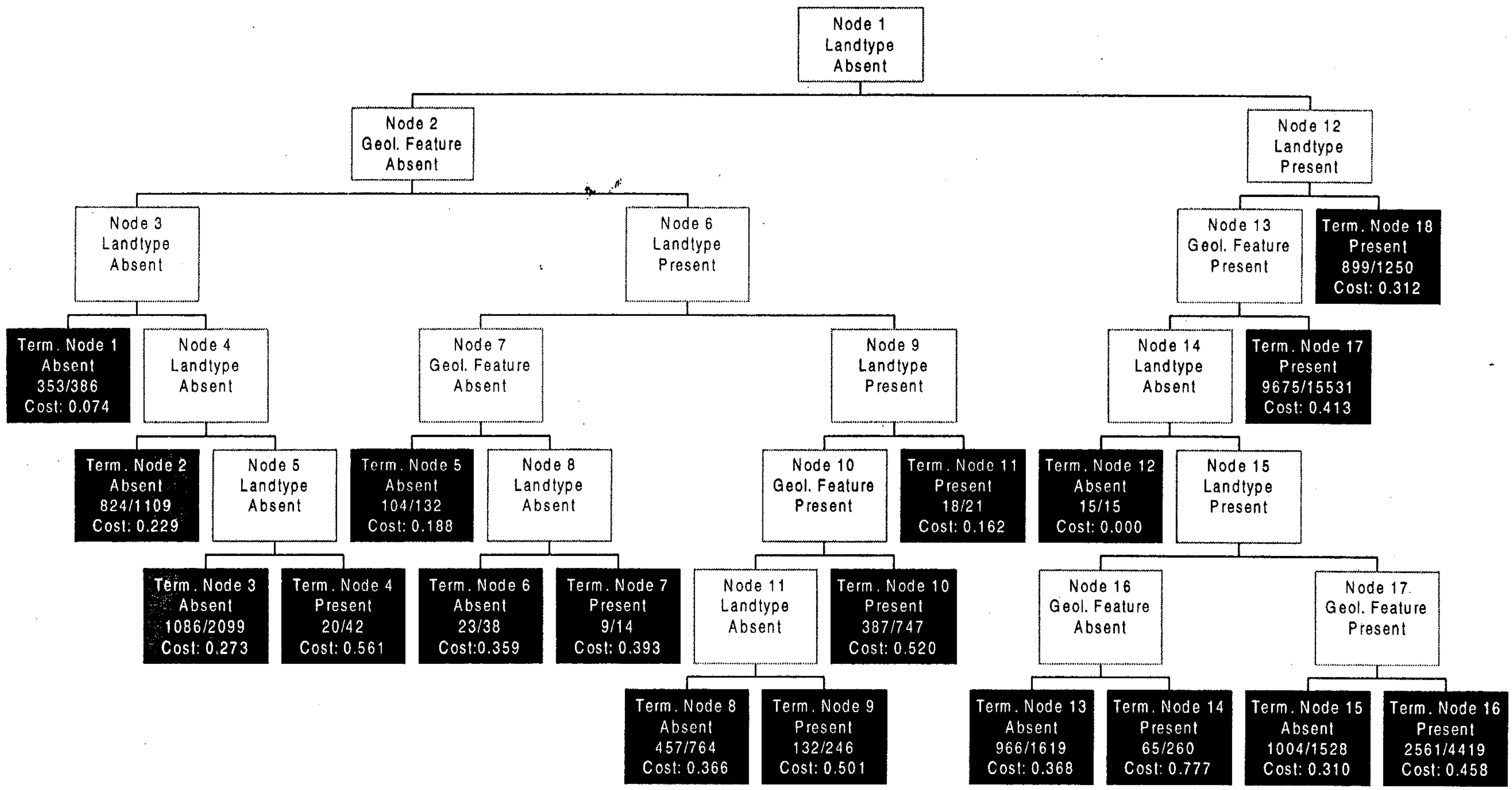

Figure 3. Classification tree predicting western white pine occurrence. Eighteen terminal node classification tree used for predicting western white pine presence or absence. Terminal nodes (shaded) show number of observations correctly classified, total number of observations and misclassification costs. Internodes show the spatial scale used in the split and whether the split was based on the presence or absence of western white pine.

operate and function. Therefore, the hierarchy may have represented a more realistic picture of how ecosystems are organized (Appendix A).

Even in this imperfect hierarchy, broader spatial scales constrained lower spatial scales (Allen and Starr 1982), and finer spatial scales explained more of the variability in western white pine occurrence and abundance then broader spatial scales (O'Neill et al. 1986) (Table 2). The strongest associations, as indicated by high chi-square p-values, occurred at the finer spatial scales and decreased as broader spatial scales were added. Landtype consistently had high p-values (0.17 for presence or absence, 0.18 for abundance, and 0.37 for productivity) followed by geological feature (0.12, for presence or absence, 0.12 for abundance, 0.22 for productivity) and then weathering (0.008 for presence or absence, 0.05 for abundance, 0.11 for productivity).

In addition to using associations among the classifier and outcome variables as an indicator of nesting, I also evaluated the structure of the CART trees and spatial patterns. For predicting the presence or absence of western white pine, the geological feature scale was used early to separate the majority of the observations into tree branches, compared to landtypes (Figure 3, node 2, node 13). Within these branches, landtypes were classified into groups with similar geological features. This resulted in individual landtypes showing both presence and absence, and the difference between the two classifications was determined by a particular geological feature. This nesting, though imperfect, was indicated when the patterns created by combining geological feature and landtype were observed (Figure 4). Geological feature classified places with western white pine being absent (western and southern portions

Table 2. Classification trees containing the weathering, geological feature, and landtype scales. Outcome variables were presence, absence, abundance (% stocking <25, 25-54, 55-74, >74), and productivity (site index at base 50 years, unknown,12, 15, 18, 21 m) of western white pine. Number of terminal nodes (Nodes) and the chi-square P-value showing the goodness-of-fit between the classifier and test data and the number (N) of observations used in the trees are shown.

Spatial Scale	Nodes	χ^2 P-value	Proportion of observations classified correctly					
			Presence / Absence N= 30,220					
			Total	Present	Absent			
P1-Weathering (Weath.)	2	0.008	0.480	0.211	0.792			
P2-Geological feature (Geol.)	2	0.12	0.587	0.670	0.491			
P3-Landtype	2	0.17	0.599	0.885	0.267			
P4-Weath. & Geol.	16	0.21	0.606	0.661	0.542			
P5-Geol. & landtype	37	0.33	0.639	0.810	0.440			
P6-Weath. & landtype	2	0.14	0.599	0.885	0.267			
P7-Weath., Geol. & landtype	37	0.33	0.639	0.810	0.440			
P8-Weath., Geol. & landtype	18	0.27	0.628	0.847	0.370			
			Abundance (classes %) N = 16,249					
			Total	<25	25-54	55-74	>74	
A1-Weathering	3	0.05	0.165	0.885	0.19	0	0	
A2-Geological feature	6	0.12	0.283	0.294	0.254	0.451	0.187	
A3-Landtype	9	0.18	0.310	0.290	0.092	0.850	0.049	
A4-Weath. & Geol.	23	0.17	0.306	0.478	0.261	0.411	0.197	
A5-Weath. & Geol.	13	0.15	0.293	0.478	0.233	0.395	0.186	
A6-Geol. & landtype	294	0.46	0.355	0.347	0.398	0.579	0.206	
A7-Geol. & landtype	66	0.38	0.362	0.306	0.297	0.637	0.232	
A8-Geol. & landtype	29	0.31	0.328	0.252	0.238	0.748	0.121	
A9-Geol. & landtype	4	0.16	0.308	0.313	0.092	0.836	0.047	
A10-Weath. & landtype	9	0.18	0.310	0.290	0.092	0.850	0.049	
A11-Weath., Geol. & landtype	293	0.46	0.356	0.354	0.399	0.578	0.066	
A12-Weath., Geol. & landtype	18	0.27	0.293	0.400	0.166	0.643	0.638	
			Site productivity (site index classes) N= 16,249					
			Total	Unknown	12 m	15 m	18 m	21 m
S1-Weathering	2	0.11	0.557	0	0	0	0.812	0.268
S2-Geology	4	0.22	0.557	0.347	0.089	0.406	0.657	0
S3-Landtype	10	0.37	0.627	0.315	0.119	0.359	0.773	0.116
S4-Weath. & Geol.	19	0.32	0.466	0.537	0.188	0.295	0.500	0.091
S5-Weath. & Geol.	8	0.26	0.450	0.551	0.089	0.406	0.452	0.091
S6-Geol. & landtype	264	0.57	0.630	0.443	0.470	0.383	0.732	0.341
S7-Geol. & landtype	72	0.51	0.640	0.398	0.233	0.365	0.768	0.232
S8-Geol. & landtype	18	0.43	0.631	0.320	0.119	0.423	0.763	0.145
S9-Weath. & landtype	10	0.34	0.627	0.315	0.119	0.359	0.773	0.116
S10-Weath., Geol. & landtype	266	0.57	0.630	0.443	0.470	0.383	0.732	0.341
S11-Weath., Geol. & landype	12	0.38	0.643	0.309	0.119	0.181	0.834	0.145

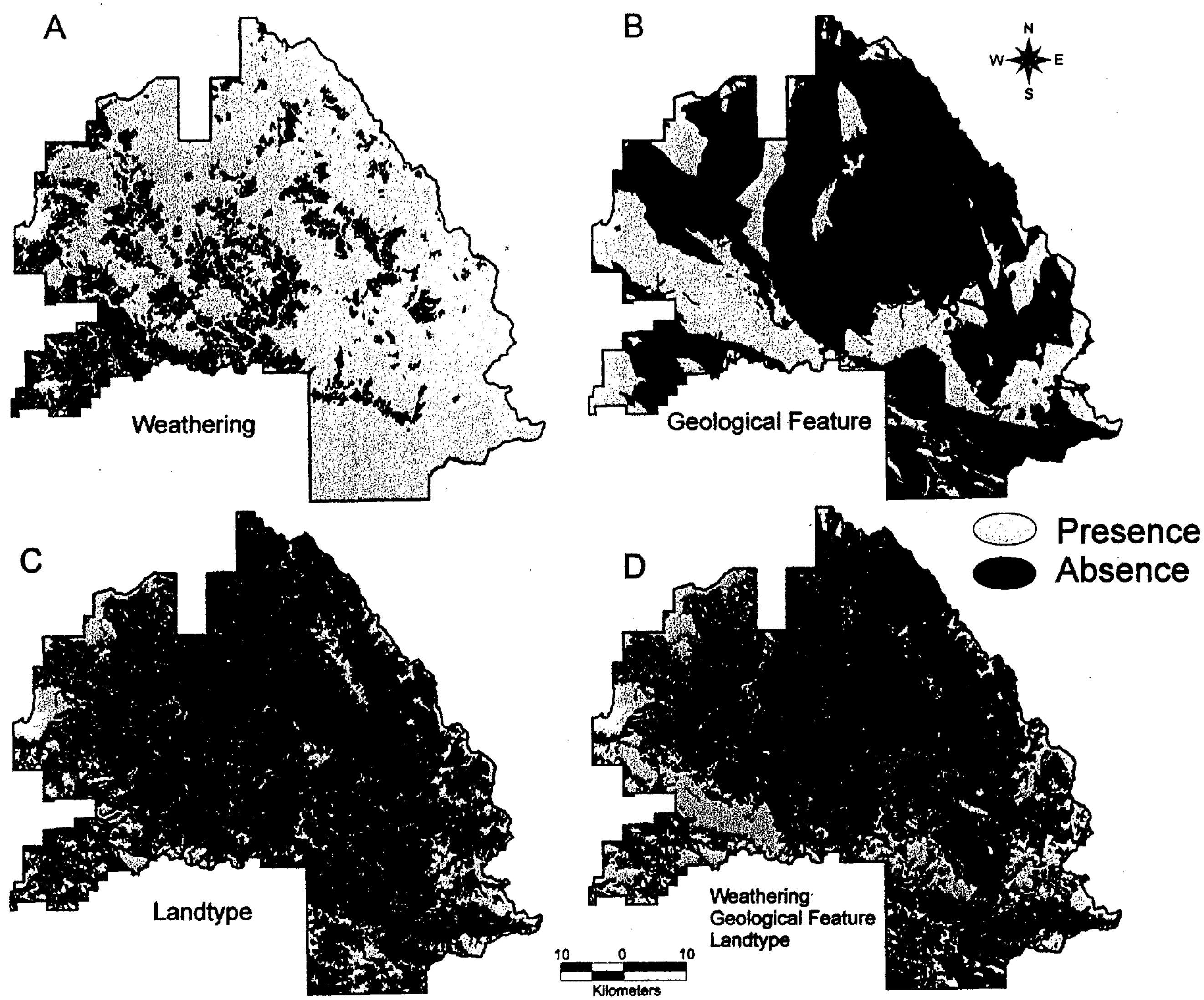

Figure 4. Illustration of historical western white pine occurrence (presence and absence) displayed on the Coeur d'Alene River Basin for three individual spatial scales (A,B, and C) and three combined spatial scales (D).

of the Basin, Figure 4B) while these same places, when observing landtypes, showed western white pine present (Figure 4C). When both of these scales were used to classify white pine occurrence it was obvious where geological features constrained the landtypes (Figure 4D) (Appendix A).

The weathering scale was not useful in relating spatial pattern in abundance, presence, or absence. Productivity (site index) was the only outcome with a non-significant (0.11) chi-square when related to weathering (Table 2). The homogeneous nature of weathering across the Basin may have contributed to its weak relationship to western white pine occurrence and abundance. This scale might have more utility in predicting western white pine outcomes when multiple areas the size of the Coeur d'Alene Basin are used.

Western white pine presence, absence, and abundance are inherently stochastic due to vagaries in seed source and disturbance patterns. The values for these outcomes depend on several factors to simultaneously occur. The timing, intensity, and location of disturbances, the climate at time of seed germination and establishment, and seed source and viability are only some of the factors determining the presence of a particular species (Agee 1993; Oliver and Larson 1990; Pickett and White 1985). For this paper, abundance had the lowest proportion of the observations classified correctly compared to presence or absence, and productivity. However, the analysis classified 64% of the observations with high abundance (55 to 74% stocking) correctly in the 18 node tree (Table 2, tree A12). The higher abundance classes dominated the Basin in 1934 and contained the greatest number of observations, thereby, contributing to the successful classification (Figure 2) (Appendix A).

Western white pine was most abundant and most productive where subsurface flow and water retention provide water throughout the growing season. These processes occur in landtypes that are highly dissected by streams, ones located adjacent to streams, those on toeslopes, or ones located in stream bottoms. These favorable settings were irrespective of slope, aspect, or elevation (Figure 5). Most places within the Basin were very productive, with many areas classified with a high (18 m) site index. The Monzonites and Syenites, alluvial deposits, Mt. Shields, St. Regis, and parts of the Prichard geological features tended to contain settings with site indexes greater than 18 m. Sites with the lowest productivity occurred on the lower member of the Prichard in the southwestern and southeastern portions of the Basin (Figure 6) (Appendix A).

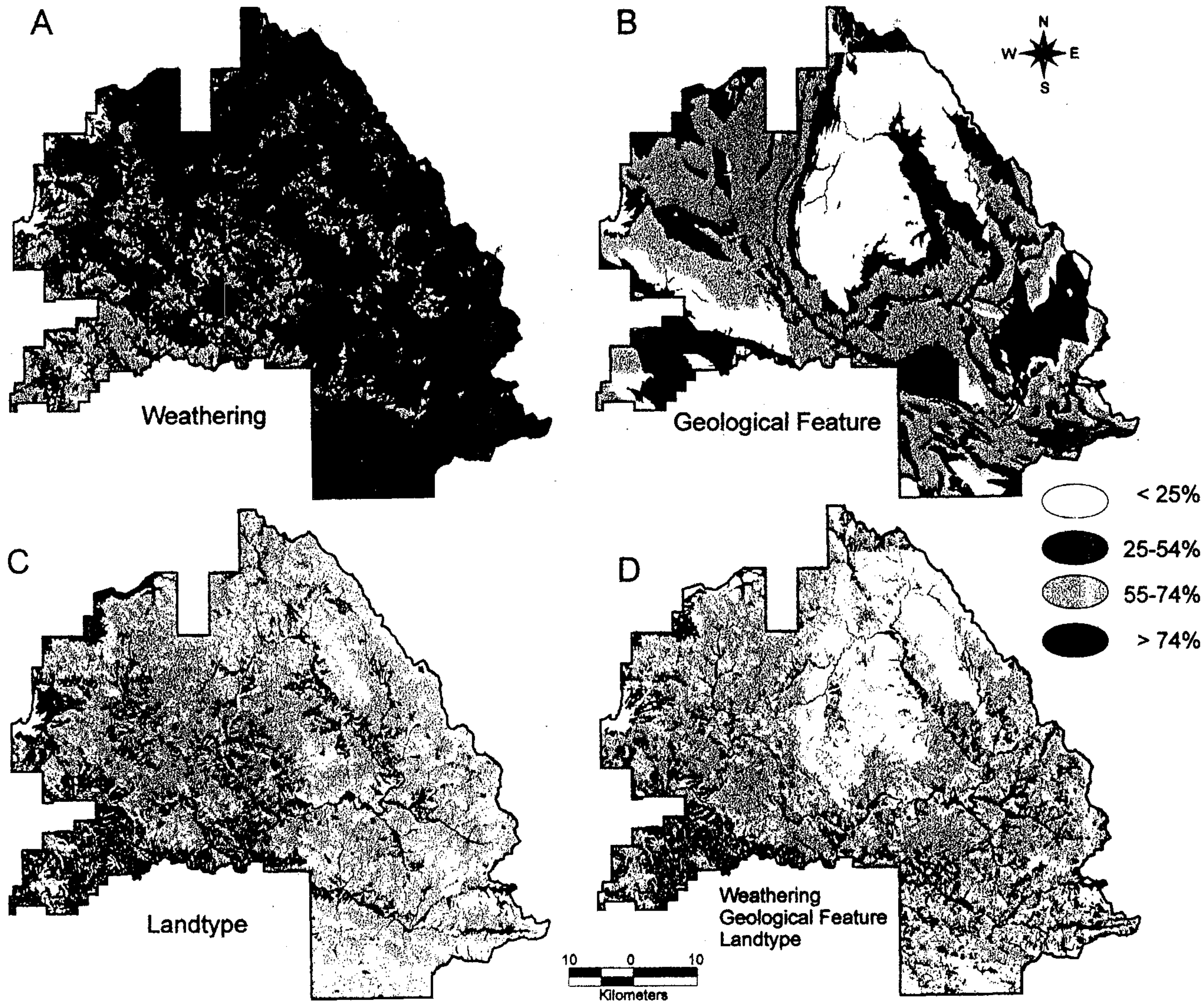

Figure 5. Illustration of historical western white pine abundance (% stocking) displayed across the Coeur d'Alene River Basin for three individual spatial scales (A,B, and C) and three combined spatial scales (D).

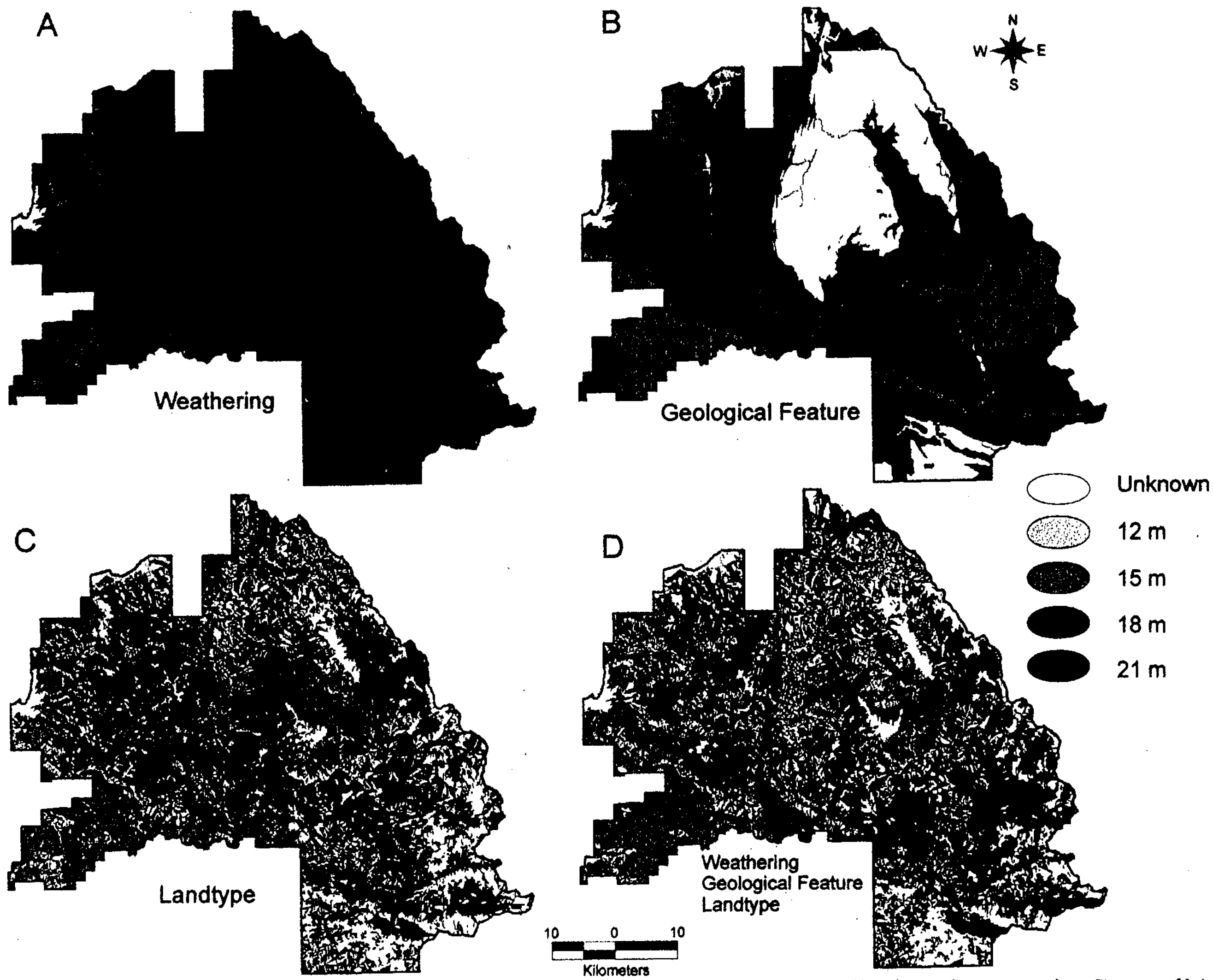

Figure 6. Illustration of western white pine site productivity (site index 50-year base) displayed across the Coeur d'Alene River Basin for three individual scales (A,B, and C) and three combined spatial scales (D). Unknown site index are areas where site index was not recorded but could support western white pine.

Study two - Canopy opening and western white pine

The following information is covered in more detail in Appendix B, "Relating western white pine growth to forest opening characteristics."

Background

In the Coeur d'Alene River Basin beginning in the 1930s, the clearcut method was commonly used, resulting in forest conditions similar to those created by stand-replacing wildfires. However, in application, clearcuts usually differ from wildfires in geographic extent (smaller than historical stand-replacing fires), shape, location, and residual structure (snags and soils). Because clearcuts are unsightly, change wildlife habitat, increase water yield, and associated roads increase soil erosion and sediment, alternatives are preferred (Bliss 2000). Shelterwood, seedtree, and individual or group selection silvicultural methods can be applied that mimic other disturbances, such as small stand-replacing and surface wildfires, insect attacks, root diseases, and wind and ice storms. However, these methods retain high forest cover and therefore favor the regeneration and development of late-seral species.

Western white pine is well suited to regenerate and develop in a variety of forest conditions. It evolved occupying environments created by many disturbances (Haig et al.1941). It grows within a wide range of landscape (elevation, aspect, slope) and microsite environments (small to large openings). However, western white pine was commonly managed using clearcuts because they were easy to apply and often the most applicable (Graham et al. 1983; Wellner 1947). Because of their frequent use, there is a tendency to view western white pine as requiring full light to survive and develop. On the other hand, Haig et al. (1941) noted that western white pine performed better under some canopy protection through age 30 years. Because of this tendency, there is no research determining how western white pine responds to different levels of canopy openings (Appendix B).

Although there is a plethora of information on gaps, canopy structure, and vegetation response in gaps, only a few studies have been conducted within coniferous forests (Coates 2000; Coates and Burton 1997, 1999; Moeur 1997; Spies and Franklin 1989). Most of this research focuses on characterizing vegetation response in openings, but rarely is this knowledge used to address management objectives (Coates 2000; d'Oliveira 2000; Myers et al. 2000). Trees grow faster and are taller in large openings compared to small openings; but there is little knowledge concerning opening thresholds, such as the size of opening required for a species to obtain a competitive advantage or the opening size needed for it to grow freely. In addition, there is limited knowledge relating canopy opening characteristics (e.g., size, shape) to common stand descriptors (e.g., tree density, height) (Crookston and Stage 1999; Mitchell and Popovich 1997).

Therefore, the objectives of the second study were to: 1) determine relations between western white pine growth and opening characteristics (e.g., visible sky, orientation, age, location, and overstory species composition), 2) determine if the relation between canopy opening attributes and western white pine growth changes because of physical setting (e.g., aspect, slope), 3) identify three canopy opening thresholds (occupancy, competitive advantage, free to grow) for western white pine, and 4) relate canopy opening attributes to stand descriptors (basal area, stand density index, trees density, size of opening) (Appendix B).

Methods

Three watersheds with diverse environments historically supporting western white pine were selected within the Coeur d'Alene River Basin (Figure 1) (Appendix B). A total of 620 young (5 to 50 years of age) western white pine were randomly selected in these watersheds growing in a wide range of forest openings, aspects, and elevations. The western white pines, associated conifers, and their biophysical environment were described in detail (Appendix B). Fisheye photographs were used to quantify the proportion of visible sky in the canopy openings. A step-wise log-linear regression procedure was used to relate the western white pine variables (basal diameter, height, factor score of growth, age) to canopy opening defined by visible sky (Appendix B). The occupancy threshold was determined using logistic regression, while the competitive advantage and free to grow thresholds were determined using fourth-degree polynomials. The dependent variable in these polynomials was the relative mean annual height increment between the selected western white pine and associated western hemlock, and the independent variable was visible sky. The thresholds were determined by observing inflection points on the response curves. To determine the optimum opening size (m^2) for western white pine development, a second-degree polynomial regression was used; visible sky was related to stand descriptors using log-linear regression.

Results and Discussion

Three western white pine descriptors--basal diameter, height, and a factor score (a combination of diameter, height and 5-year height growth)--were positively related to visible sky when adjusted for age (Figure 7). Visible sky determined from the fisheye photograph and age described 53% of the variation in height ($p = 0.0001$) (Table 3). Radiation below

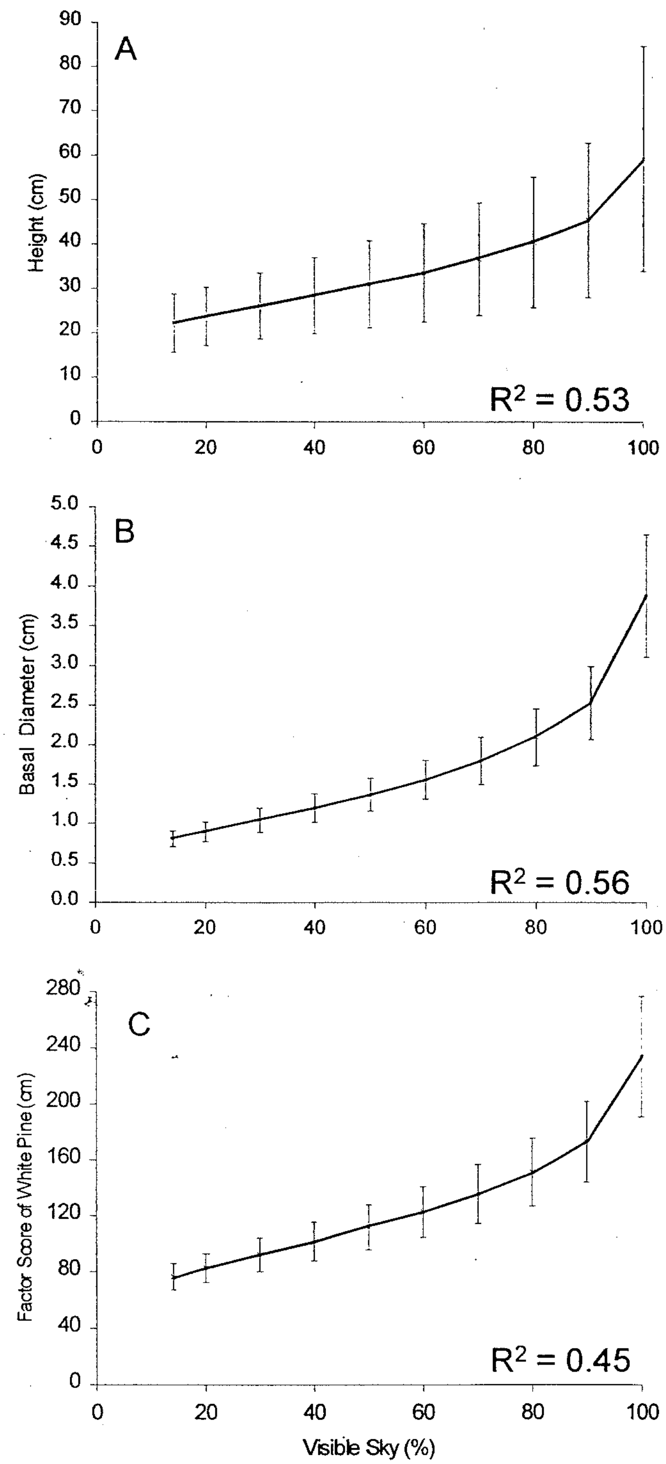

Figure 7. Western white pine growth related to visible sky. Relationship between western white pine growth and visible sky at age 10 yrs. Western white pine growth variables include (A) height, (B) basal diameter (diameter at 2.54 cm above root collar), and a (C) factor score, which is the linear combination of basal diameter, height, and last 5-years height.

Table 3. Western white pine growth related to independent variables. Results include, P-value from the partial sum of square F-tests, age as a covariate, model P-value, and adjusted R^2. Radiation reaching the canopy, aspect, and orientation were included with canopy opening and age.

Independent variables	First variable P-value	Second variable P-value	Third variable P-value	Age	Model P-value	Adj. R^2
Microsite variables			Height			
Visible sky	0.0001			0.0001	0.0001	0.53
Radiation below canopy (total)	0.0001			0.0001	0.0001	0.44
Sunfleck duration	0.0123			0.0001	0.0001	0.39
Number of sunflecks	0.0001			0.0001	0.0001	0.50
Microsite factor score	0.0122			0.0001	0.0001	0.40
Visible sky & orientation	0.0001	0.0015		0.0001	0.0001	0.54
Topographic variables						
Visible sky & total landscape radiation	0.0001	0.0222		0.0001	0.0001	0.53
Visible sky & direct landscape radiation	0.0001	0.0142		0.0001	0.0001	0.53
Visible sky & diffuse landscape radiation	0.0001	0.3155		0.0001	0.0001	0.53
Visible sky & topographic factor score	0.0001	0.6957		0.0001	0.0001	0.53
Visible sky, orientation & aspect	0.0001	0.0055	0.0001	0.0001	0.0001	0.56
Microsite variables			Basal diameter			
Visible sky	0.0001			0.0001	0.0001	0.56
Radiation below canopy (total)	0.0001			0.0001	0.0001	0.39
Sunfleck duration	0.0121			0.0001	0.0001	0.28
Number of sunflecks	0.0001			0.0001	0.0001	0.47
Microsite factor score	0.0003			0.0001	0.0001	0.30
Visible sky & orientation	0.0001	0.0035		0.0001	0.0001	0.57
Topographic variables						
Visible sky & total landscape radiation	0.0001	0.3872		0.0001	0.0001	0.56
Visible sky & direct landscape radiation	0.0001	0.2981		0.0001	0.0001	0.56
Visible sky & diffuse landscape radiation	0.0001	0.2103		0.0001	0.0001	0.56
Visible sky & topographic factor score	0.0001	0.7403		0.0001	0.0001	0.55
Visible sky, orientation & aspect	0.0001	0.0020	0.0002	0.0001	0.0001	0.58

Table 3 continued. Western white pine growth related to independent variables. Results include, P-value from the partial sum of square F-tests, age as a covariate, model P-value, and adjusted R^2. Radiation reaching the canopy, aspect, and orientation were included with canopy opening and age.

Independent Variables	First Variable P-value	Second variable P-value	Third variable P-value	Age	Model P-value	Adj. R^2
Microsite variables	Factor score of western white pine variables					
Visible sky	0.0001			0.0001	0.0001	0.45
Radiation below canopy (total)	0.0001			0.0001	0.0001	0.30
Sunfleck duration	0.0040			0.0001	0.0001	0.19
Number of sunflecks	0.0001			0.0001	0.0001	0.39
Microsite factor score	0.0028			0.0001	0.0001	0.20
Visible sky & orientation	0.0001	0.0002		0.0001	0.0001	0.46
Topographic variables						
Visible sky & total landscape radiation	0.0001	0.3744		0.0001	0.0001	0.45
Visible sky & direct landscape radiation	0.0001	0.3353		0.0001	0.0001	0.45
Visible sky & diffuse landscape radiation	0.0001	0.6350		0.0001	0.0001	0.45
Visible sky & topographic factor score	0.0001	0.4327		0.0001	0.0001	0.45
Visible sky, orientation & aspect	0.0001	0.0008	0.0001	0.0001	0.0001	0.49

the canopy, although statistically significant ($p = 0.0001$) explained less of the age-adjusted variability in height, basal diameter, or the factor score than visible sky (Table 3) (Appendix B).

The significance of landscape radiation (radiation influenced by topography) varied (Table 3). For height, both total and direct landscape radiation were significant ($p = 0.0001$), but neither explained more of the variability of western white pine growth than visible sky alone. Basal diameter was not significantly related to landscape radiation. All three dependent variables were significantly related to the number of sunflecks occurring on June 21, 1999, and the R^2 were relatively high (height 0.50, basal diameter 0.47, factor score 0.39). All of the dependent variables were significantly related to opening orientation and aspect, but the additional amount of variation explained using these variables compared to visible sky alone was small (Table 3) (Appendix B).

Three thresholds were identified relating western white pine response to visible sky (Figure 8) (Appendix B). There was a 57% probability of western white pine occupying a site with visible sky exceeding 25%, and an 80% probability of western white pine occupying the site with visible sky exceeding 45%. Western white pine gains a competitive advantage over western hemlock at 55% visible sky (Figure 8). Western white pine is free to grow when visible sky exceeds 92% (Figure 8). The slope of the response curves for basal diameter, height, and the factor score dramatically increased at approximately 92% canopy opening (Figure 7).

In all cases, basal area, stand density index, trees per hectare, and opening size were significantly related to visible sky (Figure 9B). For example, at 20% visible sky, basal area was 30 m^2 ha^{-1} (131 ft^2 ac^{-1}) and decreased to 10 m^2 ha^{-1} (44 ft^2 ac^{-1}) at 90 to 100% visible sky (Figure 9). Similar results occurred for stand density index and trees per hectare. However, only 12, 12, and 6% of the variation in basal area, stand density index, and trees per hectare were explained by visible sky, respectively. In contrast, 55% of the variability in opening size (m^2) was explained by visible sky (Appendix B).

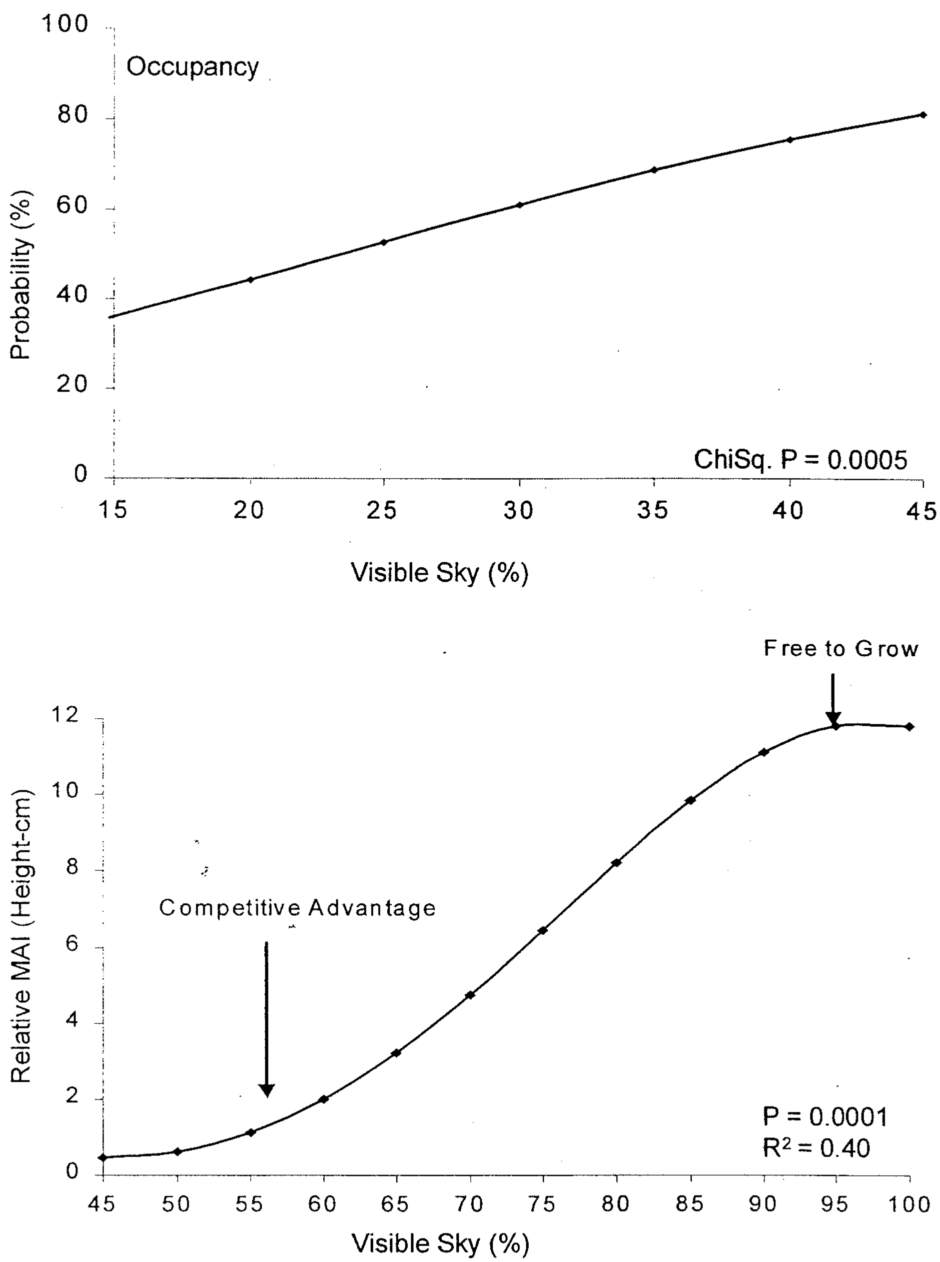

Figure 8. Occupancy, competitive advantage, and free to grow thresholds for western white pine. Canopy opening was the only independent variable used to identify thresholds.

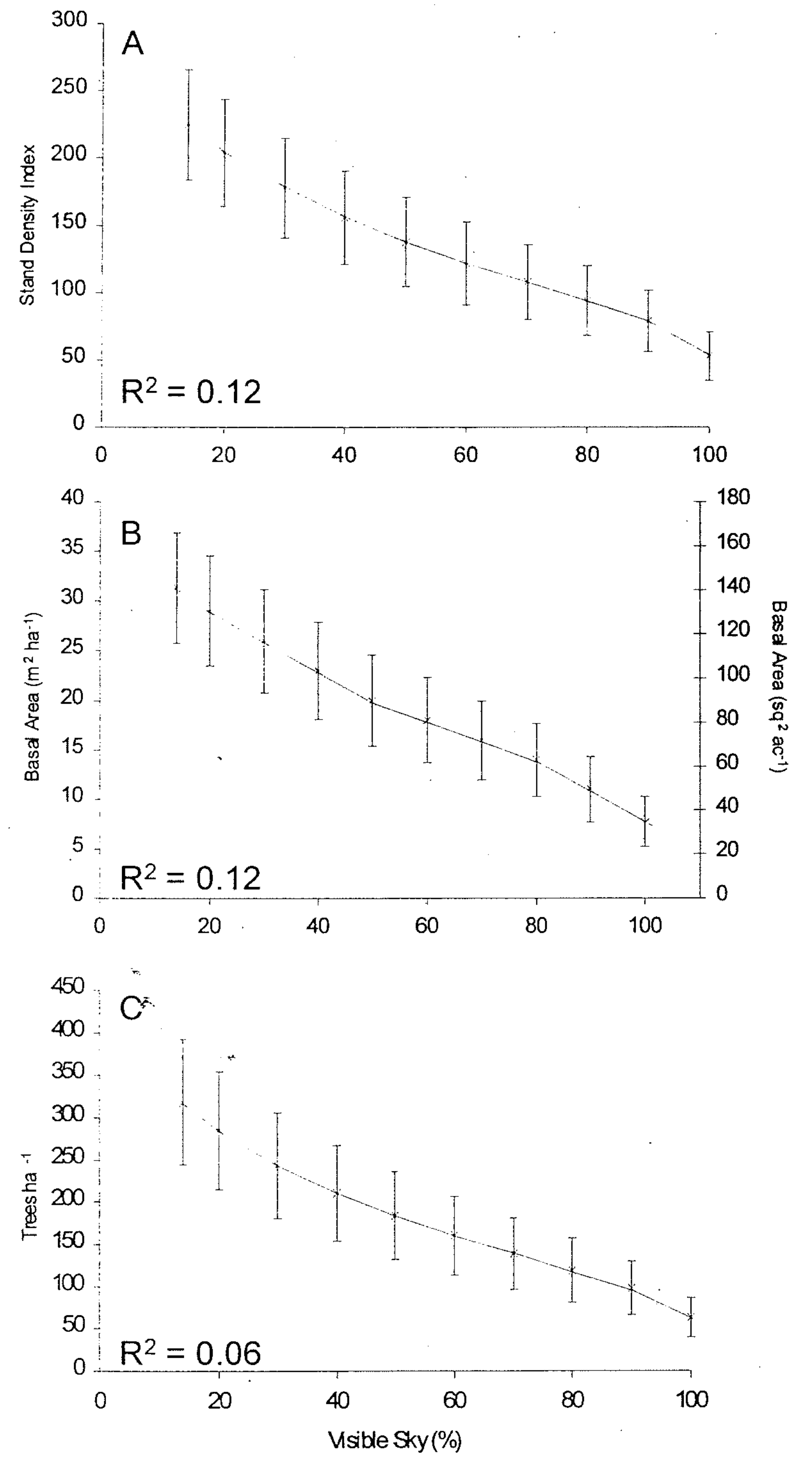

Figure 9. Percent visible sky related to stand density. Relationship between visible sky and stand density (stand density index (A), basal area (B), and trees per hectare (C). All three relationships were significant ($P = 0.0001$), but the adjusted R^2 were 0.12 for stand density index, 0.12 for basal area, and 0.06 for trees per hectare.

Study three - Western white pine growth across multiple spatial scales

The following information is covered in more detail in Appendix C, "Western white pine growth in relation to biophysical characteristics across different spatial scales in the Coeur d'Alene River Basin in northern Idaho USA."

Background

Although my first study provided knowledge on the historical occurrence, abundance, and productivity of western white pine, there is limited information on using spatial hierarchies for predicting a site-specific response. In this study, I link the information on the response of western white pine to different sized canopy openings (expressed as visible sky) to the spatial hierarchy used to describe historical western white pine forests (Appendix C). Lertzman et al. (1996) conducted a similar study when they related two spatial scales (site and gap) to processes (disturbance) important for creating forest gaps. Similarly, using a multi-scale approach, Brown (1993) linked landscape radiation to photosynthetic active radiation reaching a canopy opening. Although not a true multi-scale approach, Shen et al. (2000) related tree basal area growth to fertilization within the context of geology. None of these studies were intended to provide information on linking multiple spatial scales to a site specific response in vegetation. In this study, the objectives were to determine if broad spatial scales in addition to canopy openings (defined by visible sky) influence western white pine growth and to identify the significant interactions among the spatial scales related to western white pine growth (Appendix C).

Methods

This paper combines the spatial hierarchy defined in the Coeur d'Alene River Basin (first study, Appendix A) with the site specific western white pine information gathered across the three watersheds (second study, Appendix B). The spatial hierarchy defined for this paper included four spatial scales (canopy opening, landtype, geological feature, weathering) integrating the biophysical factors influencing site-specific vegetation. A step-wise approach using log-linear regression and linear regression was used to relate the growth of western white pine to the spatial hierarchy.

Results and Discussion

In most cases, except for weathering, adding progressively broader spatial scales explained significantly ($p \leq .05$) more of the variation in western white pine height and basal diameter when adjusted for age (Table 4). The spatial scales were linked when predicting western white pine growth as indicated by the significant interactions among the scales. Moreover, the addition of these interactions significantly added to the amount of variation explained by the models. Up to 73% of the variation in western white pine growth was explained by the spatial hierarchy including geological features, landtype, and visible sky (Table 4, equation D7) (Appendix C). An additional 2 to 18% of the variation in basal diameter and height was explained by the broader spatial scales (landtype, geological feature, weathering).

When height and basal diameter were estimated, several interactions between geological feature and landtype were significant. Some of these included the Revett formation combined with southern aspects dissected with stream breaklands, the upper

Table 4. Evaluation of spatial scales and western white pine growth (basal diameter, height, relative mean annual height increment) in different canopy openings (defined by visible sky) using the full versus reduced model hypothesis testing.

Eq. No	Model	R^2	P-value	Full model[1] SSE	Full model[1] DF	Reduced model[1] SSE	Reduced model[1] DF	F^2
				Ln basal diameter				
D1	Visible sky + age (N = 613)	0.55	0.0001	138.1	611	--	--	--
D2	**Visible sky + age** + landtype[1]	0.61	0.0001	120.5	594	138.1	611	5.1*
D3	**Visible sky + age** + geological feature	0.64	0.0001	112.5	602	138.1	611	15.2*
D4	**Visible sky + age** + weathering	0.57	0.0001	131.5	610	138.1	611	30.6*
D5	Visible sky + age + weathering + geological feature + (weathering x geological feature)	0.64	0.0001	--	--	--	--	--
D6a	**Visible sky + age** + geological feature + landtype + (geological feature x landtype)	0.71	0.0001	89.3	541	138.1	611	4.2*
D6b	**Visible sky + age + geological feature** + landtype + (geological feature x landtype)	0.71	0.0001	89.3	541	112.5	602	2.3*
D6c	**Visible sky + age + landtype** + geological feature + (geological feature x landtype)	0.71	0.0001	89.3	541	120.5	594	3.6*
D7	**Visible sky+ age + geological feature+ landtype + (geological feature** x **landtype** x visible sky)	0.73	0.0001	83.2	516	89.3	541	2.9*
				Ln height				
H1	Visible sky + age (N = 618)	0.53	0.0001	112.8	616			
H2	**Visible sky + age** + landtype	0.59	0.0001	98.9	599	112.8	616	4.9*
H3	**Visible sky + age** + geological feature	0.60	0.0001	95.7	607	112.8	616	12.0*
H4	**Visible sky + age** + weathering	0.55	0.0001	108.8	615	112.8	616	22.6*
H5	Visible sky + age + weathering + geological feature + (weathering x geological feature)[4]	0.60	0.0001	--	--	--	--	--
H6a	**Visible sky + age** + geological feature + landtype + (geological feature x landtype)	0.67	0.0001	79.2	546	112.8	616	3.3*
H6b	**Visible sky + age + geological feature** + landtype + (geological feature x landtype)	0.67	0.0001	79.2	546	95.7	607	1.9*
H6c	**Visible sky + age + landtype** + geological feature + (geological feature x landtype)	0.67	0.0001	79.2	546	98.9	599	2.6*
H7	**Visible sky +age+ geological feature + landtype + (geological feature** x **landtype** x visible sky)	0.70	0.0001	98.9	599	72.2	521	2.5*

Table 4 continued. Evaluation of spatial scales and western white pine growth (basal diameter, height, relative mean annual height increment) in different canopy openings (as defined by visible sky) using the full versus reduced model hypothesis testing.

Eq. No.	Model	R^2	P-value	Full model[1] SSE	Full model[1] DF	Reduced model[1] SSE	Reduced model[1] DF	F^2
			Relative mean annual height increment[3]					
R1	Visible sky (N = 142)	0.26	0.0001	4140	141			--
R2	**Visible sky** + landtype[1]	0.39	0.0001	3382	126	4140	141	1.9*
R3	**Visible sky** + geological feature	0.41	0.0001	3289	132	4140	141	3.8*
R4	**Visible sky** + weathering	0.26	0.0001	--	--	--	--	--
R5	Visible sky + weathering + geological feature + (weathering x geological feature)[4]	0.41	0.0001	--	--	--	--	--
R6	Visible sky + geological feature + landtype + (geological feature x landtype)[4]	0.54	0.0001	--	--	--	--	--

[1] Variables in bold are included in the reduced model and all variables are included in the full model.

[2] The F statistic tests the variable addition from the reduced to the full model with * indicating significance
($p \leq .05$).

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

[4] Overall model was significant, but weathering or landtype was not significant in the partial sum of squares.

Wallace formation combined with southern aspects with toe slopes, and northern aspects containing non-dissected stream breaklands. In addition, many interactions occurred within the St. Regis formation. No significant interactions occurred with the Monzonites, alluvials, and old gravels; however, these geological features were infrequently sampled, which could explain the lack of interactions (Appendix C).

Western white pine was able to obtain a competitive advantage over western hemlock in relatively small canopy openings with visible skies ranging from 35 to 50% on alluvials (Qa), old gravels (Qts), and St. Regis (Ysr) formations (Figure 10A). In contrast, for western white pine to gain a competitive advantage on the Revett (Yr), Burke (Ybk), Monzonites (Kms), and Striped Peak (Ysp) geological features, openings with more than 90% visible sky were required. Western white pine growing on these geological features required openings with greater than 100% visible sky (0.7 ha) to be free to grow (Figure 10B). Occupancy of western white pine occurred in smaller openings on the Striped Peak (Ysp) formation, compared to sites on the Revett (Yr) and Monzonite (Kms) formations (Figure 10C).

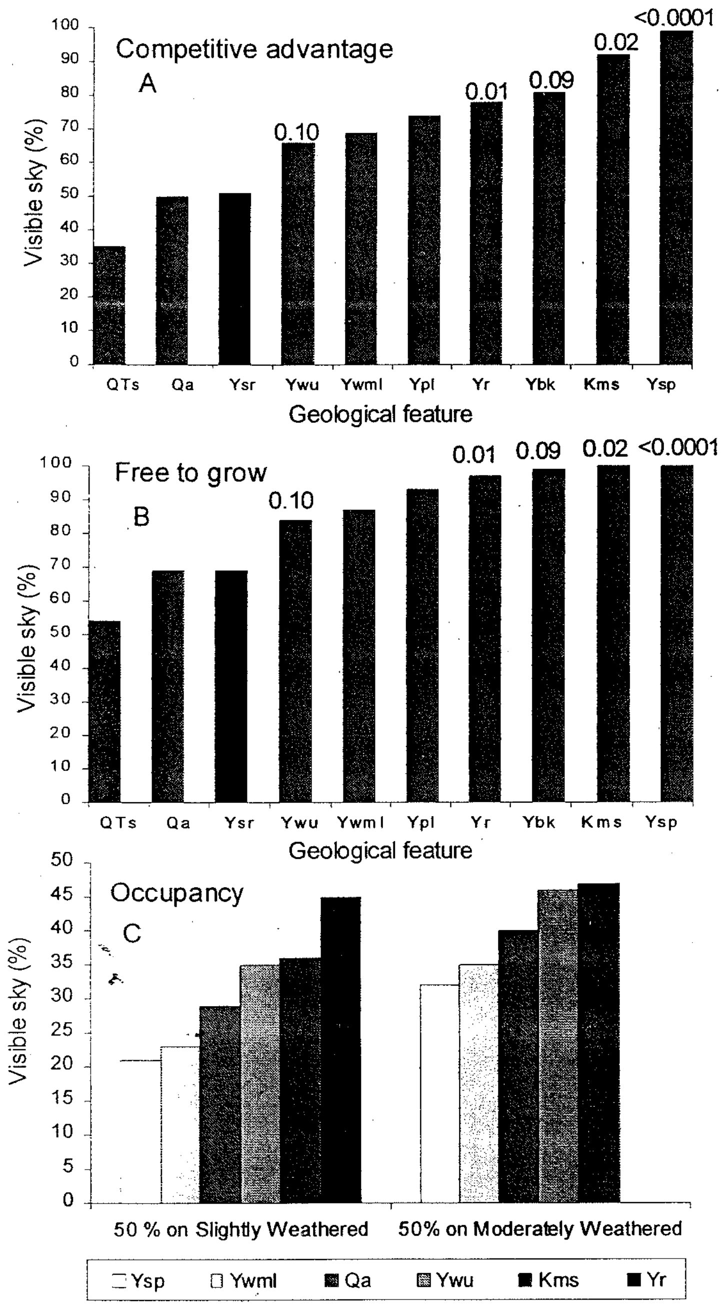

Figure 10. Geological feature influence on thresholds. The influence of geological features on the visible sky management thresholds (Appendix B). Competitive advantage (A) is when relative mean annual height increment between western white pine and western hemlock becomes positive. Free to grow (B) is when relative mean annual height increment between western white pine and western hemlock no longer increases as visible sky increases. Occupancy (C) is when three or more western white pine are established and occur on a 60-cm circular plot. Significant p-value for t-tests is shown in relation to the St.Regis (Ysr) formation for competitive advantage and free to grow. For definition of geological features refer to Appendix C, Table 2.

CHAPTER 3 - SYNTHESIS

Multiple spatial scales organized within a spatial hierarchy were used to identify a suite of biophysical characteristics influencing current growth and historical occurrence, abundance, and productivity of western white pine. Here, I synthesize the results of the three studies just described.

Where to manage western white pine

It has been suggested that increasing the abundance of western white pine in the northern Rocky Mountains should lead to more stable and sustainable forests (Hann et al. 1997; Harvey et al. 1999; Neuenschwander et al. 1999). Establishing western white pine in every place western white pine can grow would be impractical and economically impossible. A landscape perspective is required to identify locations that favor western white pine occupancy and growth.

Information from two of my studies (Appendix A and C) can be used to identify locations that favor western white pine and to establish management priorities. As I hypothesized, western white pine was historically distributed throughout most of the Coeur d'Alene River Basin. But within the Basin, I identified those kinds of places that most consistently supported western white pine. To survive and grow, western white pine prefers settings with substantial amounts of water (Graham 1990; Jackson and Spomer 1979; Minore 1979). This preference was corroborated by my results, which showed that western white pine favors landtypes that reflect high amounts of subsurface water flow and contain high amounts of surface moisture. Landtypes typifying these conditions, and those where western white pine restoration should be targeted include those dissected by streams, ones located adjacent to streams, or ones located on toeslopes. Most geological features contained western white pine, but if rapid growth is an objective, restoration activities should occur on the alluvials, old gravels, and the St. Regis geological features.

These studies also identified settings that would have a low priority for restoration. These results indicate that the granitics, basalts, and highly weathered schists would be classes of landtypes and geological features on which western white pine should not be featured. Western white pine should not be managed on high elevation, grassy mountain ridges, rock outcrops within glacial cirque basins, steep cirque headwalls within glacial cirque basins, and subalpine glaciated cirque basins. Settings on the upper member of the Prichard, and the Revett and Burke geological features should be examined closely before western white pine is planted or featured because both settings had low abundance and growth.

Western white pine management options within canopy openings

Information provided in this study complements current knowledge on western white pine management (Boyd 1959; Deitschman 1966; Ferguson et al. 1986; Graham 1988, 1990; Haig et al. 1941; Wellner 1940, 1946, 1971). Western white pine can be managed within a wide range of canopy openings as indicated by my studies (Appendix B and C). Applying this knowledge will be challenging but not impossible. Although western white pine growth will be sacrificed, unless openings are 4 to 5 ha in size; the information I provided is timely given the current reservation about clearcuts in the northern Rocky Mountains (Bliss 2000). Through the application of silvicultural treatments, a variety of stand compositions, structures, and canopy openings can be created. If seed is available, there is a high probability (55 to 80%) that through management or native disturbances, western white pine will occupy openings with 25 to 45% visible sky (basal area ≈ 120 ft^2 ac^{-1} to 80 ft^2 ac^{-1}, 28 m^2 ha^{-1} to 18 m^2 ha^{-1}). Western white pine could be planted under these conditions with assurance that they would survive and grow. But for both natural or planted seedlings to obtain a competitive advantage requires openings with at least 55% visible sky (basal area ≈ 70 ft^2 ac^{-1}, 16 m^2 ha^{-1}). Depending on the setting, stand structure, and composition, these conditions could be created initially or through further treatments. However, this window of opportunity may be 10 years or less (Deitschmann 1966; Graham 1988). To restore western white pine maintaining high forest cover requires continued treatments until the pines are free to grow or when canopy openings exceed 92% visible sky (basal area ≈ 35 ft^2 ac^{-1}, 8 m^2 ha^{-1}). To ensure that western white pine is free to grow, cultural activities (weeding, cleaning) should occur during the 10 to 30 year period after disturbances, because the species composition and future stand dynamics are largely determined during this time (Deitschman 1966; Graham 1988). Therefore, a silvicultural system incorporating these thresholds is needed that plans treatments through the life of the stand to ensure that western white pine dominates the site. In particular, my study provides information for the regeneration and young stand development phases of the silvicultural system.

Silvicultural systems should be adjusted depending on the setting (Appendix C). For stands occurring on alluvials, old gravels, and the St. Regis geological features, western white pine is able to obtain a competitive advantage over western hemlock in openings with visible skies ranging from 35 to 50% (0.2 ac, 0.08 ha). In contrast, for western white pine to gain a competitive advantage requires openings greater than 92% visible sky (1.2 ac, 0.5 ha) on the

Revett, Burke, Monzonites, and Striped Peak geological features. To achieve free to grow on these geological features, western white pine requires opening sizes greater than 100% visible sky (>1.8 ac, 0.7 ha).

Applying spatial hierarchies

I used concepts from hierarchy theory to define my spatial scales (Appendix A and C). If processes behave somewhat as if they are hierarchally nested, finer spatial scales should explain more variability in vegetation response than broader spatial scales (O'Neill et al. 1986). In my study for predicting current growth (Appendix C), this was true. The highest proportion observed of the variation in western white pine growth was explained by the finest scale (canopy opening) in a four spatial scale hierarchy (canopy openings, landtype, geological feature, weathering) (Appendix C). Similarly, landtype, the finest scale in a three spatial scale hierarchy, was strongly associated with the historical occurrence, abundance, and site productivity of western white pine (Appendix A). These are examples of where the hierarchy I defined on soil-forming processes worked quite well, even though it was not perfectly nested. But there were instances in which the broad scale (geological feature) explained more of the variation in the dependent variable than the fine (landtype) scale (Appendix C).

This inconsistency possibly occurred because I had too many landtypes, adding noise to western white pine growth estimates (Appendix C). But as hierarchy theory implies, landtypes could be grouped and constrained by geological features, a broader spatial scale, and they should constrain the variation occurring in the finer landtype scale. This did occur when the broader scales constrained the finer scales when I classified historical western white pine occurrence and abundance (Appendix A). The broader geological feature scale was used to separate observations into CART tree branches, with landtype often being nested within geological features. This indicates that the variation in western white pine growth, historical abundance, and occurrence were better explained when landtypes were linked to a higher level within the spatial hierarchy. When Fassnatcht and Gower (1998) linked forest potential vegetation types to a broader spatial scale defined on soil nutrition and moisture, 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. My results verify the hierarchical concept that spatial scales are linked, and broader scales constrain or contain finer scales (Allen and Starr 1982; Delcourt and Delcourt 1988; O'Neill et al. 1986).

Unique qualities of this research

This study provides new information that may be useful to other endeavors that include multiple spatial scales. When conducting a multiple spatial scale analysis across a large landscape, data sets become quite large, creating challenges with analysis and interpretation. I evaluated several statistical techniques and found that CART was applicable and provided interpretable results. I successfully analyzed large amounts of data (more than 45,000 observations and 1,300 unique combinations). The analysis inherently links spatial scales in classification trees and identifies combinations of spatial scales that are relatively easy to interpret.

Landscape scale analyses are often challenging because they contain inadequate data (Cherrill et al. 1995). Moreover, spatial autocorrelation should be addressed when using spatially explicit data (Cressie 1993; Gotway and Stroup 1997; Gumpertz et al. 2000;

Legendre and Fortin 1989; Payn et al. 1999; Rossi et al. 1992). The combination of my sampling design, the advantage of using a GIS platform for storing the data, and the ability to create two independent data sets in conjunction with my statistical analysis uniquely addressed both these issues (Appendix A). Because my data all existed within a GIS platform, I could select any sampling density and design. Many landtypes were small in geographic extent or were scattered throughout the drainage (e.g., narrow stream channels). To insure all landtypes were sampled, I varied my sampling density to reflect this variation. This sampling technique created a classifier data set with more than 45,000 observations. Thus, the classification trees were built upon a robust sample of all landtypes, geological features, and weathering classes. I created a second independent data set to test the classification trees using a systematic sampling technique representing the frequency distribution of my target population that had more than 30,000 observations. CART allowed me to determine misclassification costs, and, since I had a true frequency distribution of the target population in the test data set, I avoided spatial autocorrelation issues.

I defined my spatial scales to reflect the integration of short- and long-term climate, geomorphic processes (e.g., soil creep and deposition, erosion), soil weathering, bedrock, and topographic and physiographic features that influence individual plants to entire forests (Alt and Hyndman 1989; Delcourt and Delcourt 1988), making my results ecologically meaningful. My spatial scale definitions allowed me to link my results to factors influencing vegetation patterns, rather then defining my hierarchy on physical (subwatershed, watershed, river basin, region) boundaries that do not relate readily to biophysical factors. Although my hierarchy was imperfect, I was able to identify interactions among spatial scales that relate to the pattern in western white pine growth and historical occurrence, abundance, and site productivity, and at least infer what biophysical factors contribute to these relations.

The historical data I used were unique since they were spatially explicit, provided detailed information on vegetation patterns, covered all ownerships, and were relatively simple to convert to a digital format. For my application, the opportunity to make observations prior to changes in disturbance patterns caused by European settlement was invaluable. Historical information allowed me to identify settings where western white pine once existed. Additionally, these data could be used in comparative analysis of vegetation change, identify reference conditions, or complement other information sources such as fire histories to further improve inferences (Landres et al. 1999; Kaufman et al. 1994; Swetnam et al. 1999). There are some disadvantages with historical information such as being unable to evaluate errors in data collection. Fortunately, for the historical information in this study, the data standards and methods were well documented (Hutchison 1937).

Limitations

This study had some limitations. A disadvantage of forest structures defined by visible sky is that traditional density measurements were poorly related to these indices (Appendix B). I found a weak relationship between visible sky and basal area, stand density index, and trees per hectare. In contrast, Mitchell and Popovich (1997) found basal area strongly related to visible sky in pure ponderosa pine stands using a spherical densiometer. Size of opening, although a good descriptor of visible sky (Coates 2000), is not easy to estimate because of stand, tree, canopy, and crown irregularities.

There are several ways a hierarchy can be defined. I did not evaluate other spatial hierarchies using different sets of biophysical criteria (e.g., climate, disturbance), therefore, I cannot say my hierarchy was the most effective. But my hierarchy based on soil development factors using available data provided insights into ecosystem functions. The spatial hierarchy I developed not only increased our understanding on the distribution and growth of western white pine, the techniques developed in this study could be applied in landscape planning and site-specific silvicultural treatments. In particular, my results, could be used to help decision makers identify places for increasing western white pine abundance within the Coeur d'Alene River Basin and determine how to increase western white pine given the current reservation about clearcuts. Similar hierarchies could be developed to meet other management objectives. The hierarchical approach used in this study is the suggested method for implementing ecosystem management (Allen et al. 1984; Haynes et al. 1996; Kaufman et al. 1994; King 1993).

Future research

Truly answering a research question requires integrating knowledge from a wide range of studies including controlled laboratory, replicated field experiments, replicated natural experiments, and natural experiments (Diamond 1986; Ratti and Garton 1994). I had two natural experiments (Appendix A and C) and a replicated natural experiment (Appendix B). My first study (Appendix A) could be strengthened. Since all data were on a GIS platform, a replicated natural experiment could easily be conducted by changing the sampling design and creating a data set with fewer observations but would contain replication. Using results from this study, testable hypothesis concerning geological features or interactions among spatial scales could be tested. For two studies (Appendix A and C), I did not quantitatively describe or relate specific biophysical factors to the spatial scale. This would be an obvious next step. My second study (Appendix B) was a replicated natural experiment defining the relations between established western white pine and canopy opening. To affirm these relations, a controlled experiment could be conducted that examines the physiological and growth response of planted western white pine in different sized openings.

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APPENDICES

There are three appendices that contain a complete drafts of manuscript (introduction, methods, results, discussion, literature cited) written in the format reflecting a journal where it will be submitted. The appendices are:

Appendix A - Historical vegetation pattern across spatial scales - This manuscript will be submitted to Landscape Ecology

Appendix B - Canopy opening and western white pine - This manuscript was submitted to Forest Ecology and Management on March 8, 2001

Appendix C - Western white pine growth across multiple spatial scales - This manuscript will be submitted to Canadian Journal of Forest Research

Appendix A - Historical vegetation pattern across spatial scales

Characterizing historical (circa 1934) occurrence, abundance, and productivity of western white pine across multiple spatial scales of the Coeur d'Alene River Basin in northern Idaho

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Abstract

Defining multiple spatial scales hierarchically can effectively simplify the organizational structure of complex systems. Few studies link spatial scales and quantify the contribution each scale makes. Our objectives were to determine if apriori-defined spatial scales can be used to understand vegetation relations and identify linkages among the scales. The study was conducted in the Coeur d'Alene River Basin (approximately 300,000 ha) in northern Idaho. We used landtypes, geological features, and weathering to define a nested hierarchy and related these spatial scales to the historical (circa 1934) occurrence, abundance, and productivity of western white pine (*Pinus monticola*). We used 31 classification trees to identify relations between the outcome variables (presence/absence, abundance as defined by percent stocking, and site productivity as defined by site index using a 50-year base) and individual and combinations of spatial scales. By using two independent data sets (classifier data set and a test data set) and classification and regression tree analysis (CART) we were able to avoid spatial autocorrelation issues. Our spatial hierarchy was related to the outcome variables in most cases, particularly when the spatial scales were combined. The proportion of observations correctly classified for western white pine abundance was lower (16 to 36%) than the proportion classified correctly for presence or absence (48 to 64%) or for site productivity (55 to 63%). We suggest that multiple spatial scales are beneficial for use in landscape planning, and in understanding species distribution, including the presence, absence, abundance, and productivity.

Key words: hierarchy, CART, classification trees, spatial sampling, autocorrelation, species distribution, productivity, landscape analysis

1. Introduction

Defining multiple spatial scales hierarchically can effectively simplify the organizational structure of complex systems (Whyte 1967 Allen and Starr 1982; O'Neill et al., 1986). In theory, higher levels within a nested hierarchy have greater geographic extents (Delcourt and Delcourt 1988), and slower development rates (O'Neill et al., 1986), and they constrain or contain lower levels (Allen and Starr 1982). There are numerous ways to define hierarchies in forest ecosystems (Allen and Starr 1982; O'Neill et al., 1986; Urban et al. 1987; Delcourt and Delcourt 1988; Schugart and Urban 1988). For example, Delcourt and Delcourt (1988) defined nested hierarchies using the heterogeneity of vegetation patterns. Vegetative patterns are the result of biophysical processes and structures occurring at different spatial and temporal scales that sustain plant and animal communities (Delcourt and Delcourt 1988). Within short temporal (from 1 to 500 years) and fine spatial scales (from 1 to 10^6 m^2), climate, geomorphic processes, and other disturbances create forest openings that encourage the decomposition of organic matter, influence soil properties, and alter vegetation regeneration and development (Brokaw 1985; Delcourt and Delcourt 1988; Haig et al. 1941; Lawton and Putz 1988; Runkle 1982; Spies et al. 1990). The climate occurring within these scales includes seasonal patterns and short-term (from decades to centuries) weather trends and fluctuations. Geomorphic processes include soil creep, debris avalanches, deposition, eluviation (movement of material out of a portion of a soil profile), illuviation (movement of materials into a portion of a soil profile), and erosion (Brady 1974; Foth 1978; Jenny 1980; Buol et al. 1989; Sollins 1998). Biophysical factors influencing forest canopy gaps to second-order watersheds are appropriate for defining the lower levels of forest ecosystem hierarchies.

Long temporal (500 to 10,000 years) and broad spatial scales (10^6 to 10^{10} m^2) include events occurring within the Holocene and the last interglacial period (Delcourt and Delcourt 1988). Within these scales, changes in geomorphic and climatic regimes affect the dynamics of vegetation, soil weathering, and bedrock. For example, on northern Idaho landscapes, volcanic eruptions from Mount Mazama deposited ash layers, several thousand years ago, influencing vegetation (Alt and Hyndman 1989). The topographic and physiographic features underlying these depositions influence soil depth. These broad- and long-term events occur within third order and larger watersheds. The combination of processes occurring at these scales (0 to 10,000 years and 1 to 10^{10} m^2) influences individual plants to entire forests and are appropriate for defining the highest levels within forest ecosystem hierarchies (Delcourt and Delcourt 1988).

Although hierarchy theory is not new (Whyte 1967), it has only recently been used to describe and characterize ecosystems. During the 1990s, many regional and landscape assessments were conducted within the United States using multiple scales. These assessments show current and historical ecosystem characteristics such as vegetation patterns, ecosystem integrity and resiliency, and vegetation change (Quigley et al. 1996; SAMAB Report 5 1996; SNEP 1996). In these assessments, broad scales provide context for fine scales (Quigley et al. 1996; SAMAB Report 5 1996, SNEP 1996). For example, in the Columbia River Basin assessment, large river basins provided context for elements occurring at finer scales (watersheds) such as native fish strongholds or areas with high ecological integrity (Quigley et al. 1996).

Multiple spatial scales have also been used to describe rare plant habitats (Wu and Smeins 2000), characterize and relate habitat heterogeneity to fish abundance (Poizat and

Pont 1996), and predict the distribution of plant species (Cherrill et al. 1995). Wu and Smeins (2000) used three spatial scales (regional, landscape, and site) to identify potential habitat for rare plants by creating habitat suitability models for each spatial scale. At the regional scale, they classified areas as a function of soils to predict the likelihood of habitat occurring within counties or watersheds. At the landscape scale, they determined habitat suitability within stands and among multiple stands. At the site scale, information from field surveys were used to determine if a specific location was suitable for a particular rare plant.

Poizat and Pont (1996) used three spatial scales-- stream characteristic (e.g., channel or dike-fields), bank type (e.g., gravel or sand beaches), and microhabitat (e.g., turbidity, shade, shelter) --to relate juvenile fish abundance to habitat. Variations in fish abundance were better explained using multiple spatial scales compared to using a single scale. They quantified the contribution each scale made toward explaining the variation in habitat heterogeneity and fish abundance, and showed that significant interactions occurred between stream characteristic and the bank type when related to fish abundance.

Cherrill et al. (1995) used a hierarchical matrix model including three spatial scales (land class, cover type, community), to describe plant distribution. The habitat for 336 out of 570 species was identified using this model. These studies were able to describe ecosystem functions not recognizable within single scales (Cherrill et al. 1995), broader scales provided context for finer scales (Wu and Smeins 2000), and linkages among spatial scales improved fish habitat descriptions (Poizat and Pont 1996).

Few studies link spatial scales and quantify the contribution each scale makes toward inferences. Many studies using multiple spatial scales involve areas with small spatial extents, such as lakes or individual trees (O'Neill et al. 1991; Song et al. 1997;

Hinckley et al. 1998). Studies with large spatial extents usually concentrate on one spatial scale or use multiple spatial scales to provide context. They rarely attempt to find interactions among spatial scales (Collins and Glen 1991; Flather and Sauer 1996; Gustafson and Gardner 1996; Wu and Smeins 2000). In addition, spatially oriented studies seldom consider spatial autocorrelation that can bias the results, and those that do use relatively small sample sizes (Legendre and Fortin 1989; Rossi et al. 1992; Gotway and Stroup 1997; Payn et al. 1999; Gumpertz et al. 2000).

Our objectives were to determine if apriori-defined spatial scales that are hierarchically organized can be used to understand vegetation relations (broad-, mid-, and fine-scale variation) across a large landscape (>300,000 ha) and to identify linkages among the scales. Results from this study can be used to identify management priorities (landscape planning), to provide context for processes occurring at different spatial scales, and to understand population and habitat relations (Cherrill et al. 1995; Poizat and Pont 1996; Quigley et al. 1996; Wu and Smeins 2000).

2. Methods

2.1. Selected landscape

The forested landscapes of northern Idaho provided some unique opportunities. In the last 50 years, the moist forests of northern Idaho changed from landscapes containing a variety of successional stages occurring across the landscape to ones now dominated by late-seral vegetation (Hann et al. 1997; Harvey et al. 1999; Idaho Panhandle National Forest 1998) (Figure 1). Such a conversion from early-seral to late-successional vegetation would take 200 to 300 years in the absence of wildfire and human influence. As a major early-seral species, western white pine (*Pinus monticola*) plays many unique ecological roles (Leiberg 1897; Haig et al. 1941; Daubenmire and Daubenmire 1968; Larsen et al. 1980; Gale and Grigal 1987; Graham 1990; Cooper et al. 1991; Harvey 1994; Harvey et al. 1994; Minore 1979; Rehfeldt 1994). However, a combination of an exotic disease (*Cronartium ribicola*), timber harvesting, and fire exclusion led to a dramatic decline in the species (Figure 1). Since the early part of the twentieth century the species has declined by 90%, and only a fraction of its potential habitat is occupied by western white pine (Hann et al. 1997). There is considerable interest in increasing the abundance of western white pine over large landscapes (Hann et al. 1997; Harvey et al. 1999; Neuenschwander et al. 1999).

Deciding how, when, and where to efficiently increase western white pine abundance is difficult. Western white pine can grow on sites with at least 30 cm of volcanic ash soils, receiving 65 cm or more of precipitation, and occurring between 750 and 1,600 m in elevation (Haig et al. 1941; Graham 1990; Cooper et al. 1991). This area covers approximately 65% of northern Idaho. We hypothesized that multiple spatial scales would be useful in locating areas with the greatest potential for western white pine development.

2.2 Study area

We conducted our study in the Coeur d'Alene River Basin (approximately 350,000 ha), in the heart of the western white pine range (Figure 1). The Coeur d'Alene River Basin is dominated (>60%) by three potential vegetation types, grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*), that support western white pine forests (Cooper et al. 1991; Idaho Panhandle National Forest 1998). The climate of northern Idaho is influenced by the Pacific Ocean 400 km to the west. The summers are dry, and the majority of the precipitation (71 to 152 cm) occurs during the fall and winter. Annual temperatures average between 4 to 10 ^{0}C. Elevations within the Basin range from 718 to 1,875 m, but the majority of settings occur between 968 and 1,400 m (Graham 1990).

2.3 Spatial scales (independent variables)

We chose three spatial scales to reflect stable biophysical factors that integrate many soil-forming processes. We used landtypes, geological features, and weathering to define a reasonably nested hierarchy of spatial scales with extents ranging from 2 to over 200,000 ha (Table 1). The broadest scale in our hierarchy was defined using the weathering class, which reflects the relative extent to which bedrock has weathered from its presumed unweathered state (Schoeneberger et al. 1998; United States Department of Agriculture 1999) (Figure 2A). The processes incorporated into the classification occurred over the last 600 million years and altered the physical or chemical state of rocks at or near the Earth's surface without necessarily eroding or transporting the products (Bloom 1978). Three weathering classes occur in the Coeur d'Alene River Basin. Weakly weathered soils exhibit no clay development with more than 35% rock content; moderately weathered soils contain some clay with more than 35% rock content, and highly weathered soils contain high amounts of clay with less than 35% rock (United States Department of Agriculture 1999).

The mid scale of our hierarchy was defined using geological features that incorporate variations in bedrock lithology, rock class (metamorphic, igneous, and sedimentary), sediment bedding characteristics, and metamorphic structure layers (Figure 2B; Table 2). The classes in this scale, with geographic extents ranging to 33,000 ha, were also determined by processes occurring over the last 600 million years. Surface relief, hydrology, soil water-holding capacity, rock layering, rock type, surface deposits, and soil formations are some of the features recognized at this scale. In the Coeur d'Alene River Basin, the combination of these characteristics results in approximately 33 different geological feature classes (Table 2).

The finest scale, with the smallest geographic extent (2 to 2,400 ha), was defined using landtypes that identify settings based on landscape position, surface morphometry, and primary potential vegetation (Schoenberger et al. 1998; United States Department of Agriculture 1999) (Figure 2C; Table 3). Landscape position includes macrorelief such as ridgetop, sideslope, toeslope, or stream bottom. Surface morphometry describes characteristics including slope gradient and shape, and elevation. Indirectly, the influences of soil depth and topography on climate are integrated into this classification. Also, isolated areas where soil movement has occurred are recognized at this scale. The Coeur d'Alene River Basin contains five major landtype series with a total of 105 different landtypes (Table 3).

Defining spatial scales using landtypes and geology has several advantages. The settings defined by this hierarchy are relatively stable and have not changed significantly during the last 500 years (Bloom 1978). In addition, this hierarchy encompasses the soil-forming factors (climate, time, organisms, topography, initial parent material), which influence vegetation pattern (Aber and Melillo 1991; Harvey et al. 1987; Jenny 1980; Sollins 1998). The scales are somewhat nested because weathering (the broadest level) covers the largest geographic extent and has the fewest classes, and the individual categories encompass multiple geological features. Individual classes of the geological feature scale not only contain multiple landtypes, but constrain many of the soil-forming processes occurring at the landtype scale (e.g., soil deposition and erosion, clay accumulation). Moreover, soil development processes (e.g., decomposition and organic matter accumulation) occur faster within the landtype level than they do within the geological feature or weathering scale. Most importantly, data for defining this spatial hierarchy in the Coeur d'Alene River Basin was readily available from the United States Geological Survey and the Idaho Panhandle National Forests.

2.4 Distribution and abundance of western white pine (dependent variable)

Current vegetation does not provide a true reflection of western white pine habitat because white pine blister rust, timber harvesting, and fire suppression have changed the abundance and distribution of the species (Hann et al. 1997; Neuenschwander et al. 1999). The best available information for describing the distribution, abundance, and structure of vegetation in the Coeur d'Alene River Basin was a 1934 forest inventory conducted prior to the recent decline of western white pine (Hutchison 1937). These data included the major cover types (10), tree densities, and productivity classes. In addition, the species potentially occurring on areas harvested, converted to farm fields, or burned by wildfires were recorded. This information was recorded in detail (16.2-ha resolution) using a 1:31,500 map scale, covering 100% of the Coeur d'Alene River Basin (including private and publicly administered lands) (Hutchison 1937).

We created a digital copy of this historical forest information using a Geographic Information System (GIS). Each map covering about 9,000 ha of the Basin was hand drafted on mylar and scanned. The images were georectified and vectorized using Arc/Info (ESRI 1998). Chi-square was used to determine transformation accuracy based on ground control points, and a root mean square error was calculated, resulting in an error of 0.4 m. These data were attributed using the 1934, descriptions resulting in approximately 9,000 observations of historical forest composition and structure. These vector format data (weathering, geological feature, landtypes, historical forest survey) were converted to raster format with a cell size of 30 m. We sampled from this population, which contained 7,177,984 cells. Western white pine presence, absence, abundance, and site productivity were the outcome variables we used. Western white pine was deemed present if it was the designated cover type occurring in a cell. We also classified cells as present if western white pine occurred on disturbed lands prior to 1934. Cells containing cover types other than western white pine were classified as absent. For abundance, four tree density classes (<25%, 25-54%, 55-74%, or >74% stocked) were used. Western white pine site index (50-year base) including unknown, 12-, 15-, 18-, and 21-m classes, indicated site productivity (Haig 1936). Unknown site index are areas where site index was not recorded but could support western white pine. Weathering, geological feature, and landtype were the independent variables.

2.5 Sampling

Although we had a complete spatial coverage (100%) of the outcome and independent variables for the study area, we chose to select a sample. Sampling selection reflects the stochastic nature inherent in spatial data and includes random variation that allows us to quantify the predictive power of the independent variables. In addition, by drawing random samples we were able to create independent model development and testing data sets.

Classic sampling techniques (random, stratified, etc.) could not be used because the autocorrelation inherent in spatial data violates the assumption of statistical independence of sampling units. Various sampling techniques are available for optimizing spatial prediction in the face of spatial autocorrelation (McBratney et al. 1981; Yfantis et al. 1987). An equilateral triangle sampling technique appeared to best represent the spatial variation of our data. We conducted two independent samples --a set for model development and a set for testing. For the former, we weighted our sample depending on landtype frequency. This variable density sampling ensured that all landtypes, geological features, and weathering classes were represented in the data. For example, if a given landtype occurred in 0 to 6,000 cells (30 m), we sampled the three scales at 60-m intervals, and if a given landtype occurred in over 50,000 cells, we sampled at 720-m intervals. This sampling technique resulted in a model development data set containing 45,454 observations for addressing presence and absence.

For the test date set, a second triangular sampling over the entire Basin was conducted at 350-m intervals, irrespective of landtype frequency. These data represented the frequency of each landtype, geological feature, and weathering class and contained 30,220 observations. For addressing abundance and site productivity, only data with western white pine present was used in each of the data sets, resulting in 18,638 observations in the model development data and 16,249 observations in the test data.

We developed a Fortran program to sample our spatial data. The program allows geographic coordinates, a sampling density, and a sampling design to be designated. Using a specified sampling design, the program creates a flat file containing a fishnet of points. From this file, we used Arc/Info to generate a point coverage (ESRI 1998). Arc/Grid macro language was used to extract the values for each outcome and independent variable at each sample point (ESRI 1998).

2.6 Statistical analysis

Spatial statistical techniques (e.g., spatial prediction, wavelet, fractal, point process) appeared to be the most appropriate for analyzing these data (Cressie 1993). However, it became apparent that the techniques currently available for analyzing spatial data were impractical with large, rich data sets. We had 105 landtype classes, 33 geological feature classes, and 3 weathering classes, resulting in over 1,300 unique class combinations. Interpreting the coefficients with any accuracy or confidence was difficult using regression, logistic regression, or analysis of variance. Further, the residual errors were not independent or randomly distributed because of spatial autocorrelation, violating the assumptions of these analytical techniques. Techniques (kriging, cokriging, spatial regression) that adjust predictions for spatial autocorrelation are poorly suited for analyzing large (30,000 to 45,000 observations) data sets with numerous multiway interactions (over 1,000) (Legendre and Fortin 1989; Rossi et al. 1992; Cressie 1993; Goovaerts 1997; Gotway and Stroup 1997; Gumpertz et al. 2000). Algorithms and computer resources are not readily available to handle problems this large.

We used a nonparametric classification and regression tree (CART) statistical technique to estimate classification trees for western white pine presence, absence, abundance, and site index (Brieman et al.1984; Steinberg and Colla 1995). This technique partitions data using a binary decision process appropriate for both categorical and continuous data. CART can analyze complex data (many classes) with many observations. The resulting classification diagrams can be readily interpreted. Since CART is nonparametric, and does not form explicit hypothesis tests, the assumptions (residual errors independent and randomly distributed) of parametric analyses (linear regression, logistic regression, analysis of variance) do not apply or are less important. We minimized the impact of spatial autocorrelation by using two independent data sets sampled by two different methods (weighted and systematic), and two different intensities (variable and 350-m intervals). One set (classifier data) was used for developing the classification trees and one for testing the trees (test data). The test data represented the frequency distribution of the target population. Even if spatial autocorrelation existed in the test data, the outcome and independent variables were properly represented. Thus the misclassifications estimates were properly weighted by the frequencies of the variables and are therefore unbiased.

CART was used in a stepwise approach to identify relations between the outcome variables (presence and absence, abundance, and site index) and individual and combinations of spatial scales (weathering, geological feature, and landtype) (Table 4). CART produces trees with "nodes," showing where splits in the classifications occurred (Figure 3). Based on decision rules, CART classified the observations until every observation was classified correctly, or until one observation remained unclassified at a particular node, all observations in the node were the same, it contained equal proportions of classes, or there were less than 10 observations left in the node. From this maximal tree, branches were pruned and a set of subtrees were derived. The test data were classified using each of these sub-trees (>100 trees), and the best subtree with the lowest cost-complexity measure was identified by CART (not shown). The lowest cost-complexity measure is the combination of misclassification error, tree complexity (number of nodes in tree), and a cost constant (Breiman et al. 1984).

3. RESULTS

3.1 CART results and interpretation

Occasionally, when CART selected a best tree that was extremely complex, we searched for a less complex tree that still did a good job of classifying the observations. We used several factors to evaluate how well trees classified outcome variables (presence, absence, abundance, or site productivity) into categories defined by our spatial scales (weathering, geological feature, landtype). They included the chi-square goodness-of-fit statistic that compared observed frequencies to those estimated frequencies using the test data set, total number of observations correctly classified on the test data set, and how well observations were classified within the different levels of our outcome variables (Figures 3, 4, and 5; Table 4). In addition to the statistics, the number of terminal nodes per tree was evaluated to ensure that the results were meaningful and interpretable. A tree may reflect a high chi-square and classify the majority of the observations correctly, but contain over 200 terminal nodes, making it difficult if not impossible to interpret. For example, one of the trees (Table 4, tree A11) we created using all three spatial scales to classify abundance contained 293 terminal nodes and classified 36% of the observations correctly, while another 18-terminal-node tree (Table 4, tree A12) using the same three spatial scales classified 29% of the observations correctly. Hence, the 18-terminal-node tree was more than adequate for describing the relations between abundance and the spatial scales and easier to interpret than the complex 293-node tree.

We compared 31 classification trees representing individual and combinations of spatial scales for showing relations to white pine occurrence, abundance, and site productivity

(Table 4). The trees were complex and showed linkages among spatial scales when all possible spatial scale combinations were presented. The test and classifier data were similar in 29 of 31 cases as indicated by the nonsignificant ($P \geq 0.05$) chi-square statistics. In most trees, our spatial hierarchy explained to some degree, the spatial patterns of western white pine presence, absence, abundance, and site productivity. The classifier and test data were different (significant chi-square) only when weathering alone was used to classify presence, absence or abundance (Table 4, trees P1 and A1). However, when weathering alone was used to classify productivity (site index) the test and classifier data were similar (Table 4, tree S1).

For each individual tree, we used a suite of results to develop our in interpretation (Figure 3). The internodes (white) show the spatial scale and decision rule used to split the observations. Binary splitting occurs throughout the tree until observations can no longer be split and a terminal node is created. The terminal node (shaded) has the outcome from the decisions, the number of observations correctly classified, the total number of observations in the node, and the misclassification cost (calculated as 1 minus the probability of an observation being classified correctly). For example, the observations in terminal node 1 were classified as being absent of western white pine with 353 of 386 observations classified correctly, and the misclassification cost was 0.074. An individual spatial scale's contribution toward the classification is determined by following the branch from a terminal node back to the root node. The classifications in terminal node 1 (Figure 3), were a function of landtypes within a set of geological features.

3.2 Presence or absence

Classification trees containing all three spatial scales included both a 37-terminal-node and an 18-terminal-node tree (Table 4, trees P7, and P8). For classifying presence or absence, the 37-terminal-node tree only slightly outperformed the 18-terminal-node tree. The 18- terminal-node tree containing three spatial scales correctly classified 63% of the presence or absence observations (Table 4, tree P8). It also correctly classified 85% of the observations when western white pine was present and 37% of the observations when western white pine was absent. Based on the classification trees where each spatial scale was used separately, landtype appears to have a strong relationship with western white pine presence (88%), followed by geological feature (67%) and weathering (21%) (Table 4, trees P1, P2, P3). For western white pine absence, weathering (79%) and geological features (49%) were better individual classifiers than landtype (27%). Combined, weathering and geological features correctly classified 54% of the observations when western white pine was absent (Table 4, tree P4). Moreover, geological feature and landtype combined classified 44% of the observations correctly when western white pine was absent (Table 4, tree P5).

Although the 18-terminal-node tree had high success (63%) overall; there was considerable variation among terminal node misclassification costs within the tree, (Figure 3). Most of the observations (85%) with western white pine present went to the right branch. To classify absence, the split of observations was relatively clean, since the misclassification costs in the absence terminal nodes (left branch) ranged from 0.074 in terminal node 1 to 0.366 in terminal node 8. In general, the misclassifications costs within the branch classifying presence (right) were higher than the costs classifying absence. Presence misclassification costs usually ranged between 0.3 and 0.5; however, 0.8 was recorded in terminal node 14. In most cases within the presence branch, the misclassification costs increased near the branch ends, indicating a high amount of variation in these final observations.

A few landtypes and geological features tended to always have western white pine present. These landtypes occurred on valley bottoms adjacent to streams, stream terraces, alluvial fans, colluvial fans, and toeslopes (130, 131, 133, 135) (Table 5). Western white pine frequently grew in forested stream bottoms on shallow slopes (135). These landtypes were constrained by the alluvial deposits (8), a geological feature, that contained western white pine in all nodes, except when it occurred in terminal node 13 where western white pine was absent. Other landtypes favoring western white pine occurred on northerly aspects and places with abundant water (461, 463, 481). Also, settings containing quartz diorite or igneous rocks (geological feature 15) tended to support western white pine.

In contrast, several geological features and landtypes never supported western white pine. Pine did not occur on the Lakeview Limestone (2), Revett and Burke (23), or Snowslip (29) geological features. The Lakeview limestone is a steep geological feature containing sedimentary rocks with layers of limestone and dolomite containing numerous talus slopes. The Revett and Burke and Snowslip formations consist of meta-sedimentary rocks with siltite, argillite, or carbonate-siliciclastics bedrock lithologies. Also, portions of the upper member of the Prichard formation (21) consisting of argillite-silty argillite rocks contained no western white pine (Figure 2B and 4B), while the remainder of this geological feature dominated by siltite rocks was occupied by pine. Western white pine was absent on landtypes within the 300 (granitics), 500 (granitics), 600 (basalts), and 700 (highly weathered schists) series (Figures 2C and 6C; Tables 3 and 5).

The spatial scales were nested and the classifications of the fine spatial scale were dependent on the middle scale, (i.e., landtype). The geological features spatial scale was used in six splitting decisions usually occurring in the lower branch nodes (e.g., Figure 3, Nodes 2, and 13). Landtype was used 11 times for splitting and it was the first scale to be used (Node 1), but landtype was often nested within the geological feature spatial scale (e.g., Nodes 3, 6, 7, 14). For example, within terminal node 1, western white pine was absent from landtypes with talus slopes (197), high-elevation glaciated slopes (206), rock outcrops within glacial cirque basins (229), and dry glaciated slopes (209) (Tables 3 and 5). However, the presence of pine was associated with geological feature at internode 2, which caused these landtypes to also occur within terminal node 11where western white pine was present (Figure 3). Therefore, the landtypes selected in terminal node 11 were constrained by geological features that tended to favor western white pine. These geological features included glacial deposits (11), the Striped Peak formation (24), and the St. Regis formation (28). In this situation, the geological feature scale probably integrated more of the biophysical features related to western white pine presence than the fine landtype scale.

The spatial scales individually and collectively disclosed the pattern of western white pine presence or absence (Figure 6). The broad weathering scale indicated that western white pine was present in a small portion of the Basin, but only 21% of the observations where pine was present were correctly classified at this scale (Figure 6A). The geological features scale indicated that pine were absent (49% classified correctly) from the southwesterly portion of the Basin dominated by argillite-silty argillite rock types; but landtypes located in the same area showed western white pine was present (89% classified correctly) (Figure 6B and 6C). The best understanding of where western white pine historically occurred was achieved when all three scales were included (Figure 6D).

3.3 Abundance

The proportion of observations correctly classified for western white pine abundance was lower (16 to 36%) than the proportion classified correctly for presence or absence (48 to 88%) or site productivity (55 to 63%) (Table 4). Among the levels of abundance, 64% of the observations with moderate (55 to 74% stocked) to high (>75% stocked) abundance were correctly classified when all three spatial scales were used (Table 4, tree A12).

Individually, the geological features and weathering scales classified areas with low (<25% stocked) or very high abundance (>74% stocked) better than landtypes. For example, weathering classified 89% of the settings with low abundance (<25% stocked) correctly (Table 4, A1), while landtypes classified 29% correctly (Table 4, tree A3). Geological features correctly classified 25% of the observations with moderate abundance (25 to 54% stocked) correctly compared to landtypes that classified only 9% of the observations correctly (Table 4, trees A2, A3). There were two other trees that could have been selected that did not include all three spatial scales (Table 4, trees A8, A9); however, the 18-terminal-node tree containing all three spatial scales classified more observations correctly in the <25% and >74% stocking levels.

For areas with low abundance, most of the decisions were based on geological feature (Figure 4, Nodes 13-18). In contrast, for areas with high abundance, landtype along with geological features were used in the decisions (Figure 4, Nodes 1-12). As in presence or absence, most of the higher misclassifications costs occurred at the branch ends, indicating that many of these observations contained considerable variation. Of the 16,249 observations, most were initially classified with high western white pine abundance (Node 2). From this node, misclassification costs were initially low (0.029, 0.331, 0.413 in Terminal Nodes 7, 11, 12, respectively) but began to climb above 0.68 as the branch enlarged.

Among the geological features, older gravels (12) were always classified with high amounts (>55% stocking) of western white pine (Tables 2 and 6). This geological feature consists of unconsolidated old stream or river beds usually located on terraces above current stream courses. Other geological features supporting high amounts of western white pine were the gabbroic and diorite dikes (15) and the Prichard formation belt subgroup (19). However, areas with both high and low abundance occurred within the upper and lower members of the Prichard formation (20 and 21). Areas containing bedrock lithology characterized by argillite-silty argillites had low abundance, while other areas with siltite-argillite rock types had high abundance. All other geological features such as St. Regis (28), Wallace formations (31, 32, 33, 34, 35), Burke (16), Libby (17), and Mt. Shields formations (18) tended to support a wide range of western white pine abundance (Table 6).

Landtypes such as complex stream bottoms with plains, terraces, and alluvial fans (130), colluvial fans (133), and forested stream terraces (134) always contained abundant western white pine. Other landtypes tending to contain high amounts of western white pine were ridge tops (440, 490, 492, 493) and slopes that were dissected by many streams (455, 456, 457) (Tables 3 and 6). As expected, western white pine was not abundant on the dry glaciated mountain slopes (209) and rock outcrops within glacial cirque basins (229) (Tables 3 and 6).

Across the Coeur d'Alene River Basin, the areas with the highest historical abundance of western white pine occurred in the southwestern corner (Figure 7). This area corresponds to the lower member of the Prichard (20) within the geological feature spatial scale and areas containing moderately weathered soils represented in the weathering spatial scale (Figure 2A and 6D). Areas within the Striped Peak formation, belt supergroup (24), had low abundance. Much of this area was burned in 1910 by large stand-replacing wildfires, which may have influenced these results. Areas representing moderate abundance (25 to 55% stocking) were narrow strips following the streams and the St. Regis formation (28) (Figure 2B and 6D).

3.4 Site Productivity

Site productivity was the only outcome related to the weathering spatial scale as indicated by the nonsignificant chi-square (Table 4, tree S1). The tree containing all three spatial scales classified 64% of the observations correctly (Table 4, tree S11), but there was little difference among trees when landtype was included with either geological feature or weathering (0.63 to 0.64). However, none of the trees performed exceptionally well when classifying places with site indexes of 12, 15, or 21 m. Weathering classified 9% of the site index 12-m observations correctly (Table 4, tree S1) and all three scales classified 47% of the observations correctly within the 266-terminal-node tree (Table 4, tree S10). The 12-terminal-node tree containing all scales classified 83% of the observations for a site index of 18 m correctly (Table 4, tree S11).

Within the 12-terminal-node tree containing all three spatial scales, decisions were based on the landtype spatial scale, initially; however, geological features were also prominent in decisions throughout the tree (Figure 5). Most of the observations went to the right branch, with many of these observations being classified quickly in terminal node 8. Unlike the abundance and presence or absence variables, high misclassification costs were distributed throughout the tree. The lowest misclassification cost occurred in terminal node 7 with only 43 observations, and it was the only node where a site index of 12 m was classified (Figure 5).

Most places within the Coeur d'Alene River Basin were very productive, with many areas being classified with a high (18-m) site index (Figure 8; Table 7). The Monzonites and Syenites (5), alluvial deposits (8), Mt. Shields (18), St. Regis (28), and parts of the Prichard (19) geological features tended to contain settings with site indexes greater than 18 m. The sites with the lowest productivity tended to occur on the lower Prichard (20) in the southwestern and southeastern portions of the Basin (Figure 7). Observations correctly classified with low productivity in terminal node 7 were described as steep stream breaklands (106) and high-elevation talus/scree breaklands (197) (Table 7).

The complex stream bottoms with plains, terraces, and alluvial fans (130, 131), and mixtures of alluvial and colluvial fans (133) were classified as good sites (18 m) for growing western white pine (Table 7). In addition, some granitic landtypes with gentle side slopes and draws located on northerly and easterly aspects were quite productive (360, 363). Toeslopes with streams and dissected slopes occurring on all aspects were also very productive (455, 456, 463-468). These areas consistently contained high amounts of surface waterflow (Tables 3 and 6).

4. DISCUSSION

We could not define our spatial hierarchy on the actual ecosystem processes. For example, the available spatially explicit climate information represents current and not past climate. In 1934, western white pine ranged in age from 10 to over 200 years, reflecting climate occurring 70 to 300 years ago. Hence, our spatial scales needed to integrate long-term climate. We required heterogeneous data within and across watersheds that were currently available and spatially explicit for planning forest management and restoration activities, thus limiting our options to develop and map a custom spatial hierarchy integrating biophysical factors. Our historical data represent one point in time (1934), but we wanted to ensure the applicability of our results and define our spatial scales so they relate to biophysical factors that control vegetation pattern over time. Therefore, we defined a spatial hierarchy to predict vegetation pattern that integrate biological, physical, and ecological processes and structures that occur at different temporal and spatial scales (Allen and Starr 1982; O'Neill et al. 1986; Delcourt and Delcourt 1988).

Our spatial hierarchy, based on soil development was reasonably effective in classifying white pine occurrence, abundance and productivity, probably because it integrates factors such as landform (e.g., aspect, elevation, physiographic position), climate, disturbance, soil nutrition (microbial activity), and past vegetation (Jenny 1980; Delcourt and Delcourt 1988; Sollins 1998). All three spatial scales were used in the best classification trees. Landtypes reflect fine spatial scale variation within watersheds, geological features reflect variation across watersheds (mid scale), and weathering reflects long-term climate trends and variation within river basins (broad scale).

4.1 Classification performance

Our spatial hierarchy was related to the outcome variables in several classification trees, particularly when the spatial scales were combined (Table 4). In most cases, when geological feature was added to landtype, our classification improved for all three outcome variables, but in all cases, the landtype spatial scale was an important component in the hierarchy. Classification trees with the fewest number of terminal nodes containing all three spatial scales generally outperformed trees containing one or two spatial scales. Our results complement both Cherrill et al. (1995) and Poizat and Pont (1996), who also concluded that when linked together, multiple scales, explain more variation in fish abundance and plant occurrence than traditional single scale approaches.

We had mixed results on the performance of our spatial hierarchy for occurrence, abundance and productivity. When two spatial scales were used to predict site productivity and presence or absence, 45 to 64% of the observations were correctly classified (Table 4). Abundance had the lowest proportion of the observations classified correctly (16 to 36%) compared to presence, absence, or productivity (Table 4). Abundance is inherently stochastic, as it denotes seed source and disturbance patterns. The timing, intensity, and location of disturbances, the climate at time of seed germination and establishment, and seed source and viability are only some of the factors determining the dominance of a particular species (Pickett and White 1985; Oliver and Larson 1990; Agee 1993), and all could vary widely within the same landtype, geological feature, and weathering class.

For comparison, Dobbertin and Biging (1998) classified tree mortality of ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*), with accuracies between 11 and 36% using similar analytical techniques (CART). Reynolds (1994) classified spruce beetle hazard as a function of stand attributes, and was able to identify high hazard areas at least 73% of the time. Although our hierarchy had no total classification success rates greater than 64%, we were able to link the spatial scales and identify patterns in occurrence, abundance and productivity unique to different combinations of landtype, geological feature, and weathering class. Thus, our hierarchy was related to vegetation pattern across a landscape and showed the utility of using multiple spatial scales to identify vegetation patterns.

4.2 Scale definition and hierarchy theory

If processes behave somewhat as if they are hierarchally nested, then broader spatial scales should constrain lower spatial scales (Allen and Starr 1982), and finer spatial scales should explain more of the variability than broader spatial scales (O'Neill et al. 1986). As we hypothesized, our finest spatial scale (landtype) was related to the outcome variables as indicated by the consistently high p-values (0.17 for presence or absence, 0.18 for abundance, and 0.37 for productivity), followed by geological feature (0.12 for presence or absence, 0.12 for abundance, and 0.22 for productivity) and then weathering (0.008 for presence or absence, 0.05 for abundance, and 0.11 for productivity). These results suggest that landtype had an association with western white pine occurrence and abundance. The weathering spatial scale was relatively homogeneous across the Basin. Therefore it was a weak link in our hierarchy (Figure 2A). This scale might have more utility in predicting western white pine outcomes when multiple areas the size of the Coeur d'Alene Basin are used or in situations where it is more variable across the study area (Figure 2A).

The broader scales constrained the finer scales in the hierarchy we defined. For example, for predicting western white pine occurrence, abundance, and productivity, the geological feature scale was used to separate observations into tree branches, with landtype often being nested within geological features (Figure 3, Node 2, 13; Figure 4, Node 13; Figure 5, Node 9). Within these branches, geological feature constrained the landtype spatial scale by altering outcomes. Some landtypes were classified with both western white pine present and absent. Landtype 190 (rock outcrops) occurs in nodes both with western white pine present and western white pine absent (Table 5, Nodes 8 and 10), but in terminal node 10, rock outcrops occur on the Striped Peak (24) formation which was always classified as containing western white pine. The difference between the two classifications was the occurrence of a particular geological feature.

Landtypes constrained by geological features was also verified when we observed the pattern created by combining geological feature and landtype (Figure 6). By observing only the geological feature spatial scale (Figure 6B), there were places within the Basin where western white pine was classified as being absent. These same places, when observing landtypes, (Figure 6C), showed that western white pine was present. When the two spatial scales were combined, it was obvious where the geological feature spatial scale prevailed in the classification (Figure 6D). This was particularly true in the southwestern corner of the Basin (Figure 6). The broader scale, however, did not always constrain the lower spatial scale. For predicting site productivity, geological feature did not to appear to constrain landtypes because both spatial scales showed similar patterns of productivity in the southwestern corner of the Coeur d'Alene River Basin (Figure 8B and C).

The spatial hierarchy was somewhat nested, but far from perfect. Ideally, all weathering classes should contain all geological features, and all landtypes should be present within each of the geological features. These inconsistencies created classification trees with a considerable amount of noise (Table 3). For example, for classifying western white pine presence, the proportion correctly classified by the trees ranged from 0.16 to 0.77, depending on the spatial scale. Also, because of these inconsistencies, we were unable to verify if all landtypes behaved similarly within a geological feature. A fully nested hierarchy may have improved the classifications and the dependency between the classifier and test data. In the real world, ecosystems are not organized perfectly, do not have distinct lines between our classes, and inconsistencies among spatial scales add complexity toward explaining how ecosystems operate and function. Therefore, our results may represent a realistic picture of how ecosystems are organized.

4.3 Spatial scales in relation to biophysical factors

Ecological landtype was to integrate potential vegetation type, surface soil characteristics (2 m), subsurface flow, and subtle differences in topography. Western white pine prefers settings with substantial amounts of water to survive and grow (Wellner 1946; Jackson and Spomer 1979; Minore 1979; Graham 1990). This preference was corroborated when our results showed that western white pine favors landtypes that reflect high amounts of subsurface flow and contain high amounts of surface moisture. Landtypes where these processes occur include those highly dissected by streams, ones located adjacent to streams, those on toeslopes, or ones located in stream bottoms (e.g., 130, 131, 133, 463-468). Also, our results suggest that vegetation pattern was related to surface water characteristics and soil processes (total amount available, constant flow of water and nutrients, intermittent or constant supply) (Hughes and Larsen 1988; Claessen et al. 1994; Klijn 1994) captured in the landtype classification.

Landtypes disclosed areas without western white pine such as high-elevation, grassy mountain ridges (408), rock outcrops within glacial cirque basins (229), steep cirque headwalls within glacial cirque basins (241), and subalpine glaciated cirque basins (230). Western white pine was likely limited at these high elevations by temperature (Graham 1990). These results suggest that our landtype scale reflected temperature regimes. Therefore, it appears that our finest spatial scale defined by landtypes reflected fine-scale processes that influence vegetation pattern.

We intended the geological feature scale to describe regional vegetation patterns and characterize weathering processes determined by long-term climate trends and weathering potential. Geological features influence soil nutrition, water-holding capacity, and water movement through the juxtaposition of rocks (Bloom 1978). We assumed that moderately weathered soils would be productive because they contain more clay and higher water-holding capacity, and tend to be more nutritious than sands, gravels, or slightly weathered soils (Buol et al. 1989). Areas showing low productivity (Site Index 15 m), however, occurred in the southwestern corner of the Basin on moderately weathered soils (broadest scale) (Figure 2A). These settings were also associated with the lower member of the Prichard (20), which indicated low productivity (Site Index 15 m) (Figure 8B). These results may reflect the nutritional status of the geological feature as it weathers, resulting in low productive soils (Bohn et al. 1985, Moore 1998). As we intended, the geological feature spatial scale to a certain extent reflected factors that influence long-term soil development.

4.4 Patterns of western white pine occurrence, abundance, and productivity

Our spatial hierarchy did show patterns of western white pine occurrence, abundance, and productivity across a landscape, thus our results could be used in developing a landscape plan for increasing western white pine across a landscape. As we hypothesized, western white pine was historically distributed through most of the Coeur d'Alene River Basin (Figure 6D). There were only a few isolated places where western white pine was classified and observed as being absent. Landtype classes without western white pine included the granitics (500 series), basalts (600 series), and highly weathered schists (700 series). Geological features lacking western white pine included the upper member of the Prichard (21) and the Revett and Burke (23) formations. Although, western white pine can potentially grow in many places within the Coeur d'Alene River Basin, there were settings where western white pine was abundant, particularly the central portion of the Basin (Figure 7D). Only a few isolated areas were highly productive (Site Index 20), such as complex stream breaklands on northerly slopes (477) and mid-elevation dissected slopes on northerly and easterly aspects (462). Most sites within the Coeur d'Alene Basin were moderately productive (Site Index 18m).

4.5 Scientific contribution

This study provides new information which may be useful to other endeavors that include multiple spatial scales. When conducting a multiple spatial scale analysis across a large landscape, data sets become quite large, creating challenges with analysis and interpretation. We evaluated several statistical techniques and found that CART was very applicable and provided interpretable results. This technique successfully analyzed large amounts of data (more than 45,000 observations and 1300 unique combinations). The analysis inherently link's spatial scales and identifies which combinations of spatial scale categories result in a particular class by building classification trees which are easier to interpret.

Landscape scale analysis often contain inadequate data (Cherrill et al. 1995). Moreover, spatial autocorrelation is an important factor to consider when using spatially explicit data (Legendre and Fortin 1989; Rossi et al. 1992; Cressie 1993; Gotway and Stroup 1997; Payn et al. 1999; Gumpertz et al. 2000). The combination of our sampling design, the advantage of using a GIS platform for storing our data, and the ability to create two independent data sets in conjunction with our statistical analysis uniquely addressed both these issues. Because our data all existed within a GIS platform, we could select any sampling density and design. Many landtypes were small in geographic extent or were scattered throughout the drainage (e.g., narrow stream channels). To insure all landtypes were sampled, we varied our sampling density to reflect this variation. This sampling technique created the classifier data set with more than 45,000 observations. The classification trees were built upon a robust sample of all landtypes, geological features, and weathering classes. We created a second independent data set to test the classification trees using a systematic sampling technique representing the frequency distribution of our target population that had more than 30,000 observations. CART allowed us to determine misclassification costs and since we had a true frequency distribution of our target population in the test data set we avoided spatial autocorrelation issues.

The way we defined our hierarchy and interpretation of our results were ecologically meaningful. We defined our spatial scales to reflect the integration of short- and long-term climate, geomorphic processes (e.g., soil creep and deposition, erosion), soil weathering, bedrock, and topographic and physiographic features that influence individual plants to entire forests (Delcourt and Delcourt 1988; Alt and Hyndman 1989). Our spatial scale definitions allowed us to link our results to factors that influence vegetation patterns, rather then defining our hierarchy on physical (subwatershed, watershed, river basin, region) boundaries which do not relate to biophysical factors. Although, our hierarchy was imperfect, we were able to identify interactions among spatial scales that relate to the pattern in western white pine occurrence, abundance and site productivity, and at least infer what biophysical factors contribute to this relationship.

The historical data we used were unique since they were spatially explicit, provided detailed information on vegetation patterns and covered all ownerships, and were relatively simple to convert to a digital format. For our application, this opportunity to make observations prior to changes in disturbance patterns caused by European settlement was invaluable. Historical information allowed us to identify settings where western white pine once existed. Additionally, these data could be used in comparative analysis of vegetation change to identify reference conditions, or to complement other information sources such as fire histories to further improve inferences (Landres et al. 1999; Swetnam et al. 1999). There are some disadvantages with historical information, such as being unable to evaluate errors in data collection. Fortunately, for the historical information in this study the data standards and methods were well documented and published (Hutchison 1937).

The spatial hierarchy we developed not only increased our understanding on the distribution of western white pine, techniques developed in this study could be applied in landscape planning. In particular, our results, could be used to help decision makers identify places for increasing western white pine abundance within the Coeur d'Alene River Basin. Similar hierarchies could be developed to meet other management objectives. The hierarchical approach used in this study is the suggested method for implementing ecosystem management (Allen et al. 1984; King 1993; Haynes et al. 1996; Kaufman et al. 1996).

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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	Soil development time sequence	Data Source
Weathering	3	5 to 212,000 ha	current to 600 million years	IPNF[a]
Geological feature	33	5 to 33,000 ha	current to 600 million years	USGS[b,c]
Landtype	105	2 to 2,400 ha	current to 13 million years	IPNF[a]

[a] Weathering class and landtypes were provided by United States Department of Agriculture, Forest Service, Idaho Panhandle National Forests (IPNF).

[b] Geological features were supplied by the United States Geological Survey (USGS) with the classification based on individual geologic reports of study area and digital data (Hosterman 1956; Harrison and Jobin 1963; 1965; Hobbs et al. 1965; Sandpoint Quadrangle 1999; Thompson Falls Quadrangle 1999; Wallace Quadrangle 1999; Coeur d'Alene Quadrangle 2000.

[c] St. Maries Quadrangle [unpublished digital data], Derkey, P.D. Available: United States Geological Survey, Spokane, WA .

Table 2. Code and description for the 33 categories in the geological feature spatial scale.

Code	Geological feature description
2	Lakeview Limestone
4	Rennie Shale and Gold Creek Quartzite
5	Monzonite and Syenite
8	Alluvial Deposits
10	Older Glacial Deposits
11	Glacial Deposits
12	Older Gravels
13	Columbia River Basalt and Latah Formation
14	Granitic Rocks
15	Quartz Diorite or Amphibolite
16	Burke Formation, Belt Supergroup
17	Libby Formation, Belt Supergroup
18	Mount Shields Formation, Belt Supergroup
19	Prichard Formation, Belt Supergroup
20	Lower Member of the Pritchard Formation
21	Upper Member of the Pritchard Formation
22	Revett Formation
23	Revette and Burke Formations, Undivided; Belt Supergroup
24	Striped Peak Formation, Belt Supergroup
25	Striped Peak Formation, Argillite Part of Member One
26	Striped Peak Formation, Quartzite Part of Member One
27	Bonner Formation, Belt Supergroup
28	St. Regis Formation
29	Snowslip Formation, Belt Supergroup
30	Undivided Shepard Formation, Snowslip Formation, and Wallace Formation
31	Wallace Formation, Belt Supergroup
32	Middle Member of the Wallace Formation
33	Undivided Middle and Lower Members of the Wallace Formation
34	Wallace Formation, Upper Member, Undivided
35	Upper Member 1 of the Wallace Formation
36	Upper Member 2 of the Wallace Formation
37	Wallace Formation, Upper Member Three

Table 3. Codes and descriptions for 105 categories within the landtype spatial scale.

Code	Landtype description
106	Very steep stream breaklands with streams in the bottoms
110	Delta-shaped alluvial fans adjacent to major valleys on toeslopes
122	Low relief lacustrine plains or terraces with shallow slopes (0 to 5%)
130	Complex stream bottoms with plains, terraces, and alluvial fans
131	Terraces, toe slopes, and alluvial fans with moderate slopes < 40%
133	Mixes of alluvial and colluvial fans
134	Forested stream terraces, toe slopes, and fans with slopes 10 to 25%
135	Forested stream bottoms and meadows with slopes < 15%
155	Stream terraces and outwash plains (<20%) including narrow steep escarpments
190	Rock outcrop
191	Rock outcrop with minimal soil development
196	High-elevation talus/scree slopes
197	High-elevation talus/scree breaklands
198	Weathered bedrock areas prone to landslides with steep slopes (50 to 70%)
199	High-elevation talus/scree slopes with glaciated rock outcrops
200	Subalpine glaciated U-shaped valley bottoms
206	High-elevation glaciated mountain slopes (15 to 75%)
209	Dry glaciated mountain slopes (35 to 60%)
210	Subalpine glaciated mountain slopes (35 to 60%)
211	Mid- to high-elevation, undulating, alpine glaciated uplands (slopes 10 to 35%)
229	Rock outcrops in glacial cirque basins
230	Subalpine glaciated cirque basins
241	Steep cirque headwalls in glacial cirque basins
242	Steep cirque headwalls in glacial cirque basins with volcanic ash
243	Subalpine glaciated mountain slopes with glacial till
244	Glacial till with dissected, moderate slopes (35 to 55%)
245	Steep glaciated mountain slopes (>50%)
250	Glaciated mountain slide slopes, toeslopes, and foothills
253	Glaciated shallow incised draws at low to mid elevations
260	Gently sloping (<35%) glaciated midslopes and foothills
270	Glaciated sideslopes dominated by south and west aspects (30% rock)
271	Moderately steep slopes
350	Mid-elevation glaciated slopes (15 to 30%) on south and west aspects
353	Shallow and incised draws at low to mid elevations on south and west aspects
360	Gently sloping sideslopes (15 to 35%), usually on north and east aspects

Table 3 continued. Codes and descriptions for 105 categories within the landtype spatial scale.

Code	Landtype description
363	Shallow and incised draws at low to mid elevations on moderately sloped moist aspects
370	Glaciated sideslopes, ridges which are ash covered on south and west aspects
406	Open, dry, southerly aspects occurring at high elevations
407	High-elevation slopes (36 to 60%) underlain by hard metamorphic rocks
408	High-elevation, grassy mountain ridges
409	High-elevation southerly slopes (35 to 60%) with widely spaced streams
410	High-elevation northerly slopes (35 to 60%) with widely spaced streams
411	Mid- to high- elevation slopes (15 to 65%) on all aspects with many drainages
412	High-elevation southerly slopes (35 to 55%) with many drainages
413	Upper end of high elevation drainages with northerly slopes (35 to 70%)
414	Upper end of high elevation drainages with southerly slopes (35 to 70%)
415	Steep slopes (50 to 95%) with many drainages and avalanche chutes (<5,800 ft)
416	Steep slopes (50 to 95%) with many drainages and avalanche chutes (<5,200 ft)
440	Broad ridgetops with northerly slopes (10 to 35%) at high elevations
441	High-elevation slopes (10 to 35%) on southerly aspects with convex ridges
442	High-elevation slopes (10 to 35%) on southerly and westerly aspects
443	Mid- to high-elevation slopes (35 to 55%) on northerly aspects with many streams
444	Mid- to high-elevation slopes (35 to 55%) on southerly aspects with many streams
446	High-elevation slopes (35 to 55%) on south and west aspects with many streams
447	Highly dissected slopes (20 to 55%) on southerly aspects and in stream bottoms
448	Highly dissected slopes (20 to 55%) on northerly aspects and in stream bottoms
449	Mid-elevation slopes (35 to 60%) on highly dissected northerly aspects
450	Mid-elevation slopes (35 to 50%) moist sites with thick volcanic ash
451	Mid- to high-elevation slopes (35 to 55%) moist sites with thick volcanic ash
452	Mid- to high-elevation slopes (35 to 55%) northerly aspects with thick volcanic ash
455	Mid-elevation dissected toeslopes (5 to 45%) in low lands with southerly slopes
456	Mid-elevation dissected toeslopes (5 to 45%) in low lands with northerly slopes
457	Dissected slopes (20 to 55%) and ridgetops on southerly aspects
460	Low- to mid-elevation low-relief rolling uplands (slopes 10 to 25%)
461	Low- to mid-elevation dissected slopes (20 to 55%) on northerly aspects
462	Mid-elevation dissected slopes (20 to 55%) on northerly and easterly aspects
463	Low- to mid-elevation toeslopes (20 to 35%) and stream bottoms
464	Low- to mid-elevation dissected slopes (20 to 55%) on southerly aspects
465	Low- to mid-elevation dry toeslopes (20 to 35%) and stream bottoms
466	Low-elevation dissected slopes (20 to 55%) on northerly and easterly aspects

Table 3 continued. Codes and descriptions for 105 categories within the landtype spatial scale.

Code	Landtype Description
467	Dissected mid-elevation slopes (35 to 55%) on northerly aspects
468	Low-elevation dissected toeslopes (35 to 55%) on southerly aspects
469	Low-elevation slopes (15 to 65%) near streams on southerly aspects
470	Mid-elevation slopes (35 to 55%) near streams on southerly aspects
471	Mid-elevation slopes (45 to 65%) on southerly aspects with 15% rock outcrops
472	Low-elevation slopes (20 to 70%) along moderately incised streams
473	Moderately dissected slopes (20 to 55%) on southerly aspects
474	Dry timber/shrub mosaic on southerly slopes (35 ro 55%)
475	Complex stream headlands with northerly slopes (35 to 70%)
476	Dissected stream headlands with southerly slopes (35 to 70%)
477	Complex stream breaklands with northerly slopes (35 to 70%)
478	Complex stream breaklands with southerly slopes (35 to 70%)
479	Stream breaklands with rock outcrops on east - or west-facing slopes (50 to 90%)
480	Weathered breaklands on east- or west-facing slopes (45 to 90%)
481	Weathered and dissected breaklands on northerly slopes (45 to 90%)
483	Weathered and dissected breaklands on southerly slopes (45 to 90%)
488	Dissected stream breaklands on southerly slopes (60 to 80%)
489	Dissected stream breaklands on northerly slopes (60 to 80%)
490	Ridgetops on northerly slopes (10 to 35%)
491	Ridgetops on northerly slopes (0 to 40%)
492	Ridgetops on southerly slopes (10 to 35%)
493	Ridgetops on southerly slopes (0 to 40%)
515	Low-relief, rolling uplands (0 to 40%)
517	Dissected toeslopes, lowlands, and stream bottoms (5 to 35%)
518	Dissected toeslopes, lowlands, and stream bottoms on northerly slopes (20 to 45%)
557	Dissected mountain slopes and ridgetops on southerly slopes (20 to 55%)
561	Dissected mountain slopes and ridgetops on northerly slopes (20 to 55%)
562	Low- to mid-elevation slopes on northerly aspects (35 to 60%)
567	Moderately dissected slopes and narrow ridgetops on northerly aspects (20 to 55%)
573	Moderately dissected slopes and narrow ridgetops on southerly aspects (20 to 55%)
574	Low to mid-elevation slopes on southerly aspects (35 to 55%)
590	Granite mountain ridgetops
690	Basalt mountain ridgetops
717	Weathered dissected toeslopes and streams
718	Weathered siddected toeslopes and streams

Table 4. Classification trees containing the weathering geological feature and landtype scales. Outcome variables were presence or absence, abundance (% stocking <25, 25-54, 55-74, >74), and site productivity (site index at base 50 years, unknown, 12, 15, 18 21 m) of western white pine. Number of terminal nodes (Nodes) and the chi-square P-value showing the goodness-of-fit between the classifier and the test data and the number (N) of observations used in the trees are shown. Unknown site index is areas that support western white pine but no site index was given.

Spatial scale	Term. nodes	χ^2 P-Value	Proportion of observations classified correctly					
			Presence / Absence N = 30,220					
			Total	Present	Absent			
P1-Weathering (Weath.)	2	0.008	0.480	0.211	0.792			
P2-Geologic feature (Geol.)	2	0.12	0.587	0.670	0.491			
P3-Landtype	2	0.17	0.599	0.885	0.267			
P4-Weath. & geol.	16	0.21	0.606	0.661	0.542			
P5-Geol. & landtype	37	0.33	0.639	0.810	0.440			
P6-Weath. & landtype	2	0.14	0.599	0.885	0.267			
P7-Weath., geol., & landtype	37	0.33	0.639	0.810	0.440			
P8-Weath., geol., & landype	18	0.27	0.628	0.847	0.370			
			Abundance (Classes %) N = 16,249					
			Total	< 25	25-54	55-74	>74	
A1-Weathering	3	0.05	0.165	0.885	0.19	0	0	
A2-Geologic feature	6	0.12	0.283	0.294	0.254	0.451	0.187	
A3-Landtype	9	0.18	0.310	0.290	0.092	0.850	0.049	
A4-Weath. & geol.	23	0.17	0.306	0.478	0.261	0.411	0.197	
A5-Weath. & geol.	13	0.15	0.293	0.478	0.233	0.395	0.186	
A6-Geol. & landtype	294	0.46	0.355	0.347	0.398	0.579	0.206	
A7-Geol. & landtype	66	0.38	0.362	0.306	0.297	0.637	0.232	
A8-Geol. & landtype	29	0.31	0.328	0.252	0.238	0.748	0.121	
A9-Geol. & landtype	4	0.16	0.308	0.313	0.092	0.836	0.047	
A10-Weath. & landtype	9	0.18	0.310	0.290	0.092	0.850	0.049	
A11-Weath., geol., & landtype	293	0.46	0.356	0.354	0.399	0.578	0.066	
A12-Weath., geol., & landype	18	0.27	0.293	0.400	0.166	0.643	0.638	
			Site productivity (site index classes) N = 16,249					
			Total	Unk.	12 m	15 m	18 m	21 m
S1-Weathering	2	0.11	0.557	0	0	0	0.812	0.268
S2-Geology	4	0.22	0.557	0.347	0.089	0.406	0.657	0
S3-Landtype	10	0.37	0.627	0.315	0.119	0.359	0.773	0.116
S4-Weath. & geol.	19	0.32	0.466	0.537	0.188	0.295	0.500	0.091
S5-Weath. & geol.	8	0.26	0.450	0.551	0.089	0.406	0.452	0.091
S6-Geol. & landtype	264	0.57	0.630	0.443	0.470	0.383	0.732	0.341
S7-Geol. & landtype	72	0.51	0.640	0.398	0.233	0.365	0.768	0.232
S8-Geol. & landtype	18	0.43	0.631	0.320	0.119	0.423	0.763	0.145
S9-Weath. & landtype	10	0.34	0.627	0.315	0.119	0.359	0.773	0.116
S10-Weath., geol., & landtype	266	0.57	0.630	0.443	0.470	0.383	0.732	0.341
S11-Weath., geol., & landype	12	0.38	0.643	0.309	0.119	0.181	0.834	0.145

Table 5. Historical presence and absence of western white pine showing the number of observations correctly classified, the total number of observations, and which spatial scale class was assigned to each terminal node. Refer to code definitions in Tables 2 and 3 for weathering (Wea.), geological features, and landtype classes. Unknown site index are places that can support western white pine but site index was not recorded.

Term. node	Obs. classed correctly	Wea.	-----Geological features-----		-----Landtypes by series-----				
			2-19	20-37	100	200	300	400	≥500
Absent									
1	353/386	1,2,3	2,4,12,13,14 16,19	20,21,22,34,36	106,110,122 155,190,197	206,209,230 244,253,260	350,353,360 363,370	450,451,460,469	557,567,573,574 590,690,717,718
2	824/1109	1,2,3	14,16,17	20,21,22,29,31 32 34,36	196,199	242,245		406-411,413,414,441,474,492	518,561,562
3	1086/2099	1,2,3	2,4,12,13,14 16,17,19	20,21,22,23,30, 31,32,34,36				412,416,471,472,473	515,517
5	104/132	1,2,3	5,18	27,28,33	106,196,199	229,241,244		408,442,473	517,518,561,573
6	23/38	3	10	24,37	106	241,270		408,442	
8	457/764	2,3	10,11,18	25,28,33,37	155,190	230,242,245		407,409,412,413,416,441,446,447 469,471,472,492,493	
12	15/12	3	14,16,17					452	
13	966/1619	3	2,5,8,16	21,29	134	210,243		440,443,444,468,470,476,488,489 491	
15	1004/1528	2,3	2,4,13,14,19	21,23	130			415,446,447,448,449,462,464,465 466,467,475,477,478,479,480,483 490	
Present									
4	20/42	3	16	20,21,22,34		229,241		493	
7	9/14	1,3	8,11,15	24,35	199	244		473	518
9	132/246	2,3	11,18	25,28,33,37				406,410,411,474	
10	387/747	2,3	5,8,15	24,26,27,35	190	211,242,245		406,407,409-413,416,441,471 472,474,492,493	
11	18/21	2,3	11	24,28,33,35	197	206,209		414,451	
14	65/260	2,3	4,14,17,19			243		440,468,470,488,489,491	
16	2561/4419	2,3	5,8,16,17		130			415,446-449,462,464-467,475 477-480,483,490	
17	9675/15531	2,3	10,11,12,15,18	20,22,24-28 30-37	130,134	210,243		415,440,443,444,446-449,452 462 464-468,470,475-480,483,486,488 489,490,491	
18	899/1250	1,2,3	8,10-17,19	20-24,28,30 33-37	131,133,135 198	200,250		455,456,457,461,463,481,491	

Table 6. Abundance (% stocking) of western white pine showing the number of observations correctly classified, the total number of observations, and which spatial scale class was assigned to each terminal node. Refer to code definitions in Tables 2 and 3 for weathering (Wea.), geological features, and landtype classes.

Term. node	Obs. classified	Wea.	Geological features 2-19	Geological features 20-37	Landtypes by series 100	200	300	400	500
<25% stocked									
1	316/2348	2,3		24,30				411,415,446,462,463,464,466 467,470,476,477,479,480,491	
13	60/117	2,3	5,14,16	20,22,25,28,32,33,35,37		242,245		406,407,408,414,451,469	567, 573
15	58/449	3	8	22,28,32,33,35,37	190	243		440,443,444,471,488	
18	493/960	2,3	10,11,17	21,24,30,31,34,36	135,190	211,241-245		406-410,412,416,440,441,443,444 451,471,478,488, 489	
25-54% stocked									
3	139/809	2,3	5,11,17,18	20,28				447,448,449,465,468,474,475,483 493	
7	10/11	2,3	14	24,33,34,35	198	206			574
10	125/528	1,3	8,10,14,16,18	22,24,36	106,130,133 155,196,197	210		490	518, 561,562
11	5/12	2,3		24	131	200		492	
14	79/398	3	8	22,28,32,33,35,37	135	241,244		409,410,412 416,441,478,489	
55-74% stocked									
2	1134/4486	2,3	4,5,11,13,17,18	20,25,28	199			411,415,446,462,463,464,466,467 470,476,477,479,480,491	
4	144/423	2,3		24,25,30				447,448,449,465, 468, 474,475 483,493	
5	1444/4442	2,3	8,10,12,14,15,16,19	21,22,23,26,27,31-37	199			411,415,446,447,448,449,462-468 470,474,475,476,477,479,480,483 491,493	
6	62/147	2,3	8,15,16,18	20-22,24,28,33-35,37	134,191			413,452,472	
8	4/7	3	11	28,33	155,197	230			
17	67/249	3	16	20,25,26	190	241,243		409,410,412,416,440,441,443,444 471,478,488	
>74% stocked									
9	183/157	1,3	5,11,12,15,17,19	20,21,28,30-34,37	130,133,196	210		490	518,557,561
12	330/439	1,2,3	8,10,11,12,14,15,16 19	20,21,22,28,33,34	131	200,209,229 250		455,456,457,461,473,481,492	517,590
16	48/67	3	5,14,18,19	27	190	244		409, 410,412,440,441,444,471,478 488,489	

Table 7. Site productivity (site index at 50 years) of western white pine showing the number of observations correctly classified, the total number of observations, and which spatial scale class was assigned to each terminal node. Refer to code definitions in Tables 2 and 3 for weathering (Wea.), geological features, and landtype classes. Unknown site index are places that can support western white pine but site index was not recorded.

Term. node	Obs. classified	Wea.	Geological features		Landtypes by series				
			2-19	20-37	100	200	300	400	≥500
Unknown									
6	38/488	1,2,3	17,19	22,24,28				441,457,462,472,473,490	517
9	40/82	2,3	16	20,25,26,28,32		241,245		406,408,414,416,451	
12	672/1677	2,3	10,11,17	21,22,24,30,31 33,34,35,36,37	135, 190	211,241-245		406-410,412,414,415,416,440,443 444,451,469,471,477,478,488,489	573
Site index 12 m									
7	24/43	2,3	8,10,11,16	20,21,22,24,28,33	106,134,155,197	250		492	
Site index 15 m									
2	69/574	1,2,3	13,15,16	33, 34, 37				462,490	518,557 561,567
3	127/235	1,2,3	8,12,14,18	21,36				441,446,456,462,472, 473,490	517,518 561 562,567,574 590
5	217/267	1,2		20				457,461,472,473	517
Site index 18 m									
8	8811/ 11944	2, 3	4,5,8,10-19	20,21,22,23,24,26 27,28,30-37	122,130,131,133 191,196,199	200,206,209,210 229,230,246,270	360 363	411,413,446-449, 452,460 463-468 470,474-477,479,480 481,483,486,491,493	677,678
10	398/567	3	5,8,14-16,18,19	20,25,26,27,28,32	135,190	242-244		407,410,415,440,441,443,471,478488,489	573
Site index 21 m									
1	17/72	1,2,3	15,16	33,34	198			441,457,472,473	
4	18/247	1,2,3		20				455,456,462,490	
11	5/32	3	5,16,18	20,27,28				409,412,444	

Figure Captions

Figure 1. Historical (1930s) and current (1996) western white pine presence within the northern Rocky Mountain region (Hann et al. 1997). Study area is the 350,000-ha Coeur d'Alene River Basin.

Figure 2. Illustrations of each spatial scale by broad categories. The spatial scales include (A) weathering, (B) geological feature, (C) landtypes, and (D) western white pine abundance (circa 1934). Refer to Tables 2 and 3 for geological feature, landtype labels, and associated definition.

Figure 3. Eighteen-terminal-node classification tree used for predicting historical presence or absence of western white pine. Terminal nodes (shaded) show number of observations correctly classified, total number of observations, and misclasification costs. Internodes show spatial scale used in the split and whether the split was based on the presence or absence of western white pine.

Figure 4. Eighteen-terminal-node classification tree used for predicting historical western white pine abundance (% stocking), using only observations containing western white pine. Terminal nodes (shaded) show number of observations correctly classified, total number of observations, and misclasification costs. Internodes show spatial scale used in the split and whether the split was based on the stocking level of western white pine.

Figure 5. Twelve-terminal-node classification tree used for predicting western white pine site productivity (site index 50-year base), using only observations containing western white pine. Terminal nodes (shaded) show number of observations correctly classified, total number of observations, and misclasification costs. Internodes show spatial scale used in the split and whether the split was based on site index level of western white pine.

Figure 6. Historical white pine occurrence (presence and absence) displayed on the Coeur d' Alene River Basin for three individual spatial scales (A, B and C) and three combined spatial scales (D).

Figure 7. Historical western white pine abundance (% stocking) displayed across the Coeur d' Alene River Basin for three individual spatial scales (A, B, and C) and three combined spatial scales (D).

Figure 8. Western white pine site productivity (site index 50-year base) displayed across the Coeur d'Alene River Basin for three individual scales (A, B, and C) and three combined spatial scales (D). Unknown site index are areas where site index was not recorded but could support western white pine.

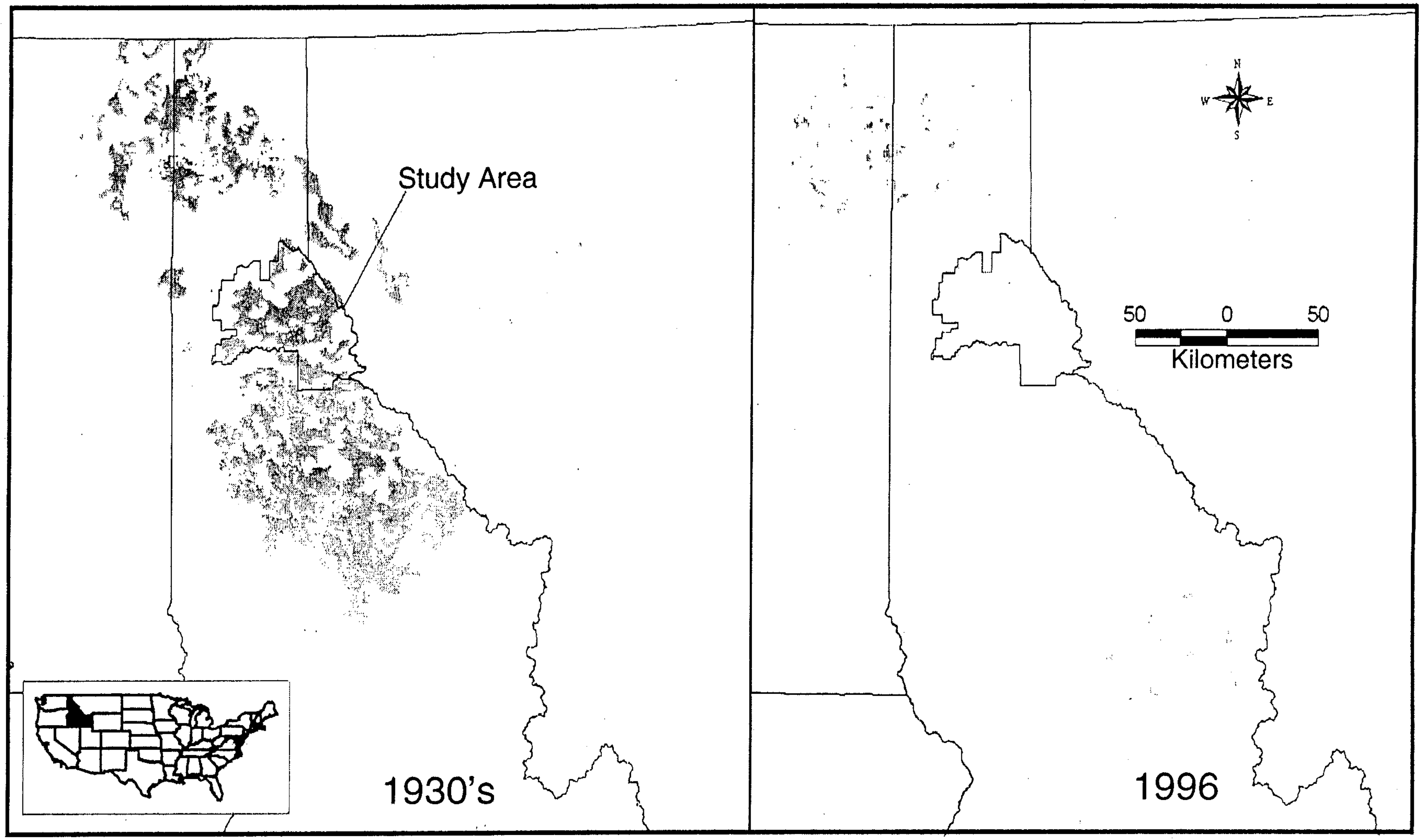

Figure 1

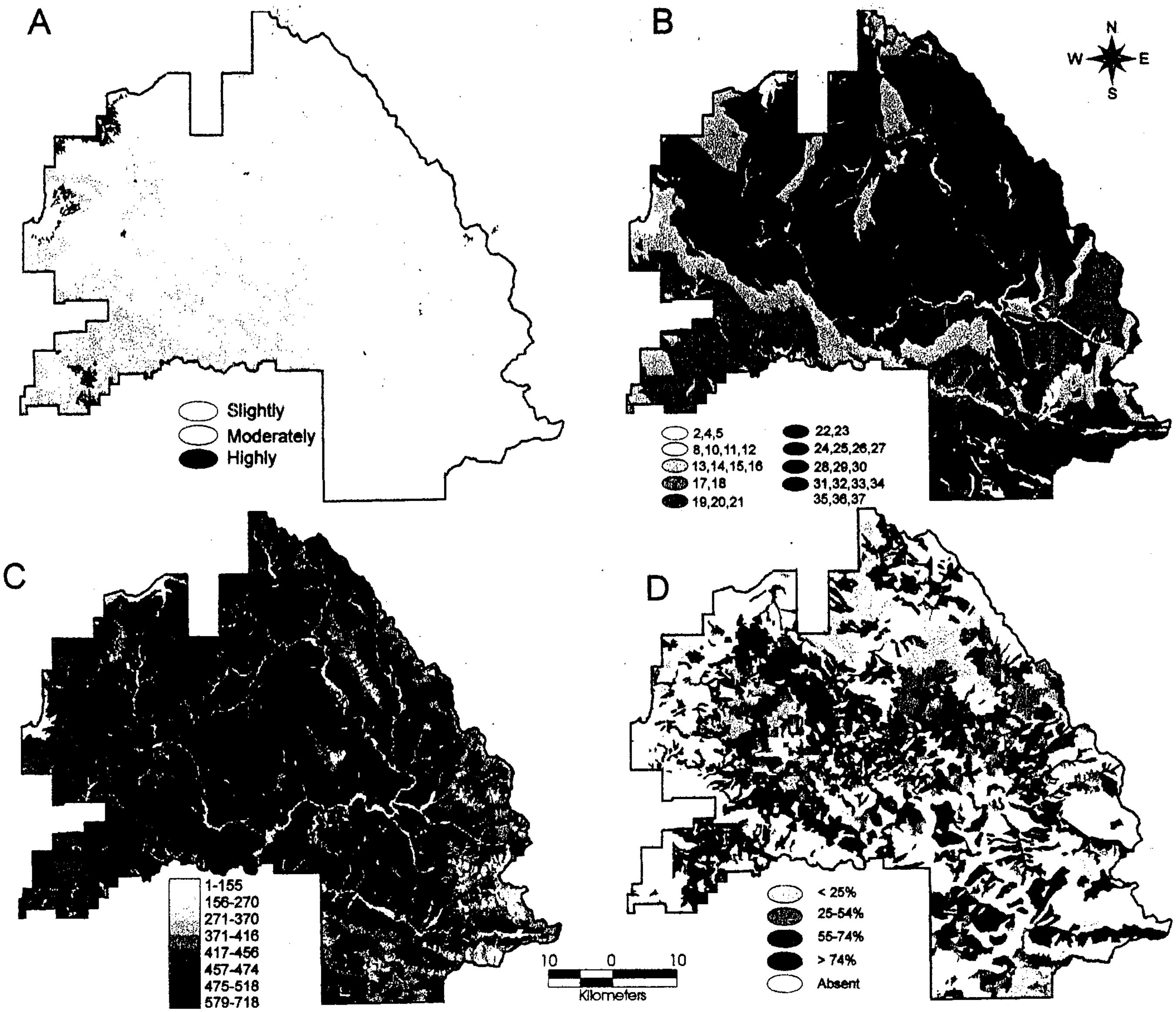
A
Slightly
Moderately
Highly
B
N
W
E
S
2,4,5
8,10,11,12
13,14,15,16
17,18
19,20,21
22,23
24,25,26,27
28,29,30
31,32,33,34
35,36,37
C
1-155
156-270
271-370
371-416
417-456
457-474
475-518
579-718
D
< 25%
25-54%
55-74%
> 74%
Absent
10
0
10
Kilometers

Figure 2

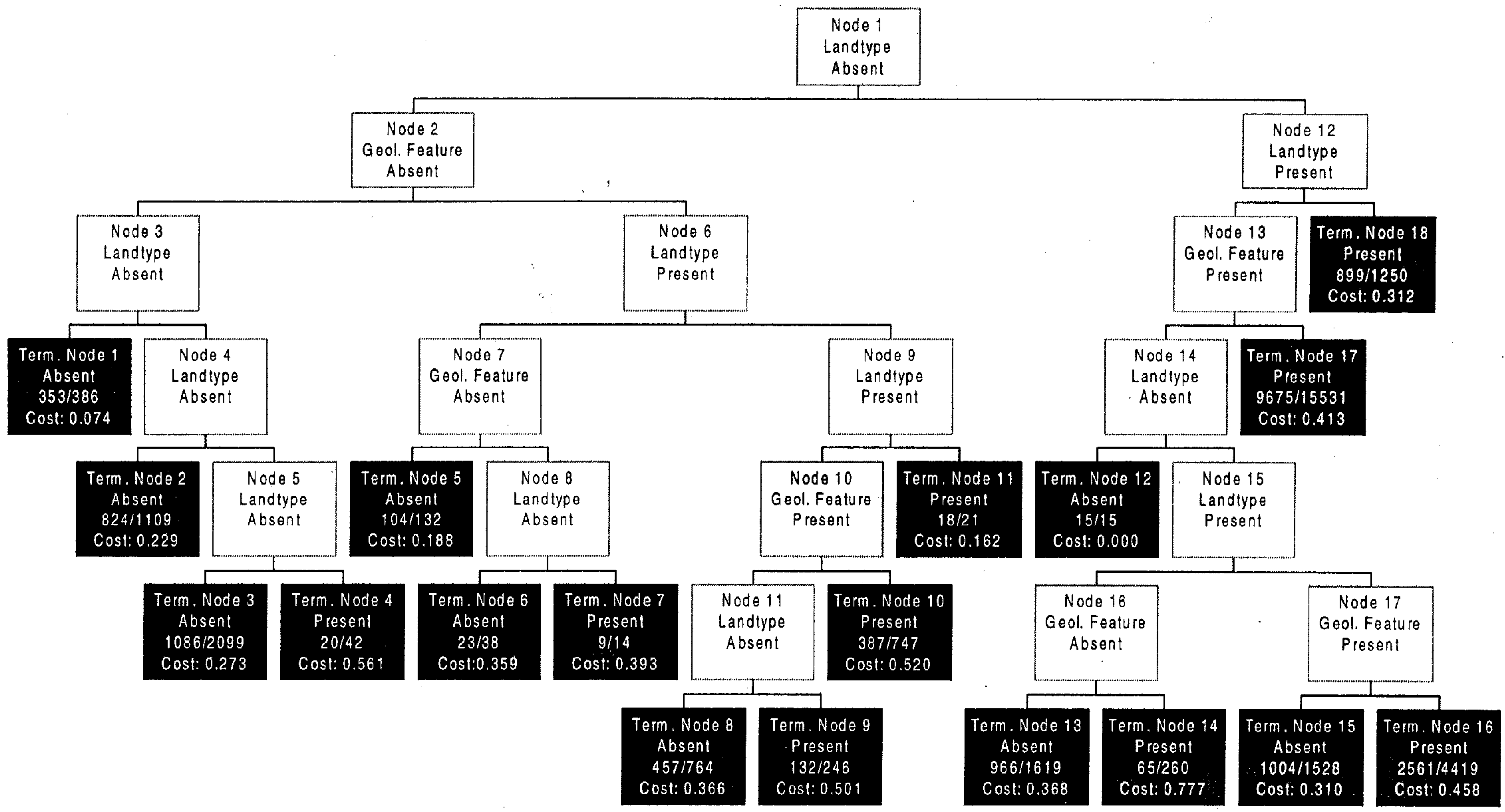
Node 1
Landtype
Absent
Node 2
Geol. Feature
Absent
Node 12
Landtype
Present
Node 3
Landtype
Absent
Node 6
Landtype
Present
Node 13
Geol. Feature
Present
Term. Node 18
Present
899/1250
Cost: 0.312
Term. Node 1
Absent
353/386
Cost: 0.074
Node 4
Landtype
Absent
Node 7
Geol. Feature
Absent
Node 9
Landtype
Present
Node 14
Landtype
Absent
Term. Node 17
Present
9675/15531
Cost: 0.413
Term. Node 2
Absent
824/1109
Cost: 0.229
Node 5
Landtype
Absent
Term. Node 5
Absent
104/132
Cost: 0.188
Node 8
Landtype
Absent
Node 10
Geol. Feature
Present
Term. Node 11
Present
18/21
Cost: 0.162
Term. Node 12
Absent
15/15
Cost: 0.000
Node 15
Landtype
Present
Term. Node 3
Absent
1086/2099
Cost: 0.273
Term. Node 4
Present
20/42
Cost: 0.561
Term. Node 6
Absent
23/38
Cost:0.359
Term. Node 7
Present
9/14
Cost: 0.393
Node 11
Landtype
Absent
Term. Node 10
Present
387/747
Cost: 0.520
Node 16
Geol. Feature
Absent
Node 17
Geol. Feature
Present
Term. Node 8
Absent
457/764
Cost: 0.366
Term. Node 9
Present
132/246
Cost: 0.501
Term. Node 13
Absent
966/1619
Cost: 0.368
Term. Node 14
Present
65/260
Cost: 0.777
Term. Node 15
Absent
1004/1528
Cost: 0.310
Term. Node 16
Present
2561/4419
Cost: 0.458

Figure 3

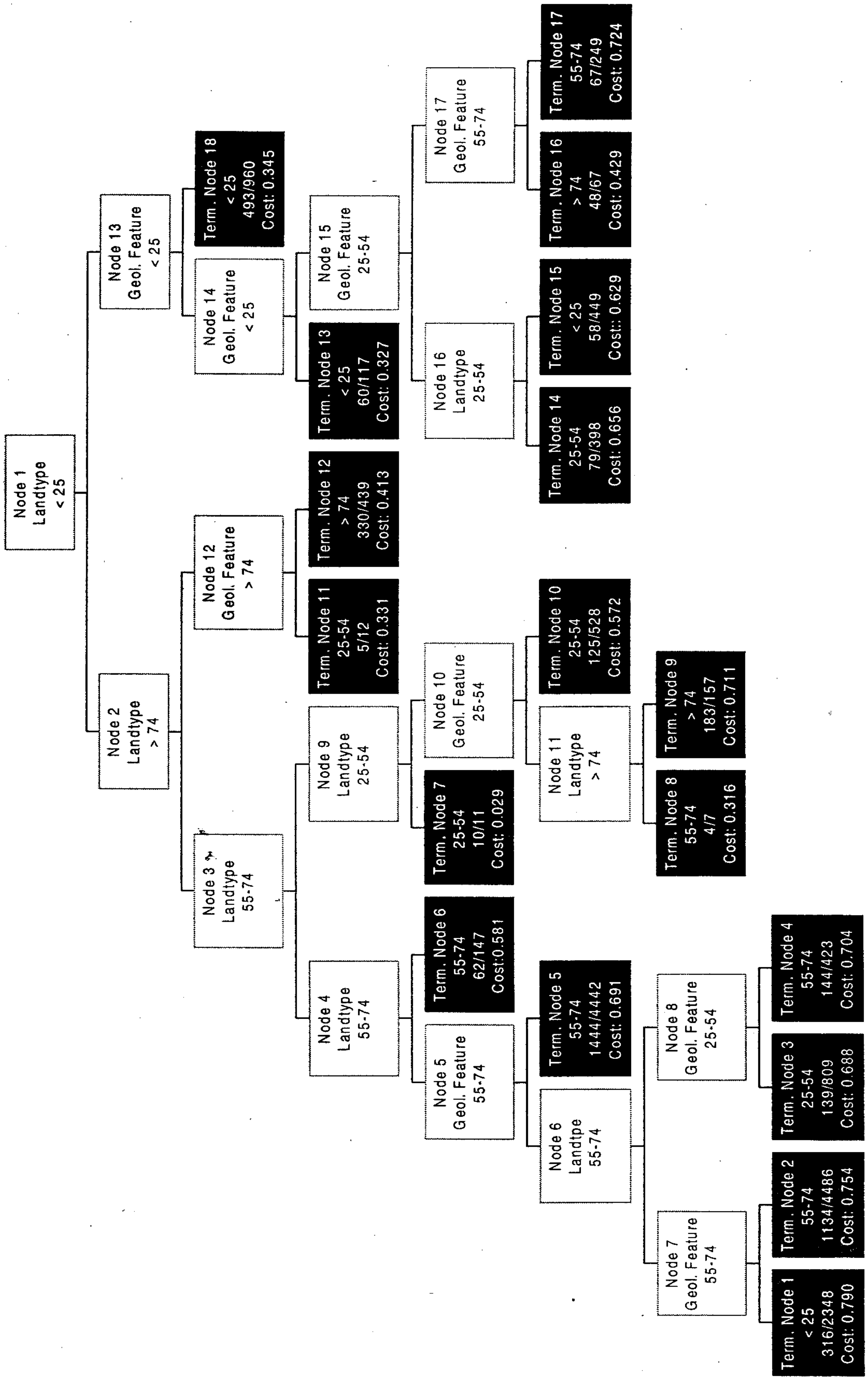
Node 1
Landtype
< 25
Node 2
Landtype
> 74
Node 13
Geol. Feature
< 25
Node 3
Landtype
55-74
Node 12
Geol. Feature
> 74
Node 14
Geol. Feature
< 25
Term. Node 18
< 25
493/960
Cost: 0.345
Node 4
Landtype
55-74
Node 9
Landtype
25-54
Term. Node 11
25-54
5/12
Cost: 0.331
Term. Node 12
> 74
330/439
Cost: 0.413
Term. Node 13
< 25
60/117
Cost: 0.327
Node 15
Geol. Feature
25-54
Node 5
Geol. Feature
55-74
Term. Node 6
55-74
62/147
Cost:0.581
Term. Node 7
25-54
10/11
Cost: 0.029
Node 10
Geol. Feature
25-54
Node 16
Landtype
25-54
Node 17
Geol. Feature
55-74
Node 6
Landtpe
55-74
Term. Node 5
55-74
1444/4442
Cost: 0.691
Node 11
Landtype
> 74
Term. Node 10
25-54
125/528
Cost: 0.572
Term. Node 14
25-54
79/398
Cost: 0.656
Term. Node 15
< 25
58/449
Cost: 0.629
Term. Node 16
> 74
48/67
Cost: 0.429
Term. Node 17
55-74
67/249
Cost: 0.724
Node 7
Geol. Feature
55-74
Node 8
Geol. Feature
25-54
Term. Node 8
55-74
4/7
Cost: 0.316
Term. Node 9
> 74
183/157
Cost: 0.711
Term. Node 1
< 25
316/2348
Cost: 0.790
Term. Node 2
55-74
1134/4486
Cost: 0.754
Term. Node 3
25-54
139/809
Cost: 0.688
Term. Node 4
55-74
144/423
Cost: 0.704

Figure 4

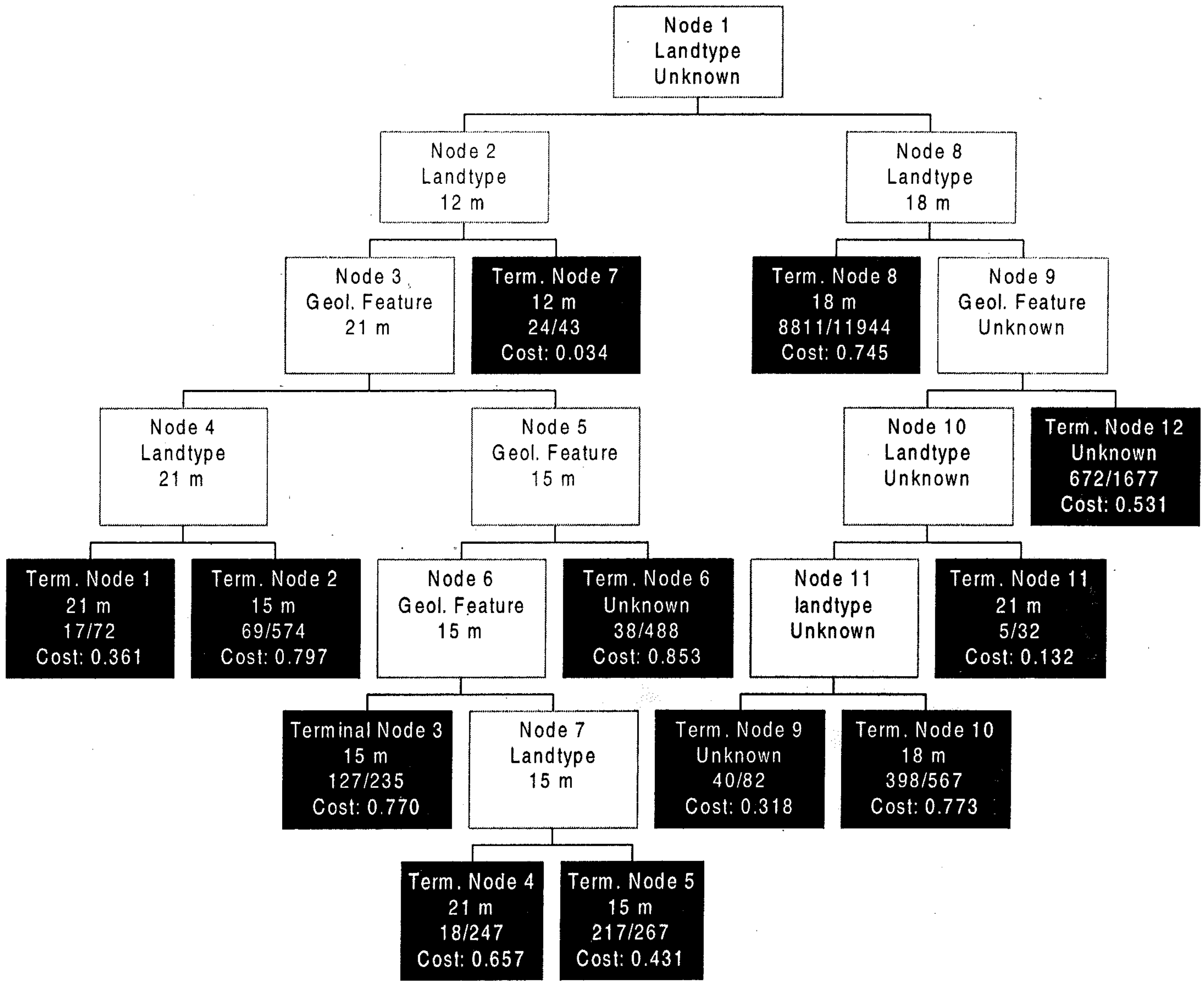
Node 1
Landtype
Unknown
Node 2
Landtype
12 m
Node 8
Landtype
18 m
Node 3
Geol. Feature
21 m
Term. Node 7
12 m
24/43
Cost: 0.034
Term. Node 8
18 m
8811/11944
Cost: 0.745
Node 9
Geol. Feature
Unknown
Node 4
Landtype
21 m
Node 5
Geol. Feature
15 m
Node 10
Landtype
Unknown
Term. Node 12
Unknown
672/1677
Cost: 0.531
Term. Node 1
21 m
17/72
Cost: 0.361
Term. Node 2
15 m
69/574
Cost: 0.797
Node 6
Geol. Feature
15 m
Term. Node 6
Unknown
38/488
Cost: 0.853
Node 11
landtype
Unknown
Term. Node 11
21 m
5/32
Cost: 0.132
Terminal Node 3
15 m
127/235
Cost: 0.770
Node 7
Landtype
15 m
Term. Node 9
Unknown
40/82
Cost: 0.318
Term. Node 10
18 m
398/567
Cost: 0.773
Term. Node 4
21 m
18/247
Cost: 0.657
Term. Node 5
15 m
217/267
Cost: 0.431

Figure 5

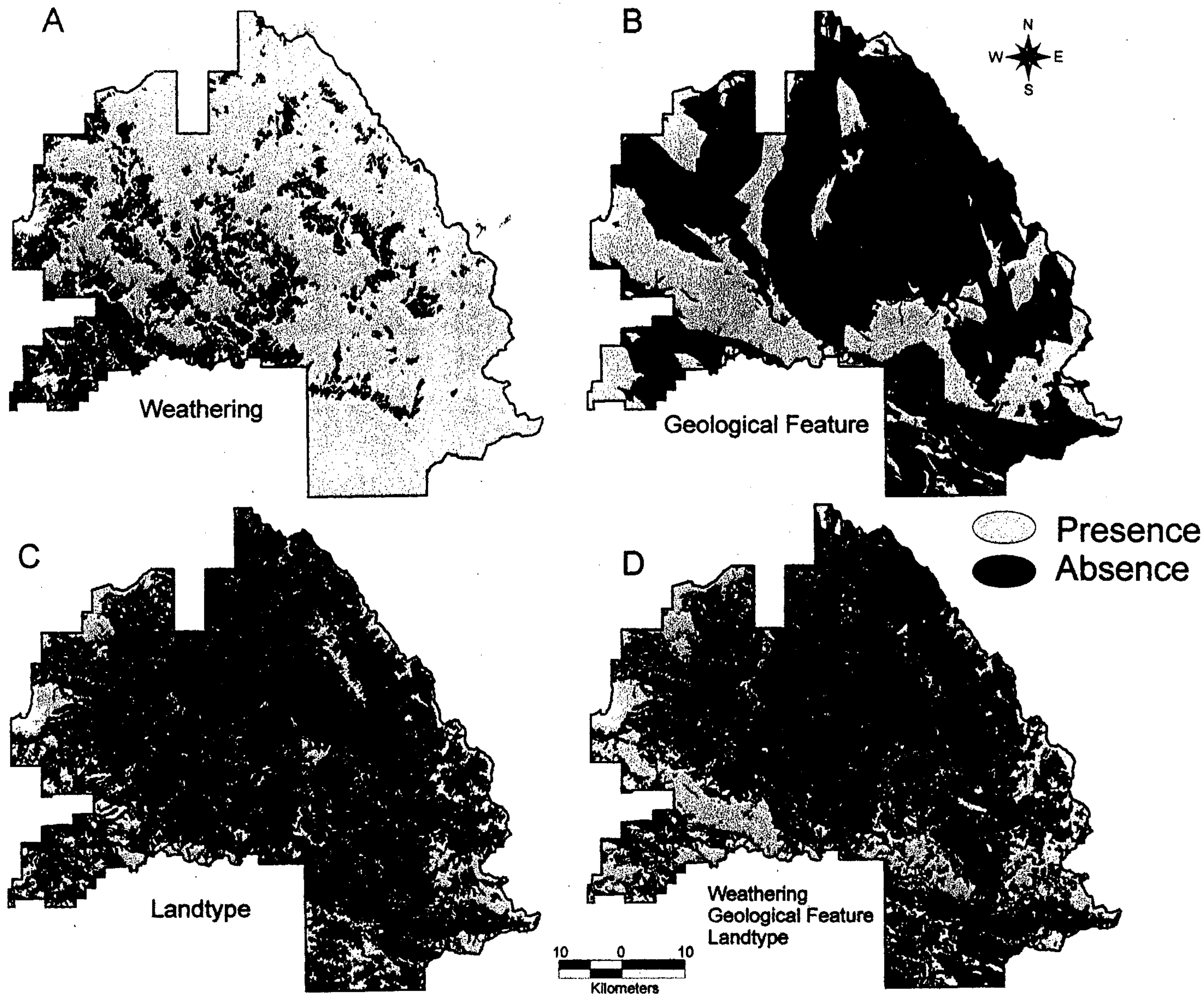
A
Weathering
B
Geological Feature
N
W
E
S
C
Landtype
D
Weathering
Geological Feature
Landtype
Presence
Absence
10
0
10
Kilometers

Figure 6

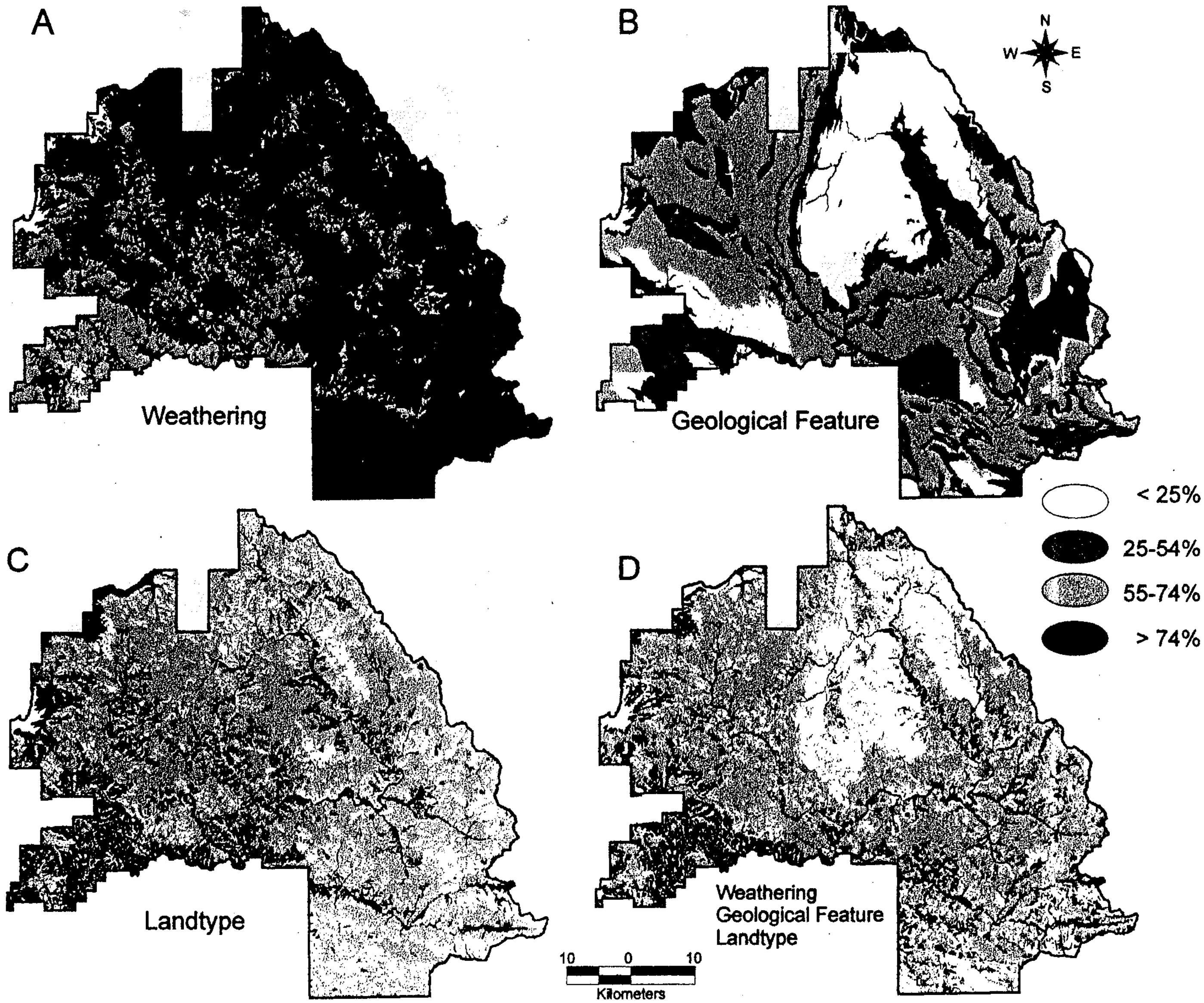
A
Weathering
B
Geological Feature
N
W
E
S
< 25%
25-54%
55-74%
> 74%
C
Landtype
D
Weathering
Geological Feature
Landtype
10
0
10
Kilometers

Figure 7

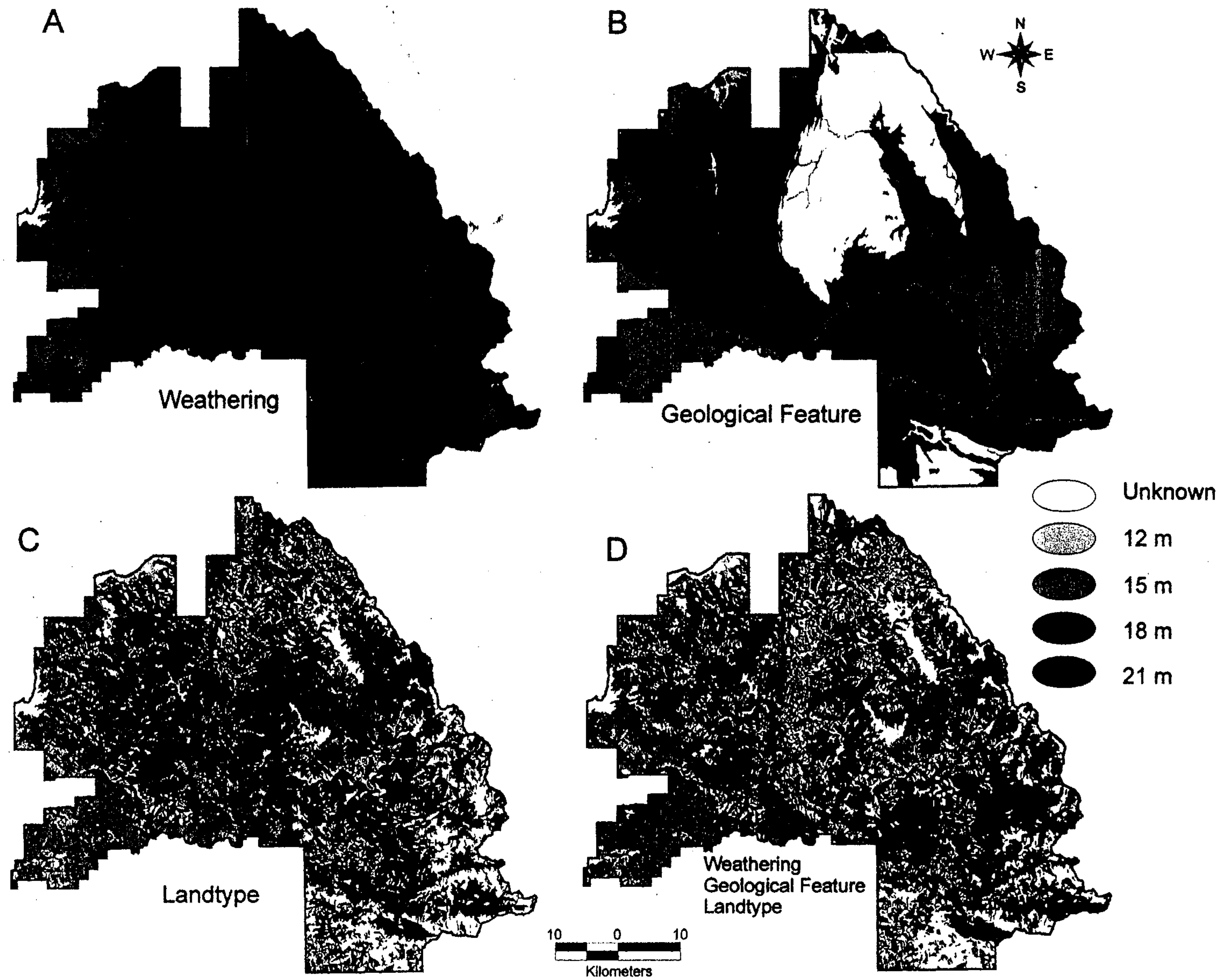
A
Weathering
B
N
W
E
S
Geological Feature
C
Landtype
D
Weathering
Geological Feature
Landtype
Unknown
12 m
15 m
18 m
21 m
10
0
10
Kilometers

Figure 8

Appendix B - Canopy opening and western white pine

Relating Western White Pine Growth to Forest Opening Characteristics

by

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Forest Ecology and Management

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Abstract

Forest canopy openings ranging from 2 m^2 to 15 ha in size are created by ice storms, fires, and other disturbances. Trees occurring in the northern Rocky Mountains of North America evolved with different levels of tolerance for growing in these openings. Because of timber harvesting, fire exclusion, and disease, the abundance of western white pine (*Pinus monticola*) has declined in the northern Rocky Mountains by over 90% from what occurred in the early 1900s. Because of laws and regulations, clearcutting – once favored as the method for managing western white pines -- is now used infrequently. This study was conducted to develop an understanding of how western white pine regenerates and grows in a variety of opening sizes and to provide information useful for managing the species in openings smaller than clearcuts.

We sampled 620 young (5 to 50 yr.) western white pines growing in a variety of canopy opening sizes stratified by aspect and elevation, and dispersed across three watersheds in northern Idaho. Using factor analysis and log-linear regression, age adjusted basal diameter ($R^2 = 0.56$), height ($R^2 = 0.53$), and a factor score ($R^2 = 0.45$) were positively related to canopy openings (measured by % visible sky), ranging from 14 to over 100% visible sky, as quantified from a vertical fisheye photograph taken at the midcrown of each tree. Western white pines occupy sites with >25% visible sky, have a competitive advantage with >55% visible sky and are free to grow with >95% visible sky. Optimum western white pine growth occurs with openings >5 ha. Traditional density indices (basal area, trees per hectare) related poorly to % visible sky.

Keywords: thresholds, tolerance, gaps, canopy, fisheye photographs

1. Introduction

1.1. Background

Forest canopy openings[1] are areas free of trees where new or residual understory plant communities develop (Gysel, 1951; Bray, 1956; Minckler and Woerhelde, 1965; Runkle, 1992). Opening attributes (opening size, orientation, location, age, overstory species) influence light, temperature, moisture, nutrient cycling, root biomass, and other biophysical factors that shape the operational environment (interaction of biophysical factors with the plant) that influences the composition, regeneration, and growth of ground-level vegetation, including small trees (Spomer 1973; Grubb, 1977; Canham, 1989; Norman and Campbell, 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). Barik et al., (1992) showed more light (photon flux) reaches the forest floor in openings compared to areas under a closed canopy in subtropical forests of India. Relative humidity, soil moisture, and litter depth decreased as opening size increased. Similarly in subtropical forests within the People's Republic of China, as opening size increased, soil moisture decreased, which was correlated with decreases in nutrient release, decomposition, and microbial activity (Zhang and Liang, 1995). Higher temperatures and greater temperature fluctuations occur at ground level in forest openings compared to similar sites under closed canopies (Haig, 1936).

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[1]For this paper we define "opening" as a gap in the canopy between 2 m^2 and 15 ha in size. This definition encompasses the size range used in gap ecology (Runkle, 1992).

In the northern Rocky Mountains of North America, trees evolved with different autecological (individual plant species and their relationship to their environment) characteristics allowing them to compete and successfully grow in different size openings (Haig, 1936; Haig et al., 1941; Minore, 1979). In openings, higher temperatures cause soil surface layers to dry faster and deeper than corresponding layers under a canopy. Western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) root penetration is too shallow to obtain moisture in the lower soil layers as they dry. Therefore these species are less likely to survive in large openings. In contrast, western larch (*Larix occidentalis*) and ponderosa pine (*Pinus ponderosa*) roots penetrate soil layers quickly enough to obtain moisture from the lower soil layers as they dry, allowing them to regenerate and survive in large openings (Haig et al., 1941). This subtle difference in growth habitats gives western larch and ponderosa pine a greater tolerance[2] than western hemlock and western redcedar for growing in dry conditions.

Western larch, ponderosa pine, and lodgepole pine (*Pinus contorta*) have low tolerance for growing under closed canopies (Haig et al., 1941). These species grow rapidly, maximizing use of available nutrients, light, and water (Haig et al., 1941). Western hemlock and western redcedar tolerate closed canopy conditions, enabling them to germinate and survive indefinitely in dense shade. Western white pine (*Pinus monticola*) has moderate tolerance, allowing it to grow within a wide range of microenvironments. However the species cannot readily compete with western hemlock and western redcedar in very closed

[2]"Tolerance" is the capacity of an organism to tolerate unfavorable environmental conditions.

growing conditions (Haig et al., 1941). Similarly, it cannot compete readily with western larch under very open conditions (Haig et al., 1941).

Disturbance type (ice storms, volcanic eruptions, disease, fire), extent (fine or coarse-scale), frequency (time between disturbances), and severity (amount of forest vegetation and forest floor and soil removed) create a variety of canopy openings that influence subsequent species composition (White and Pickett, 1985; Stewart, 1986; Lorimer, 1989; Spies and Franklin, 1989; Oliver and Larson, 1990; Moeur, 1997). Openings created by single-tree mortality favor the regeneration and growth of late-seral or tolerant species (White and Pickett, 1985; Moeur, 1997). In the northern Rocky Mountains, even western hemlock, which is very tolerant, requires fine-scale disturbances (individual tree mortality) to regenerate and grow (Spies and Franklin, 1989; Moeur, 1997). In contrast, depending on the severity and extent, large openings (>2 ha) created by stand-replacing events, such as fires, which favor early-seral and intolerant species. For example, in some places within the northern Rocky Mountains, shrub or lodgepole pine communities developed after repeated wildfires while single fires perpetuated western white pine and western larch-dominated stands (Larsen, 1929; Shiplett and Neuenschwander, 1994). Medium size (0.5 to 2 ha) openings were created by fires, wind and ice storms, insect attacks, and root diseases, provide a wide range of microenvironments favoring many plant species. A variety of species such as western white pine, Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), western redcedar, and western hemlock will regenerate in such openings (Haig et al., 1941; Wellner, 1946).

1.2. Problem

Scientists have suggested the abundance of western white pine, a major early-seral species in the moist forests of the northern Rocky Mountains, should be increased because it plays many ecological roles (e.g., genetic plasticity, grows over a wide range of environments, unique morphological characteristics, resistant to many endemic diseases and insects, and is a long-lived seral) (Leiberg, 1897; Haig et al., 1941; Daubenmire and Daubenmire, 1968; Minore, 1979; Larsen et al., 1980; Graham, 1990; Cooper et al., 1991; Harvey, 1994; Rehfeldt, 1994; Harvey et al., 1999; Neuenschwander et al., 1999). An exotic disease (*Cronartium ribicola*), timber harvesting, and fire exclusion contributed to a sharp decline in western white pine abundance. Since the early part of the 20th century, when this species dominated many northern Idaho forests (Fig. 1). The species now dominates on less than 10% of the area it formerly occupied (Hann et al., 1997; Idaho Panhandle National Forests, 1998). There is considerable interest in not only increasing amounts of western white pine locally but in managing and conserving western white pine over landscapes (Hann et al., 1997; Harvey et al., 1999; Neuenschwander et al., 1999).

There is no research determining how western white pine responds to different levels of canopy openings. Western white pine evolved to occupy environments created by many disturbances. This evolution allows it to grow within a wide range of landscape (elevation, aspect, slope) and microsite environments (small to large openings). However, western white pine was commonly managed using clearcuts, because they were easy to apply and often the most applicable (Wellner, 1947, Graham et al., 1983). Because of their frequent use, there is a tendency to view western white pine as requiring full light to survive and develop. Haig et al., (1941) noted that western white pine up to 30 years old performed better under some canopy protection.

Silviculturally, many opening characteristics can be created favoring a particular species complex. In the northern Rocky Mountains, the clearcut method has been primarily used, which can mimic opening characteristics created by stand-replacing wildfires. However, in application, clearcuts usually differ from wildfires in geographic extent (smaller than historical stand replacing fire), shape, location, and residual structure (snags and soils). In contrast, few silvicultural methods (shelterwood, seedtree, individual or group selection) were applied within the region mimicking other fire scale disturbances (small stand-replacing and surface wildfires, insect attacks, root diseases, wind and ice storms) that were historically very prevalent.

Forest management in the northern Rocky Mountains has changed. Large clearcuts, among other things, were unsightly, changed wildlife habitat, and increased water yield, and associated roads increased soil erosion and sediment (Bliss, 2000). Changes caused by clearcuts often violated laws and regulations aimed at protecting wildlife and clean water. Therefore, to regenerate and sustain forests, silvicultural methods need to mimic disturbances other than large stand-replacing wildfires. In many cases, these methods need to leave high forest cover that tends to favor late-seral species. We hypothesize that western white pine is well suited to regenerate and develop in these and other forest conditions.

Although there is a plethora of information on gaps, canopy structure, and vegetation response in gaps, most studies have been in tropical or deciduous forest settings, with few studies occurring within coniferous forests (Spies and Franklin, 1989; Spies et al., 1990; Coates and Burton, 1997, 1999; Moeur, 1997; Coates, 2000). Most research concentrated on characterizing gaps and vegetation response but rarely linked this knowledge to address management objectives (Coates, 2000; d'Oliveira, 2000; Myers et al., 2000). Linking management actions and gap characteristics can be accomplished by identifying thresholds of vegetation response as a function of canopy opening. In addition, these thresholds can further our understanding of vegetation dynamics by linking biophysical factors to gap characteristics. Therefore, our study objectives were to: (1) determine relations between opening characteristics (opening size, edge, orientation, location, overstory species composition) and vegetation response (western white pine growth), (2) determine if the relation between western white pine growth and canopy opening attributes changes because of physical setting (aspect, topographic position), (3) identify three canopy opening thresholds (occupancy, competitive advantage, free to grow) for western white pine, and (4) relate canopy opening attributes to stand descriptors (basal area, stand density index, trees per acres, size of opening) that can be used to design silvicultural methods.

2. Methods

2.1. Study area

Three watersheds with diverse environments (Deception is 1500 ha, Jordan is 7 500 ha, and Beaver is 20 000 ha) historically supporting western white pine were selected within the Coeur d'Alene River Basin (Fig. 1). The watersheds were dominated (90%) by three potential vegetation types, -- grand fir, western hemlock, and western redcedar, -- that support western white pine (Cooper et al., 1991; Idaho Panhandle National Forest, 1998). Young western white pine were growing in these watersheds over a wide range of forest openings, aspects, and elevations providing substantial variation useful for understanding western white pine dynamics within canopy openings.

2.2. Sampling design

Data from at least 192 sample plots covering a variety of opening attributes were collected within each of three watersheds (Fig. 1). A sampling matrix representing eight broad aspect classes (northeast, southeast, southwest, northwest) and elevation classes (low, high) were used to ensure plot location occurred across different topographic settings (Table 1). Twenty-four plots were located within each aspect and elevation classification. These plots were distributed among three canopy openings (under canopy, small, large) ranging from 0.001 to 15 ha in size. Within each opening classification, four plots were located near the edge and four were located near the center.

2.3. Data collection

Within each combined watershed, aspect, and elevation class, locations representing the opening sizes were located, using a random number generator, until the sampling matrix was filled (Table 1). Within each elevation, aspect, and opening class, two western white pine trees were randomly selected, one near the center and one near the edge. All data were placed within the context of the selected tree that was the experimental unit. After the 576 cells of the sampling matrix were filled, additional plots were added to ensure sampling of all possible settings where western white pine could potentially grow. These areas included closed canopy conditions, steep south slopes, and other places tending to disfavor western white pine occupancy. If multiple western white pines occurred in these conditions, the site was sampled and added to the study. A total of 620 western white pines (5 to 50 yr.) growing in a variety of canopy openings on a variety of topographic settings were sampled.

2.4. Dependent variables

The growth characteristics of the randomly selected western white pines were the dependent variables. Selected trees ranged from 20 to 700 cm in height, were well established (5 yr or older), and free of obvious damage (no blister rust stem cankers, no obvious branch cankers, no broken tops, no obvious bark or stem damage). Although trees with obvious blister rust were not sampled, some selected western white pine trees could be infected with blister rust. However, there is no evidence that blister rust impacts tree growth until the tree stem is encircled by a canker (Bingham et al., 1973; Hoff and Steinhoff, 1980; Hoff, 1984). Moreover, most seedlings (62%) regenerating under tree canopies die before 3 years of age. Western white pines surviving beyond 3 years 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, 5-year height growth (height increment for the last 5 years), age (total age 2.5 cm above root collar), and stem diameter 2.5 cm above root collar. In addition, crown length and crown width (length of four low branches with green needles taken in the four cardinal directions) were recorded. From these data, mean annual height increment (cm), mean annual diameter increment (cm), crown ratio (%), crown shape (ratio of crown length over crown width), and crown diameter (cm) were calculated.

2.5. Independent variables

Independent variables were separated into four classes: understory tree attributes, opening attributes, surrounding overstory tree attributes, and landscape attributes. A circular plot (60-cm radius) was used to quantify and characterize trees surrounding the selected western white pine. Because these plots can contain hundreds of trees, tree 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. The following measurements were obtained on selected trees: total height from root collar to base of terminal bud, age (total age 2.5 cm above root collar), and stem diameter 2.5 cm above the root collar. From these measurements, crown ratio, crown shape, and mean annual height and diameter increment were calculated.

The second class of data described opening attributes using a vertical fisheye photograph (Lawton and Putz, 1988; Runkle, 1992; Coates and Burton, 1997; HemiView, 1997). The camera lens was level with the camera top facing magnetic north and centered over the stump at a height equal to mid-crown 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 180^0 view of the overstory canopy.

The vertical fisheye photographs were developed and placed on compact disks. Using these photographs and digital analysis software (HemiView, 1997), we quantified visible sky (proportion of visible sky), total radiation (mol m^{-2} $year^{-1}$), diffuse radiation, and direct radiation above and below the canopy. Sunfleck duration (hours day^{-1}) and number of sunflecks were quantified for the solstice on June 21, 1999. 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; HemiView, 1997).

Other opening attributes complementing the photographic data were: distance to opening edge, size, location, elevation, aspect, slope, orientation, topographic position, slope configuration, canopy height, dominant species in canopy, and seed wall density. Distance to opening edge was the distance from the selected tree to bole of a tree greater than15 cm diameter breast height (1.5 m) in the four cardinal directions (north, west, south, east) (Runkle, 1992). Opening area was calculated using the following formula: area = pi*length*width/4 (Runkle, 1992). Location (longitude and latitude) was estimated using a 1:24 000 topographic map. Opening orientation was the azimuth of the longest axis in relation to the selected western white pine. Topographic position defined the position of the selected western white pine in its relation to stream confluence, ridge top, lower third slope, middle third slope, upper third slope, bench, lower headwall, middle headwall, upper headwall, or valley bottom adjacent to stream channel (Camp et al., 1997).

The third class of data described the overstory trees. In some cases, opening attributes accounted for trees surrounding a relatively large opening (20 m^2). However, when an overstory existed it was described using a probability proportional to size plot. A 8 m^2 ha^{-1} angle gauge defined the plot, and trees greater than 15 cm diameter breast height were tallied by species and 5 cm diameter classes (e.g., 10 to 14.9 cm).

The amount of landscape radiation reaching each plot was estimated. These data were generated using a digital elevation model and TopoView Software (Fu and Rich, 1999).

This software estimated total hours of sunlight (hours $year^{-1}$) and total solar radiation (watts m^{-2}). These values were adjusted for shading by mountains, sun path specific to the time of year, longitude, latitude, aspect, and elevation.

3. Analysis

3.1. Exploratory analysis

The analysis was designed to develop relations between western white pine growth descriptors and biophysical factors. Therefore, results had to be both biologically and statistically relevant. To ensure biological relevancy, we placed the variables into six classes: (1) variables characterizing western white pine growth: height, basal diameter, mean annual height and diameter increment, last 5-year height increment, and tree age, (2) variables characterizing tree form: crown shape, crown ratio, needle retention, and crown diameter, (3) variables describing the competing environment of the selected western white pine: number of additional western white pine on the microsite plot and their mean annual height increment, number of species other than grand fir and western hemlock species on the microsite plot, number of western hemlock on the microsite plot and their mean annual height increment, and number of grand fir on the microsite plot and their mean annual height increment, (4) variables characterizing the environment surrounding the western white pine: visible sky (%), yearly below-canopy radiation, number of sunflecks and total sunfleck duration for June 21, 1999, and opening orientation, (5) variables characterizing the environment influenced by topography: proportion visible sky from landscape position, yearly landscape radiation (direct, diffuse, total), and aspect, and (6) variables describing stand characteristics: basal area, trees per hectare, species composition, stand density index, and size of opening.

We conducted exploratory analysis of individual and combinations of independent (visible sky) and dependent variables (height, diameter, crown ratio) 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 scatter plots, correlation coefficients, principal component analysis, and factor analysis.

Results from these procedures provided an indication of transformations appropriate 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). A sine and cosine transformation of orientation and aspect suggested by Stage (1976) was used. However, we determined that classifying orientation into four classes (0 to 45, 45 to 90, 90 to 135, and 135 to 180 degrees) and aspect into eight classes (0 to 45, 46 to 90, 91 to 135, 136 to 180, 181 to 225, 226 to 270, 271 to 315, and 316 to 360 degrees) provided both significant and interpretable results.

3.2. Statistical analysis

Three new variables were created as a result of the factor analysis: (1) a factor score (linear combination of variables that were related to each other using an adhoc method outlined by Johnson (1998)[3], which combined dependent growth variables (basal diameter, height, 5-year height growth), (2) a factor score, which combined independent microsite variables (visible sky, sunfleck duration, and number of sunflecks), and (3) a factor score that combined independent topographic variables (proportion of visible landscape sky and hours of radiation reaching a landscape position).

Using scatter plots, relations between the dependent western white pine variables (e.g., height, crown ratio) and the independent microsite variables (e.g., proportion of visible sky, radiation below canopy) were evaluated. According to the scatter plots, all dependent variables, were related to the microsite independent variables. Many of the scatter plots showed a non-linear relationship between dependent and independent variables. Therefore, in the statistical analysis, log-linear regression (ln(y) = x) was used rather than linear regression.

A step-wise log-linear regression procedure was used to relate the dependent variables to the independent microsite variables. The first step was to determine which dependent variable had the strongest relationship to the independent microsite variables. This was accomplished by relating visible sky to each dependent western white pine variable. The results from the partial sum of squares F-tests, coefficient of determination (R^2), adjusted

[3]The adhoc method used in this analysis is to create a variable by taking the average of the standardized variables that were identified as being correlated in the factor analysis (Johnson, 1998).

coefficient of determination (adj. R^2), and behavior of residual errors were used to evaluate the goodness-of-fit of the regressions (Table 2). The dependent variables, height, basal diameter, and a factor score combing white pine growth variables, (factor score), were selected for use in later analysis along with age as a covariate because they had the highest adjusted R^2 (0.53 for height, 0.56 for diameter, and 0.45 for the factor score) (Table 2). Crown diameter also had a high adjusted R^2 (0.49). However, because it was strongly correlated with basal diameter, we decided to use basal diameter rather than crown diameter, keeping in mind as basal diameter increased so did crown diameter. Mean annual height and diameter increment and 5-year height increment had lower adjusted R^2 and were not selected (Table 2).

The second step was to evaluate the other microsite variables to determine which variables best explained the variation in basal diameter, height, and the factor score. The relation between selected western white pine growth variables and other microsite variables along with age as a covariate were investigated (Table 3). Visible sky and opening orientation along with age were selected as the primary microsite variables because they had the highest adjusted R^2 (0.54 for height, 0.57 for basal diameter, and 0.46 for the factor score) when related to the selected dependent variables. Three models were created as a result of these two steps, each having a different dependent variable (basal diameter, height, and the factor score) (Table 4).

To the three models containing visible sky, orientation, and age along with each dependent variable, we added topographic variables (aspect, landscape radiation, radiation duration) to determine if they significantly contributed to describing western white pine growth. Because aspect was the only variable that improved the adjusted R^2 (0.56 for height, 0.58 for basal diameter, and 0.49 for factor score), it was added to the set of three models (Table 3). There were no interactions among the independent variables.

To identify the three thresholds (occupancy, competitive advantage, free to grow) we used visible sky as the only independent variable because in previous analyses visible sky was the strongest variable explaining western white growth (Table 2). For occupancy, we estimated the probability of having three or more western white pine (including the sample tree) on the microsite plot as a function of visible sky (Fig. 2). The logistic regression was weighted by the number of western white pine occurring on the microsite plot.

Relative mean annual height increment (RELMAI) between the selected western white pine and western hemlock (RELMAI = western white pine mean annual height increment (MAI)- western hemlock MAI) located on the microsite plot was used to determine competitive advantage and free to grow. A fourth degree polynomial regression relating RELMAI to visible sky was used to identify response curve inflection points, thereby providing estimates of competitive advantage and free to grow thresholds (Fig. 2).

Because we sampled a wide range of openings (0.001 to 15 ha in size), we used last 5-years height growth and mean annual height increment to estimate the optimum opening size for western white pine growth using a second degree polynomial regression (Fig. 3). To relate visible sky to stand descriptors (basal area ha^{-1}, stand density index, trees ha^{-1}, and size of opening) we used log-linear regression (Fig. 4 and 5).

4. Results

The three western white pine descriptors, basal diameter, height, and the factor score, were positively related to visible sky when adjusted for age. Visible sky determined from the fisheye photograph and age described 53% of the variation in height (Table 3). Radiation below the canopy and age although significant (p = 0.0001) explained less of the variability in height, basal diameter, or the factor score (Table 3). Landscape radiation significance varied depending on the independent variable. For height, total and direct landscape radiation were significant (p = 0.02 and 0.01, respectively) but did not explain the variability of western white pine growth any more than visible sky alone. In contrast, landscape radiation values were not significantly (p = 0.39, 0.30, 0.21) related to basal diameter. Number of sunflecks occurring on June 21, 1999 was significant for all three variables and had relatively high adjusted R^2 for height (0.50), basal diameter (0.47), and the factor score (0.39), but because this value was calculated as a result of visible sky, we decided visible sky was a better descriptor of the microenvironment around the western white pine. Orientation and aspect, were significantly (at least 0.0020 for orientation and p = 0.0002 for aspect for predicted basal diameter) related to all the dependent variables (Tables 3 and 4). Although the increase in adjusted R^2 was small compared to visible sky, both these variables increased the amount of variation explained in basal diameter, height, and the factor score (Tables 3 and 4).

Because we described openings larger than what the fisheye photograph captured (approximately 0.7 ha), we had western white pines growing in canopy openings ranging from 14 to over 100% visible sky. As visible sky increased, so did age-adjusted western white pine basal diameter, height, and factor score (Fig. 6). Although opening orientation and aspect did not describe much more of the variability than visible sky alone, they did have a significant influence on western white pine growth (Table 4). Southwest-facing aspects and openings oriented southeast to northwest (91 to 180) had the smallest age-adjusted western white pines. In contrast, openings oriented northeast to southwest (0 to 90) on northeast-facing aspects had the larger (age-adjusted) trees across all canopy openings (Fig. 7). There were no interactions among visible sky, aspect, or orientation, indicating that western white pine grew similarly across canopy openings regardless of aspect or orientation.

For western white pine to occupy a site, there has to be seed and the site needs to favor germination and seedling establishment. Under a dense canopy, 65% of the seedlings will die by age 3 years. After this time, survival increases and seedlings that become established can live for long periods (Haig et al., 1941; Wellner, 1965). All trees we measured were at least 5 years old, often much older. Therefore, we assumed seedlings we measured, in addition to the sampled western white pine, occupied the microsite. However, stochastic events could create conditions favorable for ideal but anomalous seedling germination. Therefore, we conservatively based our definition of occupancy on three or more western white pines occurring on a 60 cm radius circular plot at least 5 years old. Our results showed there was a 57% probability of western white pine occupying a site at a 25% visible sky (Fig. 2). At 45% visible sky there was an 80% probability of western white pine occupying the site (Fig. 2).

Competitive advantage and free to grow were estimated using inflection points on a regression curve relating relative mean annual increment (RELMAI) to visible sky ($p = 0.0001$ and $R^2 = 0.40$) (Fig. 2). Within the western white pine cover type, western hemlock (a shade tolerant species) is one of western white pine's key competitors in small canopy openings (Haig et al., 1941; Boyd, 1980; Graham, 1990). Our results showed that western white pine gains a competitive advantage (RELMAI became positive) over western hemlock between 50 to 55% visible sky (Fig. 2). Free to grow (RELMAI stabalizes) begins to occur at 92% visible sky (Fig. 2). Similarly, when observing the relation of basal diameter, height, and the factor score to visible sky, the slope of these response curves dramatically increased at approximately 92% visible sky (Fig. 6).

Using our data we identified the size of opening required to optimize western white pine growth. We related 5 year height growth and mean annual height increment to visible sky. Our results show an inflection point occurring on the regression curve approximately at an opening size of 4 to5 ha (Fig. 3).

The third objective of this study was to relate visible sky to more traditional forest inventory measurements. In all cases, there was a statistically significant relation between visible sky calculated from the fisheye photograph and basal area, stand density index, trees per hectare, and size of opening. For example, at 20% visible sky, basal area was 30 $m^2 ha^{-1}$ (139 $ft^2 ac^{-1}$) and decreased to 10 $m^2 ha^{-1}$ (45 $ft^2 ac^{-1}$) at 90 to 100% visible sky (Fig. 4). Similar results occurred for stand density index and trees per acre. However, only 12, 12, and 6% of the variation in basal area, stand density index, and trees per hectare, were explained by visible sky, respectively (Fig. 4). In contrast, 55% of the variability in opening size was explained by visible sky (Fig. 5).

Although all cases, overstory species was significant, it only explained a small amount of the variation in basal area, stand density index, trees per hectare, and opening size. Lighter crowned western white pine and lodgepole pine tended to allow more visible sky through the canopy compared to the heavy crowned western hemlock and grand fir. In areas with no overstory trees, such as patches or strips, surrounding species composition significantly ($p < 0.0001$) influenced opening size (Fig. 5). For example, if heavy crowned trees dominated the surrounding overstory, canopy openings greater than 4500 m^2 were needed to achieve free to grow. In contrast, if light crowned trees dominated the surrounding overstory, a 2500 m^2 opening would provide the same environment (Fig. 5).

5. Discussion

5.1. Radiation and growth

Landscape radiation is an important component influencing vegetation composition over time and space (Daubenmire, 1943; Daubenmire and Daubenmire, 1968; Garnier and Ohmura, 1970; Pope and Lloyd, 1974; Cooper et al., 1991), leading to the assumption that opening location on the landscape (ridge versus valley bottom) would affect how gaps influence vegetation development. Surprisingly, although statistically significant, direct, diffuse, or total landscape radiation when combined with visible sky did not improve estimates of western white pine height or the factor score over visible sky alone (Table 3). Moreover, it did not significantly influence diameter growth. The amount of radiation (intensity and duration) reaching a landscape position is highly variable depending on 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; Pope and Lloyd, 1974; Hutchison et al., 1980). It appears the combination of these factors produced such a variation that we were unable to relate western white pine growth to topographic associated light levels. Another possible reason we found no relationship between western white pine development and the amount of direct radiation reaching a landscape position was that direct radiation was totally intercepted by the overstory canopy and diffuse radiation was similar across landscape positions (Anderson, 1970; Pope and Lloyd, 1974).

We found significant relations with growth and number of sunflecks, and sunfleck duration, leading us to infer that western white pine growth was more responsive to direct radiation than to diffuse radiation. If most direct radiation was intercepted by the overstory canopy, then sunflecks were the only source of direct radiation reaching the surface. In our study, height, basal diameter, and factor score were negatively related to the number of sunflecks (adjusted $R^2 = 0.50$ for height, 0.47 for diameter, 0.39 for the factor score) and positively related to sunfleck duration (Table 3). Below canopy radiation, although significant ($p = 0.0001$), explained a smaller proportion of the variation in western white pine growth (0.44 for height, 0.39 for diameter, 0.30 for the factor score) than did number of sunflecks. Characterizing sunflecks may be a better descriptor of how canopy openings influence light environments in the understory than using radiation measurements (ratios, proportions, or other direct measurement) from above and below the canopy (Wellner, 1946; Anderson, 1966; 1970; Hutchison and Matt, 1977; Ustin et al., 1984; Canham et al., 1990; Smith et al., 1992).

5.2. Canopy Opening and Other Attributes and Their Influence on the Operational Environment

For western white pine to develop and mature it requires not only sufficient light, but also enough moisture and nutrients at the right temperature for photosynthesis and subsequent growth to occur. Canopy opening, as measured by percent visible sky, explained more of the variation in western white pine growth (0.53 for height, 0.56 for diameter, and 0.45 for the factor score) than below canopy radiation alone (0.44 for height, 0.39 for diameter, and 0.30 for the factor score), suggesting that canopy opening integrates other factors, in addition to radiation, that influence vegetation dynamics. Such factors may include variation in night and day temperatures, soil moisture, nutrient dynamics, and relative atmospheric water demand (Haig, 1936; Jemison, 1934; Norman and Campbell, 1989; Zhang and Liang, 1995; Barik et al., 1992; Brown, 1993). Jemison (1934) noted that soil surface temperatures, evaporation rates, and absolute humidity were significantly different among overstory densities (no canopy, 50% canopy, full canopy) in forest cover types similar to the ones we used in this study. This climatic variation can have a major effect on seedling establishment and growth (Jemison, 1934; Haig, 1936; Grubb, 1977; Jackson and Spomer, 1979; Canham, 1989; Veenendall et al., 1995).

Canopy opening, as measured by percent visible sky, likely integrates the availability of nutrients and water to understory vegetation. In the northern Rocky Mountains, western hemlock and grand fir (heavy crowned species) use more water and nutrients (Minore, 1979; Harvey et al., 1999), providing less water and nutrients to ground level vegetation compared to forests dominated by western white pine and western larch (light crowned species). The species-rich understories historically occurring in western white pine forests, are very different from the sparse understories occurring in western hemlock dominated forests today (Haig et al., 1941; Cooper et al., 1991; Harvey et al., 1999).

We compared western white pine growing in different combinations of aspects and opening orientations. Our results showed trees were taller at a given age in openings oriented northeasterly (0 to 45^0) and occurring on northeasterly aspects (Fig. 7) compared to trees growing in other opening orientations and aspects (Fig. 7). Pope and Lloyd (1974) showed that solar radiation (direct and diffuse) received on easterly and westerly aspects are relatively equal, northerly aspects receive less radiation than east or west facing aspects, and southerly aspects receive more radiation than east or west facing aspects. Possibly western white pine is similar to grand fir that has high potential conductance, low acclimation ability, and relatively high osmotic potential at incipient plasmolysis, indicating that it prefers a relatively constant and high water supply (Jackson and Spomer, 1979). If so, this indicates that western white pine would grow poorly on orientations and aspects where moisture is limited or is more inconsistent, which may be more prevalent on southerly aspects.

5.3. Thresholds

Within the moist forests of the northern Rocky Mountains, up to 10 tree species and several shrub and forb species all compete for site occupancy, creating a species rich ecosystem. Several factors contribute to high species richness in these forests such as: life-form, phenological differences and tolerance for unfavorable conditions, fluctuations in the environment combined with small differences in the competitive ability between species, the balance between intraspecific and interspecific competition, production of alleopathic substances, soil, microbial and plant interactions, and a wide range of environments that are created by a wide range of disturbances (Haig et al., 1941; Daubenmire and Daubenmire, 1968; Grubb, 1977; Minore, 1979; Lorimer, 1989; Spies and Franklin, 1989; Oliver and Larson, 1990). For an ecosystem to maintain such species richness, many of these mechanisms must be present (Grubb, 1977; Bazzaz, 1979; Swaine and Whitmore, 1988; Spies and Franklin, 1989; Whitmore, 1989). For western white pine to take advantage of these environments seed must be present and western white pine has to establish, and occupy the site before the more tolerant species (Fig. 2). To gain a competitive advantage and be free to grow it has to both simultaneously occupy the site first and grow faster then its competitors (Grubb, 1977; Reader et al., 1995).

Occupancy depends on seed source availability (Fig. 2). Reader et al., (1995) found that at least 93% of the variation in seedling establishment was explained by overstory species density. Today, western white pine abundance has decreased drastically, making seed scarce compared to what it was historically (Hann et al., 1997; Neuenschwander et al., 1999) (Fig. 1). Even with this decrease in abundance, we found canopy openings (defined by visible sky) where western white pine had a high probability (55 to 82%) of occurring (Fig. 2). Our results verify observations made by early researchers who stated that western white pine can regenerate and grow, although slowly, under high overstory canopy densities (Larsen, 1924; Haig, 1936; Wellner, 1936; Haig et al., 1941). Similarly, eastern white pine (*Pinus strobus*) can regenerate and grow in hardwood canopy gaps (Messier et al., 1999).

We attempted to identify competitive advantage and free to grow with both western hemlock and grand fir. We succeeded using western hemlock (Fig. 4) but failed with grand fir. We found, given the same age, western white pine tended to grow faster than grand fir, thus western white pine always had a competitive advantage over grand fir. However, if disturbances create gaps with less than 25% visible sky, grand fir is able to establish prior to, and exclude western white pine from becoming established (Jackson and Spomer, 1979; Minore, 1979; Foiles et al., 1990; Graham, 1990). Even when additional disturbances increase the size of these small openings, other tree species are unable to establish, even though canopy conditions favor their establishment and growth (Ferguson et al., 1986; Ferguson and Carlson, 1993; Mitchell and Arnott, 1995). In our study, as opening size increased, growth of all species including the tolerant species increased (Fig. 8). Similar results were noted by Coates, (2000). If a disturbance such as a wildfire creates a canopy opening with a visible sky greater than 25%, our results show that western white pine has the ability to occupy the site. In such openings, western white pine would likely gain a competitive advantage over western hemlock and grand fir provided future disturbances increase the size of the opening (Fig. 5).

Applying knowledge gained form this study to restore western white pine forests will be challenging but not impossible. Although, growth will be sacrificed in openings less than 4 to 5 ha in size (Fig. 3), these thresholds provide a means for managing and sustaining western white pine in the northern Rocky Mountains given the current reservation about clearcuts (Bliss, 2000). A range of canopy opening sizes can be created through silvicultural treatments or by native disturbances where these thresholds may be applied. If seed is available, with 25 to 45% canopy opening (visible sky) would give rise to a 55 to 80% probability that western white pine would regenerate (Fig. 2a). Moreover, planted western white pine would survive in these conditions. Western white pine growing under these conditions would need to be released through overstory removal to ensure the pines obtain a competitive advantage and become free to grow. To achieve competitive advantage would require at least 55% visible sky. While free to grow would require 92% visible sky. Depending on the setting, this window of opportunity may be 10 years or less (Fig. 4b). In addition, during the 10 to 30 years after a disturbance, the species composition and future stand dynamics are largely determined, indicating that cultural activities (weeding, cleaning) should occur during this time (Deitschman, 1966; Graham, 1988).

A disadvantage of forest structures defined by visible sky is that traditional density measurements were poorly related to this measurement. We found a weak relationship between visible sky and basal area, stand density index, and trees per hectare. In contrast, Mitchell and Popovich (1997) found basal area strongly related to visible sky in pure ponderosa pine stands using a spherical densiometer. Size of opening, although a good descriptor of visible sky (Coates 2000) is not easy to estimate because of stand, tree, canopy, and crown irregularities. Although opening size was a better descriptor of visible sky than stand density indices it only explained 55% of the variation. Even with these weak relationships, depending on stand structure and composition conditions to achieve competitive advantage and free to grow can be accomplished with openings of 3000 to 5000 m^2 or with residual basal areas less than 15 m^2 ha^{-1} (approx. 68 ft^2 ac^{-1}) (Fig. 4 and 5). At this threshold there is a high probability that mid-aged western white pine will be in the dominant overstory.

There are many studies, characterizing vegetation response as a function of canopy opening size (Canham, 1989; Bradshaw, 1992; Coates and Burton, 1997; 1999; Coates 2000), however, we did not find any study where thresholds such as occupancy, competitive advantage, or free to grow were identified. The techniques we developed to identify the thresholds are unique, and could be used in other ecosystems. Because canopy opening limits vegetation establishment and growth (Norman and Campbell, 1989), it is an ideal variable for investigating vegetation dynamics among different species over time and space. This study disclosed relations among canopy opening characteristics and vegetation response and how biophysical settings affected these relationships. In addition, it provided insight on how species regenerate, grow, and compete and provided information for making informed management decisions.

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Table 1
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. Factor score combined basal diameter, height, and 5-year height growth.

Aspect	Plot location	Low elevation openings			High elevation openings			
		Under (<.1 ha)	Small (<.5 ha)	Large (>1 ha)	Under (<.1 ha)	Small (<.5 ha)	Large (>1 ha)	Total
Azimuth (degrees)		Number of Plots						
0 to 90	Edge	4	4	4	4	4	4	24
	Center	4	4	4	4	4	4	24
91 to 180	Edge	4	4	4	4	4	4	24
	Center	4	4	4	4	4	4	24
181 to 270	Edge	4	4	4	4	4	4	24
	Center	4	4	4	4	4	4	24
271 to 360	Edge	4	4	4	4	4	4	24
	Center	4	4	4	4	4	4	24
Total		32	32	32	32	32	32	192

Table 2
Log-linear regression was used to analyze the data. For each dependent variable, the significance level (P-value) from the partial sum of squares F-test, model P-value, and adjusted R^2 were used to evaluate the contribution each variable made to the relations between the dependent and independent variables. Visible sky was transformed using the arcsine of the square root. All dependent variables were transformed using the natural log, except for crown shape, which was transformed using the square root.

Dependent variables	Independent variables			
	Visible sky P-value	Age	Model P-value	Adjusted R^2
Height	0.0001	0.0001	0.0001	0.53
Basal diameter	0.0001	0.0001	0.0001	0.56
Factor score	0.0001	0.0001	0.0001	0.45
5-year height growth	0.0001		0.0001	0.26
Mean Annual Increment-height	0.0001		0.0001	0.25
Mean Annual Increment-diameter	0.0001		0.0001	0.41
Crown shape (crown diameter x height)	0.0001	0.3176	0.0001	0.12
Crown ratio	0.0001	0.8168	0.0001	0.12
Needle retention	0.0087	0.0001	0.0001	0.06
Crown diameter	0.0001	0.0001	0.0001	0.49

Table 3
The evaluation of independent variables predicting western white pine height, basal diameter, and a factor score. Significance levels (P-value) from partial sum of square F-tests for each independent variable, over all model significance, and adjusted R-squares were used for determining significant relations. Age was a covariate in all models.

Independent variables	First variable P-value	Second variable P-value	Third variable P-value	Age	Model P-value	Adj. R^2
Microsite variables			Height			
Visible sky	0.0001			0.0001	0.0001	0.53
Radiation below canopy (total)	0.0001			0.0001	0.0001	0.44
Sunfleck duration	0.0123			0.0001	0.0001	0.39
Number of sunflecks	0.0001			0.0001	0.0001	0.50
Microsite factor score	0.0122			0.0001	0.0001	0.40
Visible sky & opening orientation	0.0001	0.0015		0.0001	0.0001	0.54
Topographic variables						
Visible sky & total landscape radiation	0.0001	0.0222		0.0001	0.0001	0.53
Visible sky & direct landscape radiation	0.0001	0.0142		0.0001	0.0001	0.53
Visible sky & diffuse landscape radiation	0.0001	0.3155		0.0001	0.0001	0.53
Visible sky & topographic factor score	0.0001	0.6957		0.0001	0.0001	0.53
Visible sky, orientation & aspect	0.0001	0.0055	0.0001	0.0001	0.0001	0.56
Microsite variables			Basal Diameter			
Visible sky	0.0001			0.0001	0.0001	0.56
Radiation below canopy (total)	0.0001			0.0001	0.0001	0.39
Sunfleck duration	0.0121			0.0001	0.0001	0.28
Number of sunflecks	0.0001			0.0001	0.0001	0.47
Microsite factor score	0.0003			0.0001	0.0001	0.30
Visible sky & opening orientation	0.0001	0.0035		0.0001	0.0001	0.57
Topographic variables						
Visible sky & total landscape radiation	0.0001	0.3872		0.0001	0.0001	0.56
Visible sky & direct landscape radiation	0.0001	0.2981		0.0001	0.0001	0.56
Visible sky & diffuse landscape radiation	0.0001	0.2103		0.0001	0.0001	0.56
Visible sky & topographic factor score	0.0001	0.7403		0.0001	0.0001	0.55
Visible sky, orientation & aspect	0.0001	0.0020	0.0002	0.0001	0.0001	0.58

Table 3 continued
The evaluation of independent variables predicting western white pine height, basal diameter, and a factor score. Significance levels (P-value) from partial sum of square F-tests for each independent variable, over all model significance, and adjusted R-squares were used for determining significant relations. Age was a covariate in all models.

Independent variables	First variable P-value	Second variable P-value	Third variable P-value	Age	Model P-value	Adj. R^2
Microsite variables	Factor Score of Western White Pine Variables					
Visible sky	0.0001			0.0001	0.0001	0.45
Radiation below canopy (total)	0.0001			0.0001	0.0001	0.30
Sunfleck duration	0.0040			0.0001	0.0001	0.19
Number of sunflecks	0.0001			0.0001	0.0001	0.39
Microsite factor score	0.0028			0.0001	0.0001	0.20
Visible sky & opening orientation	0.0001	0.0002		0.0001	0.0001	0.46
Topographic variables						
Visible sky & total landscape radiation	0.0001	0.3744		0.0001	0.0001	0.45
Visible sky & direct landscape radiation	0.0001	0.3353		0.0001	0.0001	0.45
Visible sky & diffuse landscape radiation	0.0001	0.6350		0.0001	0.0001	0.45
Visible sky & topographic factor score	0.0001	0.4327		0.0001	0.0001	0.45
Visible sky, orientation & aspect	0.0001	0.0008	0.0001	0.0001	0.0001	0.49

Table 4
Three log-linear models showing the relations among western white pine descriptors and microsite, topographic, and stand descriptors (Coeff.) coefficients) and standard errors (SE). Significance (P < .05) denoted by '*'.

Independent Variables		Dependent variables (Y)					
		Height		Basal diameter		Factor Score	
		Coeff.	SE	Coeff.	SE	Coeff.	SE
		ln Y = Visible sky + age					
Intercept		3.06*	2.92	- 1.38*	0.081	- 2.44*	0.18
Visible sky		0.83*	0.70	1.32*	0.069	1.66*	0.10
Age		0.066*	0.060	0.065*	0.0032	0.071*	0.0046
		ln Y = Visible sky + age + orientation					
Intercept		3.036*	0.076	- 1.41*	0.084	- 2.47*	0.12
Visible sky		0.83*	0.062	1.31*	0.069	1.64*	0.10
Orientation	0 to 45^0	0.074	0.048	0.10*	0.054	0.14*	0.078
	46 to 90^0	0.067	0.050	0.13*	0.056	0.15*	0.081
	91 to 135^0	- 0.099*	0.051	- 0.08	0.056	- 0.16*	0.082
	136 to 180^0	0.00		0.00		0.00	
Age		0.066*	0.0028	0.066*	0.0031	0.072*	0.0045
		ln Y = Visible sky + age + orientation + aspect					
Intercept		2.99*	0.085	- 1.44*	0.095	- 2.85*	0.14
Visible sky		0.84*	0.061	1.33*	0.068	1.67*	0.098
Orientation	0 to 45^0	0.068	0.48	0.09*	0.053	0.13*	0.077
	46 to 90^0	0.046	0.05	0.10*	0.053	0.12	0.080
	91 to 135^0	- 0.092		- 0.082	0.056	- 0.15*	0.080
	136 to 180^0	0.00		0.00		0.00	
Aspect	0 to 45^0	0.22*	0.062	0.21*	0.069	0.36*	0.10
	46 to 90^0	0.025	0.065	- 0.063	0.073	- 0.012	0.10
	91 to 135^0	- 0.078	0.062	- 0.076	0.069	- 0.12	0.10
	136 to 180^0	0.13	0.068	0.15*	0.076	0.24*	0.11
	181 to 225^0	0.044	0.064	0.050	0.076	0.091*	0.11
	226 to 270^0	- 0.064	0.064	- 0.054	0.071	- 0.13	0.10
	271 to 315^0	- 0.065	0.069	- 0.057	0.077	- 0.082	0.11
	316 to 360^0	0.00		0.00		0.00	
Age		0.067*	0.0028	0.067*	0.0031	0.073*	0.0044

Figure Captions

Fig. 1. Change in western white pine abundance since the 1930's. Study area includes three watersheds (Deception Creek, Jordan Creek, and Beaver Creek) within the Coeur d'Alene River Basin.

Fig. 2. Three thresholds (occupancy, competitive advantage, free to grow) were identified using visible sky as the only independent variable. For occupancy, we estimated the probability of having three or more western white pine (including the sample tree) on a 60 cm radius circular microsite plot. Logistic regression was weighted by the number of western white pine occurring on the microsite plot. Relative mean annual height increment (RELMAI) between the selected western white pine and western hemlock (RELMAI = MAI-height of western white pine − average MAI-height of western hemlock) located on the microsite plot was used to determine competitive advantage and free to grow. A fourth degree polynomial regression relating RELMAI to visible sky was used to identify response curve inflection points, thereby providing estimates of competitive advantage and free to grow thresholds. All models were significant at P = 0.0001.

Fig. 3. Opening size for optimum western white pine growth ranges from 3.5 to 4.5 ha for both MAI-height (A) and 5-year height growth (B). To estimate opening size for optimum western white pine growth we used a second degree polynomial and related Mean Annual Increment-height (A) and last 5-year height growth (B) to opening size. The model was significant at P = 0.0001.

Fig. 4. Relationship between visible sky and basal area (A), stand density index (B), and trees per hectare (C). Although the three relationships were significant (P = 0.0001), the Adjusted R^2 were low.

Fig. 5. Relationship between opening size and visible sky. The relationship was significant (P = 0.0001) with visible sky explaining 55 % of the variation in opening size. Heavy crowned species include grand fir, western hemlock and western redcdear. Light crowned trees include western larch, western white pine, and lodgepole pine. Dotted lines represent three thresholds: occupancy, competitive advantage, and free to grow. For occupancy, we estimated the probability of having three or more western white pine (including the sample tree) on a 60 cm radius circular microsite plot as a function of visible sky. For competitive advantage and free to grow, we used relative mean annual height increment (RELMAI) between the selected western white pine and western hemlock (RELMAI = MAI-height of western white pine – average MAI-height of western hemlock) located on the microsite plot as a function of visible sky. For each species, an approximate estimate of opening size can be ascertained for each threshold.

Fig. 6. Relationship between western white pine growth variables and percent visible sky at age 10. Western white pine variables include (A) total tree height, (B) basal diameter (diameter 2.54 cm above root collar), and (C) a factor score that is the linear combination of basal diameter, height, and last 5-year height. The factor score uses an adhoc method for combining correlated variables that averages correlated standardized variables (Johnson 1998). Age was a significant covariate in all three relationships. Age was a significant covariate. Model significance was P=0.0001.

Fig. 7. Relationship between western white pine basal diameter aspect, and orientation at age 10 with visible sky of 100%. Comparison between different opening orientations across two different aspects. Tree basal diameter is greater when openings are oriented northeast and are located on northeast aspects than tree basal diameter when they occur in southeast oriented openings given the same aspect. Age is a significant covariate in the model. Model significance was P = 0.0001 with an $R^2 = 0.58$.

Fig. 8. Relationship between visible sky and three species–(WH) western hemlock, (GF) grand fir, and (WWP) western white pine. All species responded similarly as visible sky increased.

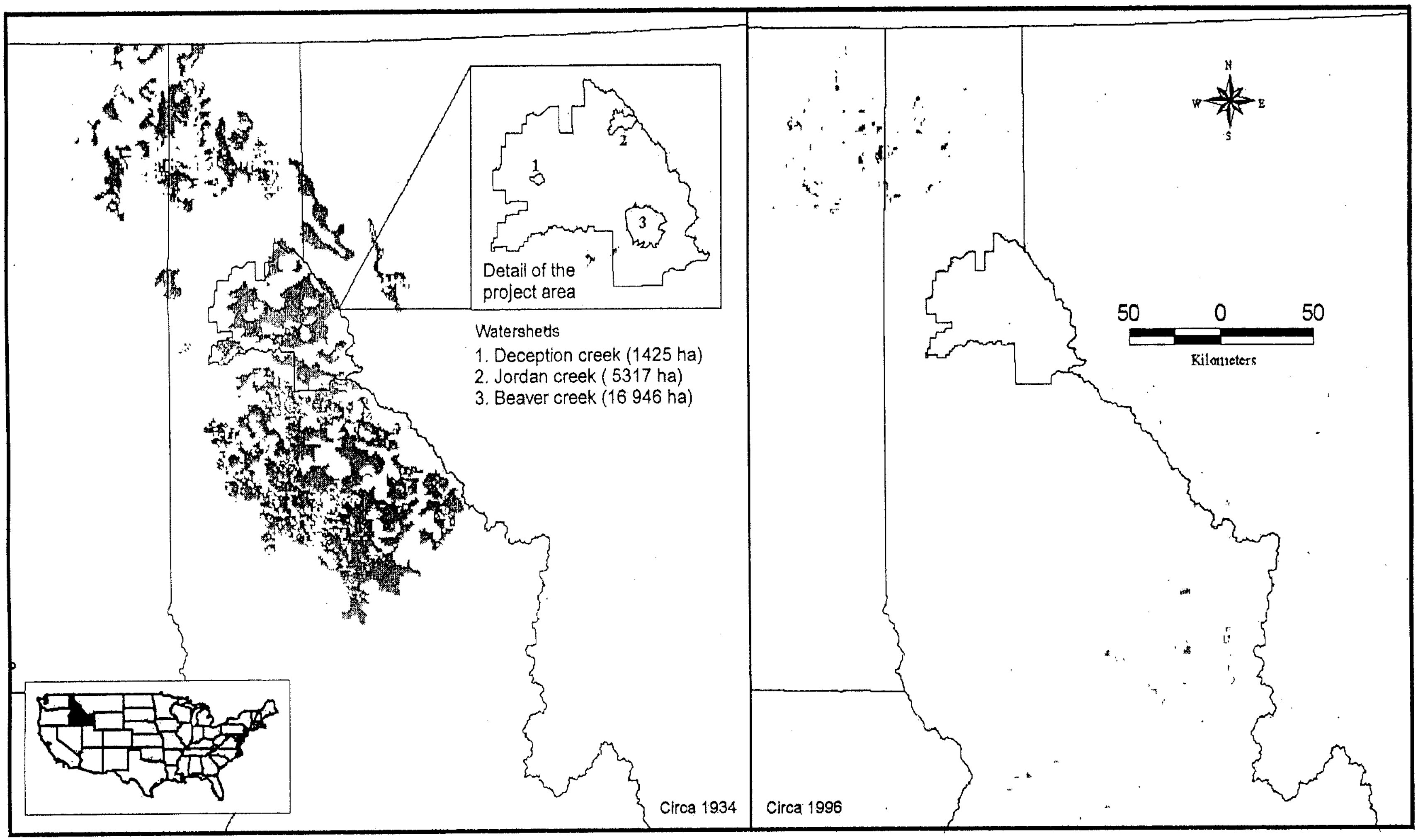

Detail of the project area
1
2
3
Watersheds
1. Deception creek (1425 ha)
2. Jordan creek (5317 ha)
3. Beaver creek (16 946 ha)
Circa 1934
Circa 1996
N
W
E
S
50
0
50
Kilometers

Fig. 1

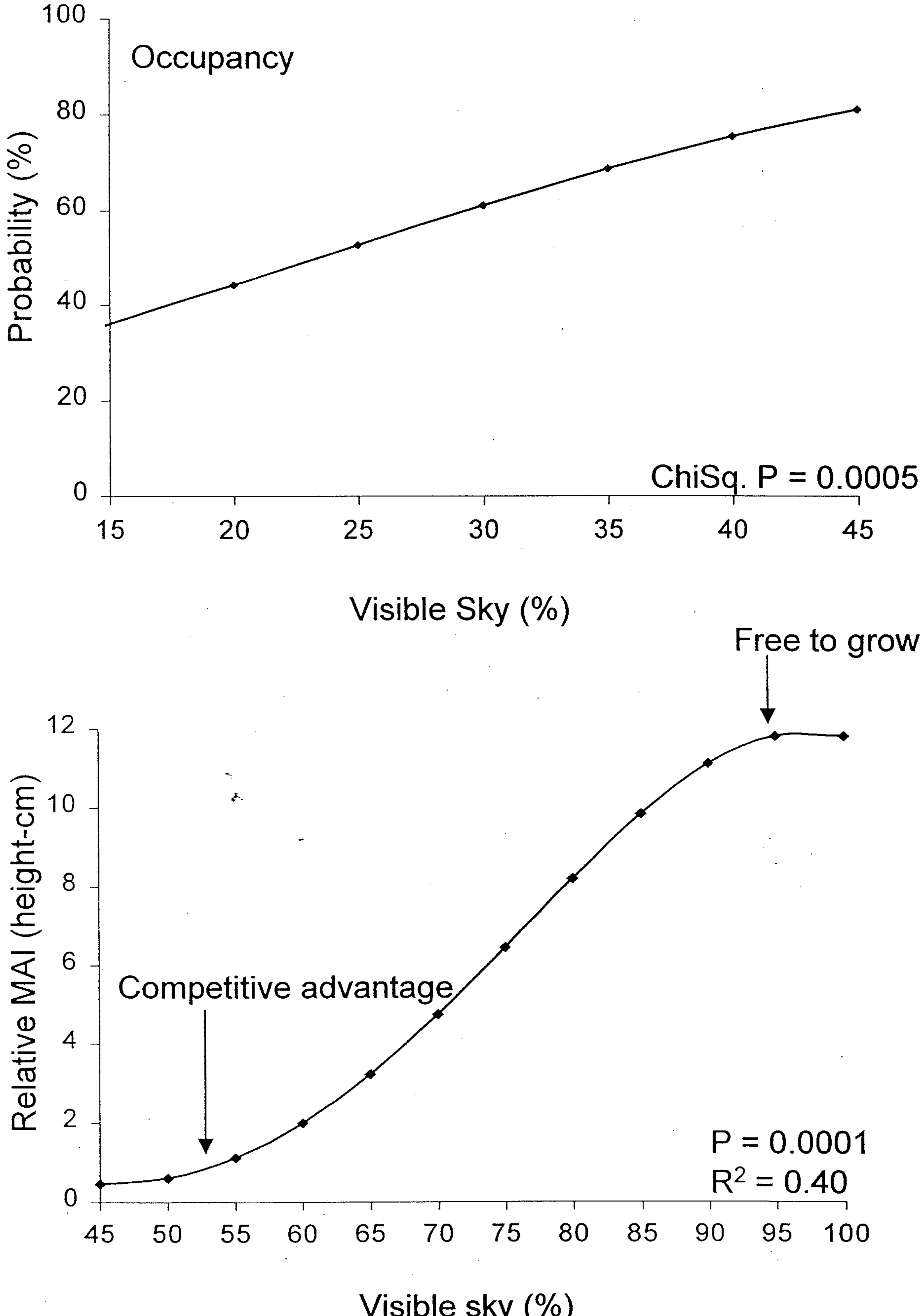

100
Occupancy
80
60
40
20
0
Probability (%)
ChiSq. P = 0.0005
15
20
25
30
35
40
45
Visible Sky (%)
Free to grow
12
10
8
6
4
2
0
Relative MAI (height-cm)
Competitive advantage
P = 0.0001
R2 = 0.40
45
50
55
60
65
70
75
80
85
90
95
100
Visible sky (%)

Fig. 2

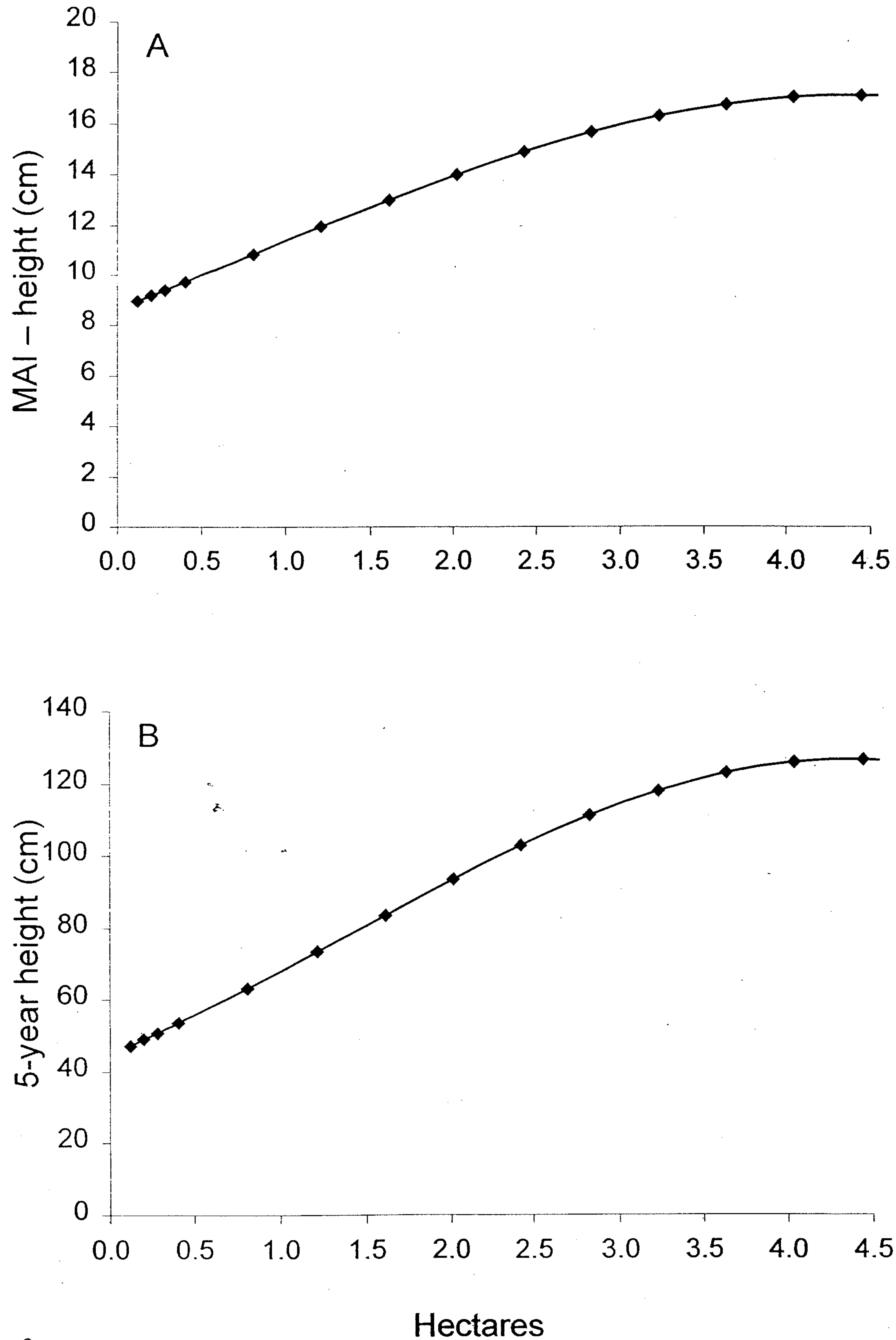
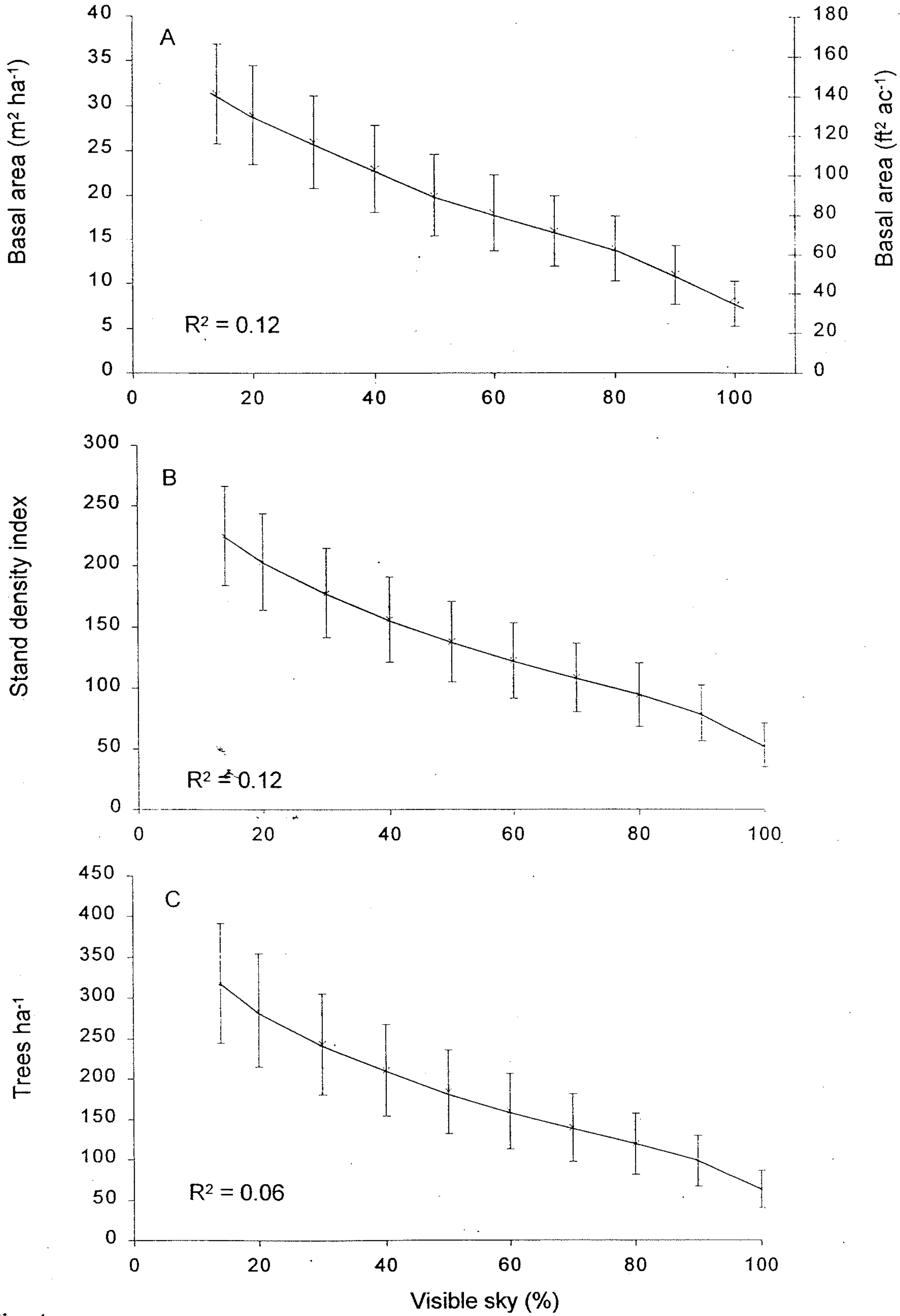
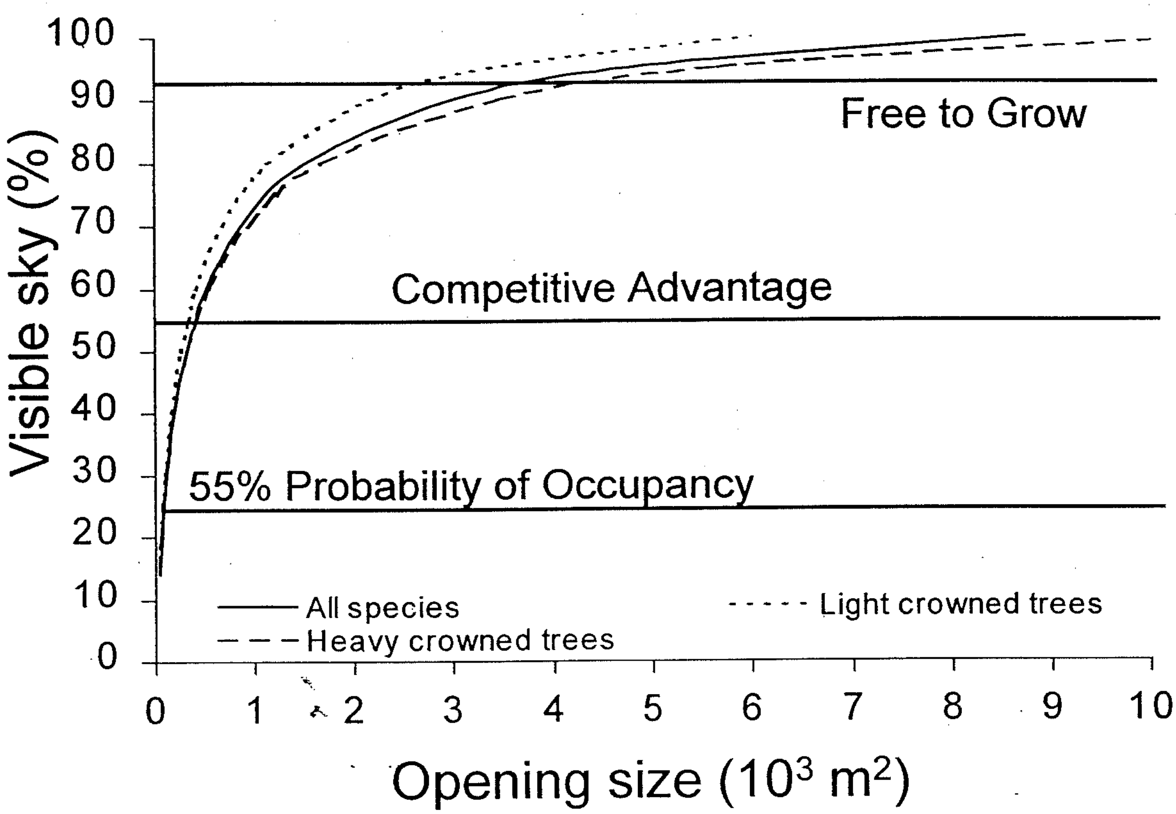

A
MAI – height (cm)
20
18
16
14
12
10
8
6
4
2
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
B
5-year height (cm)
140
120
100
80
60
40
20
0
Hectares

Fig. 3



A
Basal area (m² ha⁻¹)
Basal area (ft² ac⁻¹)
R² = 0.12
B
Stand density index
R² = 0.12
C
Trees ha⁻¹
R² = 0.06
Visible sky (%)

Fig. 4



100
90
80
70
60
50
40
30
20
10
0
Visible sky (%)
Free to Grow
Competitive Advantage
55% Probability of Occupancy
All species
Heavy crowned trees
Light crowned trees
0
1
2
3
4
5
6
7
8
9
10
Opening size (10^3 m^2)

Fig. 5

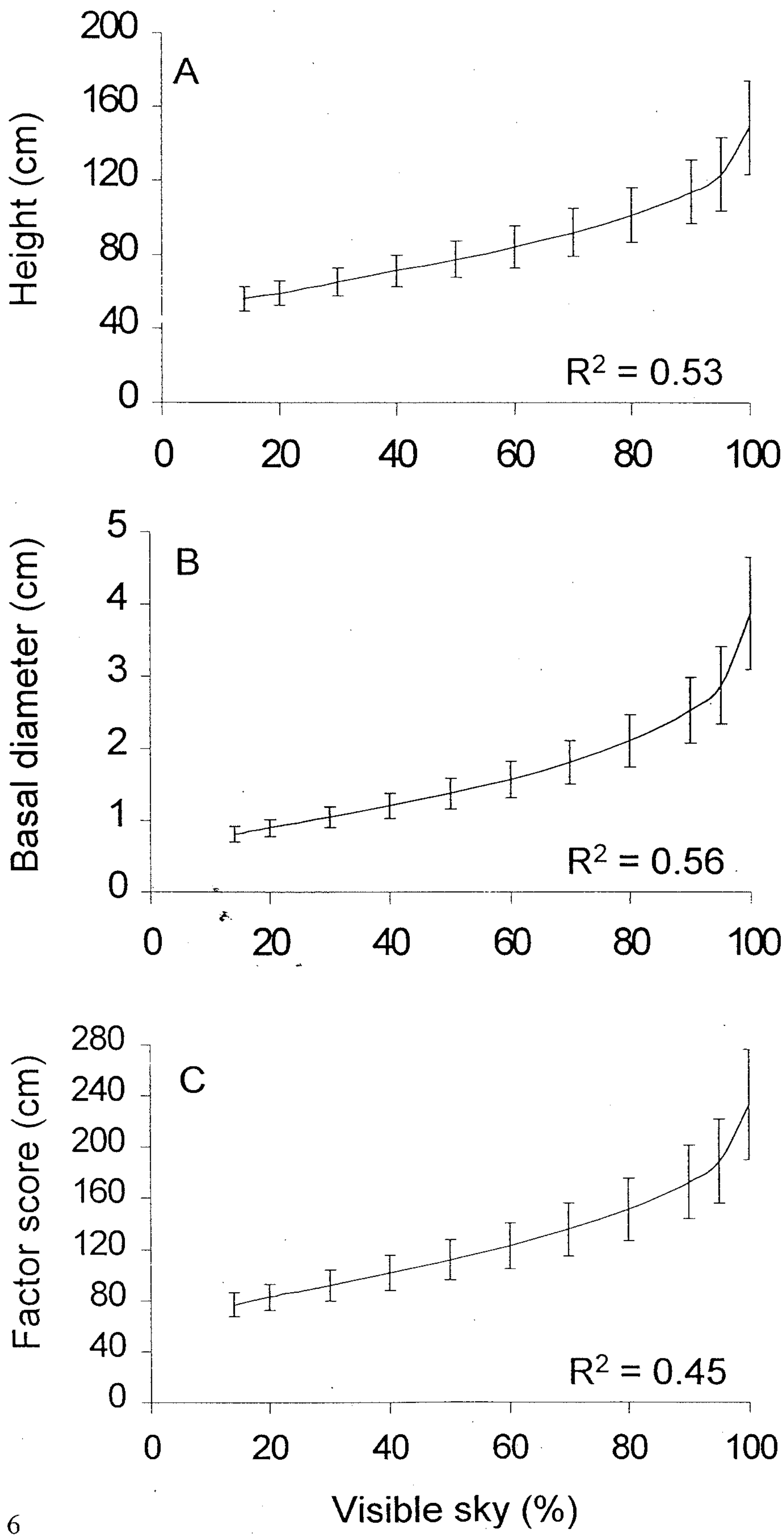

200
160
120
80
40
0
Height (cm)
A
R² = 0.53
0
20
40
60
80
100
5
4
3
2
1
0
Basal diameter (cm)
B
R² = 0.56
0
20
40
60
80
100
280
240
200
160
120
80
40
0
Factor score (cm)
C
R² = 0.45
0
20
40
60
80
100
Visible sky (%)

Fig. 6

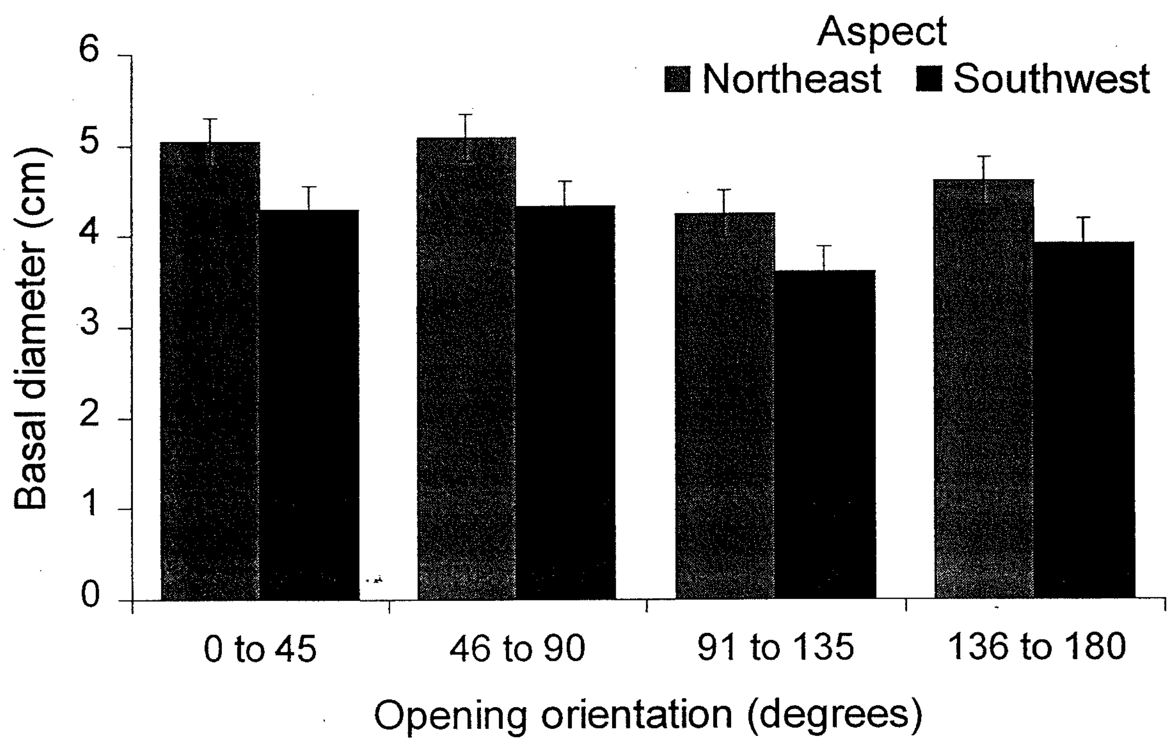

Aspect
Northeast
Southwest
6
5
4
3
2
1
0
Basal diameter (cm)
0 to 45
46 to 90
91 to 135
136 to 180
Opening orientation (degrees)

Fig. 7

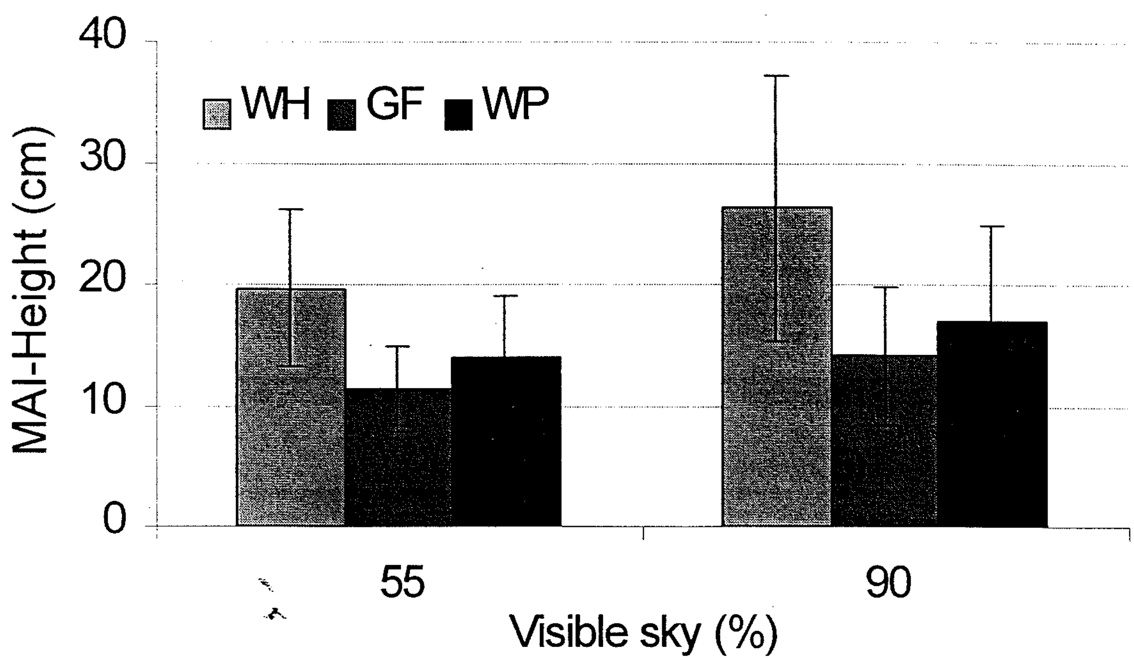


Fig. 8

Appendix C - Western white pine growth across multiple spatial scales

Western white pine growth in relation to biophysical characteristics across different spatial scales in the Coeur d'Alene River Basin, in Northern Idaho USA

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Abstract: Many studies have quantified tree regeneration and growth beneath canopies in forest ecosystems, but results are seldom placed within the context of broad-scale biophysical factors. Mapped landscape characteristics for three watersheds were integrated to create a spatial hierarchy reflecting biophysical factors (e.g., climate, soil formation, disturbance) that influence growth of young western white pine (*Pinus monticola* Dougl. Ex D. Don) under a range of canopy openings. The spatial hierarchy included: canopy opening (as defined by percent visible sky), landtype, geological feature, and weathering. Study sites were within the 350,000 ha Coeur d'Alene River Basin in northern Idaho. Using log-linear regression in a step-wise approach, interactions and individual scale contributions were identified for describing the variation in western white pine growth. For estimating western white pine basal diameter, the model explained 73% of the variation; and for estimating height the model explained 70% of the variation. The interaction among spatial scales explained up to 16% of this variation and better described vegetation response than any single spatial scale. These results complement the extensive site-specific knowledge about western white pine regeneration and development by linking landscape attributes to a site specific vegetation response.

Introduction

Ecosystem processes (e.g., disturbance, soil development, and climate) influence vegetation pattern at multiple spatial scales. For example, growth and abundance of vegetation results from interactions among topography, climate, disturbance, soil processes (formation and cycling), time, and vegetation (both current and historical) (Jenny 1980; Pickett and White 1985; Crawley 1986; Matérn 1986; Delcourt and Delcourt 1988; Oliver and Larson 1990; Dale 1999). These interactions result in 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). (Spatial pattern is the arrangement of plants or groups (patches) of plants that exhibit a certain amount of predictability [Dale 1999].) Large 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, within a forest, stand disturbances (e.g., windthrow, insects, and 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 patterns of birds and vegetation (Cherrill et al.1995; Song et. al. 1997; Hinckley et al. 1998; Saab 1999). 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 were either too fine (individual leaf) or too broad (tree) to effectively study physiology mechanistically. Song et al. (1997) determined factors that influence canopy structure by first modeling three-dimensional individual trees (fine-scale) and then building a stand canopy (broad- scale) with these trees. From this multi-scale approach they determined that species composition and tree density influenced shape and size of crowns and subsequent patch size. Saab (1999), used three spatial scales: microhabitat (local vegetation characteristics), macrohabitat (cottonwood forest patch characteristics), and a landscape (surrounding vegetation types and land uses) to study patterns of bird distribution and abundance. Her results showed that landscape patterns most influenced 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 the occurrence of plant distribution (presence or absence data) by using a series of matrices (one matrix per scale). They found that 59% of the 570 plant species were significantly related to the hierarchy. These studies used multiple scales, in most cases with significant results, to understand spatial pattern and structures (landscape features, vegetation characteristics). These studies did not always link spatial scales. Inferences were made within a single spatial scale (Saab 1999), fine-scale data were summarized to address broad-scale questions (Song et al. 1997; Hinckley et al. 1998), or scales were linked using probabilities of fine-scale information occurring at the broad spatial scale (Cherrill et al. 1995). 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; Parsons et al. 1994; Wilczynski and Pickett 1993; Veenendall et al. 1995; Zhang and Zak 1995; Coates and Burton 1997). While these studies contributed 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, and soils). Lertzman et al. (1996) used two spatial scales (forest and 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 total sun per day (a macroclimate factor) had a positive linear relation to the amount of photosynthetically active radiation reaching a gap, 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 objectives requires a knowledge of how fine-scale disturbances are influenced and constrained by processes and structures at broad-scales (Quigley and Arbelbide 1997). However, defining and using multiple spatial scales can be challenging. Hierarchy theory can be used to identify relevant spatial scales (Allen and Starr 1982; Klijn 1994). Scales are nested, and in general, higher levels within the hierarchy have a broader spatial extent 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, 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 vegetation 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 we think influence western white pine (*Pinus monticola* Dougl. ex D. Don) growth under a range of canopy openings. We expected that western white pine growth was influenced by the variation in canopy opening size. But we also hypothesized that variables at other spatial scales, would further improve and refine our predictions. Instead of summarizing results within a spatial scale, or grouping fine-scale data to address broad-scale responses, we will pinpoint the influence broad spatial scales have on an tree growth under a canopy by sampling across spatial scales. Our objectives were to determine if broad spatial scales, in addition to canopy opening size, influence western white pine growth and to identify the significant interactions among spatial scales when they are related to western white pine growth. Linking across spatial scales will show hierarchy theory is useful for understanding seedling and sapling growth. In addition, linking spatial scales and subsequent interactions could influence site specific silvicultural decisions (regeneration and intermediate treatments).

Methods

Spatial hierarchy

The spatial hierarchy we defined included four spatial scales (site, landtype, geological feature, weathering class) integrating the biophysical factors that we believe influence site-specific vegetation response (Table 1). The finest 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). The next broader spatial scale uses a landtype classification, based upon landform, elevation, potential vegetation, slope gradient and shape, aspect, and microrelief (United States Department of Agriculture 1999). This scale represents the variation in soil depth as well as the topographic features that influence surface climate, potential moisture, and overstory tree composition and structure. We defined our third scale using a geological feature classification that is based on parent material (Coeur d'Alene Quadrangle 2000; Harrison and Jobin 1963; 1965; Hobbs et al. 1965; Hosterman 1956; St. Maries Quadrangle[1]; Thompson Falls Quadrangle 1999; Wallace Quadrangle 1999). The classification represents variation in bedrock lithology, sediment bedding characteristics, metamorphic structure layers, and rock color and size. These characteristics influence surface relief, hydrology, water holding capacity, nutrition, and soil formation (Godron 1994; Shen et al. 2000). The broadest scale in our hierarchy was weathering, which classifies settings based on the relative extent to which bedrock has weathered as compared to its presumed, un-weathered state (Schoeneberger et al. 1998; United States Department of Agriculture 1999). This scale reflects long-term climate and geologic processes.

Scales defined by landtype, geological feature and weathering vary spatially, have different geographic extents, and are somewhat inherently nested (Table 1). Broader scales (geological feature, weathering) contain finer scales (soil depth is indirectly integrated into landtypes); and processes (erosion, and organic matter decomposition) occur faster at the finer scales than processes (soil weathering) occurring at broader scales. Landtype, geological feature, and weathering are relatively stable and have not changed significantly during the past 500 years. Isolated areas where soil movement has occurred were recognized in the landtype classification. In addition, these spatial scales integrate soil-forming factors (climate, time, organisms, topography, initial parent material) that also influence vegetation pattern (Jenny 1980; Aber and Mellilo 1991; Sollins 1998). Canopy opening changes relatively rapidly both temporally and spatially compared to the other scales, but it influences many critical elements (light, moisture, heat) important for tree growth.

Selected landscape

We selected three watersheds (Jordon, Beaver, and Deception) within the 350,000 ha Coeur d'Alene River Basin in northern Idaho in the United States (Fig. 1). The same area was used in a related study (Jain et al. Appendix B) to define relations among opening characteristics (opening size, edge, orientation, age, location, overstory species composition, soil substrate, disturbance severity and type) and western white pine seedling or sapling growth. 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.), and western redcedar (*Thuja plicata* Donn ex D. Don) (Cooper et al. 1991; Idaho Panhandle National Forests 1998), that contained young western white pine growing a wide range of canopy opening. The geology, soils, and topography are diverse, providing substantial variation useful for understanding western white pine growth within our spatial hierarchy.

Digital information on weathering, geological features, and landtype for these three watersheds were obtained from the Idaho Panhandle National Forests, Idaho Geological Survey, and the United States Geological Survey. The finest scale data were obtained from Jain et al. (Appendix B) who randomly located 620 (approximately 200 plots per watershed) plots that were stratified across two elevations, four aspects, and a range of canopy opening sizes (Table 1). Jain et al. (Appendix B) located plots along transects ($\leq$30 m in length and two to four plots per transect) in a mosaic of canopy conditions, making individual plots difficult to locate. Therefore, the start of each transect was located using a global positioning system and located on a topographic map (1:24,000). The transects and their affiliated plots were associated with their respective weathering, geological feature, and landtype using a geographic information system (GIS) (Fig. 2). Six-hundred-twenty observations of western white pines, canopy openings, and weathering, geological feature, and landtype classes were included in the data. Table 2 and 3 show the number of observations occurring in each weathering, geological feature, landtype, and geological feature/landtype combination.

For each plot, Jain et al. (Appendix B), described the physical environment (canopy size, orientation, slope position, and overstory tree density) and the characteristics (height, basal diameter, crown ratio, age, crown height) of a western white pine. We used their canopy opening (as defined by % visible sky) data obtained from a fisheye photograph to represent our finest spatial scale and western white pine height and basal diameter adjusted for age to represent a site specific vegetation response. In addition, Jain et al. (Appendix B), identified three thresholds (occupancy, competitive advantage, and free to grow) as a function of canopy opening (visible sky). Probability of three or more western white pine occurring on a microsite was used for estimating occupancy, and relative mean annual height increment between western white pine and western hemlock was used for estimating competitive advantage and free to grow. They determined western white pine had a competitive advantage at 55% visible sky, free to grow was achieved at 92% visible sky. We hypothesized that these thresholds would change as a function of our spatial hierarchy. We used our spatial hierarchy, relative mean annual height increment, number of trees per microsite plot, and the values for competitive advantage and free to grow from Jain et al. (Appendix B), to test this hypothesis.

Analysis

Exploratory analysis of the data 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. Normal probability plots and histograms were used to determine if the data were normally distributed and to suggest appropriate transformations.

The analysis used the log-linear model Jain et al. (Appendix B), developed for estimating height and basal diameter (ln of height or basal diameter = percent visible sky + age) (Table 4). Percent visible sky was transformed using the arcsine of the square root (Kirk

1995), and age was a covariate. Visible sky and age explained 55% of the variation in basal diameter and 53% of the variation in height (Jain et al. Appendix B), (Table 4, equations D1 and H1). Using this model and a step-wise approach, we identified interactions and individual scale contributions toward describing the variation in western white pine growth (Table 4). In some cases, the overall model was significant, but an individual spatial scale was not when observing the partial sum of squares (Table 4, equations D5, H5, R4). For example, this occurred when geological feature was added to weathering and visible sky to estimate basal diameter. The overall model was significant, but weathering and the interaction between weathering and geological feature were not significant in the partial sum of squares (Table 4, equation D5). Therefore, weathering was not considered in later analysis.

When both the overall model and main effects were significant, hypothesis testing was conducted by evaluating the predicted square errors from the full model (e.g., Table 4, D7) versus predicted square errors from the reduced model (e.g., Table 4, D6), (Dielman 1996). A significant F-statistic (Table 4, last column), residual error behavior (residual errors were checked for normality and independence) plus an increase in the R^2 (Table 4, column 1) indicated whether the addition of a spatial scale improved the relationship with western white pine growth. This iterative process was conducted until all relevant combinations of the spatial scales had been evaluated.

The interaction of landscape and site operational environments (Spomer 1973) determine if a western white pine can survive, have a competitive advantage, and be free to grow (Jain et al. Appendix B), (Fig. 3). The site environment (canopy opening size) interacts with landscape conditions (landtype and geological feature and weathering) to shape the environment in which a tree establishes and develops. To evaluate the relationship between the site and landscape environment we first related relative mean annual height increment to visible sky (Table 4, equation R1). We again used step-wise linear regression to determine which spatial scale along with visible sky significantly contributed toward describing the variation in relative mean annual height increment (Table 4, equations R1-R6). In the analysis, geological feature and landtype were significant. However, no significant T-tests occurred among landtypes; therefore, we used only geological feature (Table 4, equation R3). Using equation R1 (relative mean annual increment = visible sky) we determined the relative mean annual height increment at each visible sky threshold. For competitive advantage, we fixed the visible sky at 55% and solved the equation resulting in a relative mean annual height increment of 4.3 cm, and for free to grow we fixed the visible sky at 92%, resulting in a relative mean annual height increment of 7.3 cm. We used each of these values in the model containing geological feature (relative mean annual increment = visible sky + geology) and solved for visible sky (Fig. 3, Table 4, equation R3). For occupancy, we used the same step-wise approach using logistic regression rather than linear regression to determine if our spatial scales in addition to visible sky significantly predicted occupancy (Table 5, equations O1-O6). The equation was solved and provided a probability of occupancy as a function of weathering, geological feature, and visible sky.

Results

Sampling across spatial scales

A diverse set of weathering classes, landtypes, and geological features were sampled by Jain et al. (Appendix B), (Table 2). Within the weathering scale, weakly and moderately weathered classes had high sampling densities (620 plots). The highest sampling density occurred within the weakly weathered class (519 of 620) and was distributed across the three watersheds (Table 2). 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.

Within the Coeur d'Alene River Basin, the geological features were not related to topographic settings, were members of the metamorphic belt series, and contained similar rock types. Differences among geological features were subtle; only varying by weathering state, composition (quantities and type of rocks), and structure (layering). Some of the more distinguishable differences included whether they were unconsolidated (Qa, Qts) or consolidated (all others) (Table 2). Both Wallace formations (Ywml, Ywu) have layers of carbonate and contain diverse rock types, compositions, and structures. Monzonite (Kms), Burke (Ybk), lower member of Prichard (Ypl), Revett (Yr), and St. Regis (Ysr) formations all have a limited range of rock types except for the lower Prichard, which has the potential to create more acidic soils as it weathers. All of the geological features were sampled in Beaver Creek. Deception and Jordan Creek are more homogeneous. Each drainage only has two (Jordan) or three (Deception) geological features (Table 2). Deception Creek is much smaller

(1500 ha), which may contribute to the low number of geological features it contains. In contrast, Beaver Creek is 20,000 ha and has greater geological diversity (Fig. 2).

A diversity of landtypes occurred in all three watersheds (Table 2). Both northern and southern aspects included both non-dissected and dissected stream breaklands (477, 480, 483, 488). There were landtypes with diverse rock and soil particle sizes (cobbles to clay size) that are focal points for water and nutrients and contain soil substrates favoring root growth such as toeslopes (131), stream bottoms (130), alluvial and colluvial fans (133); southern aspects where one to three streams come together to form a basin (468); and northern aspects adjacent to stream drainages. Ridge tops on northern aspects in two weathering classes (490, 491) were also sampled; but since weathering did not differ significantly and weakly weathered northern aspect ridge tops (491) had a low sampling size (three), we combined these two landtypes. Excluding these two landtypes, sampling density ranged from nine plots on southern aspects with non-dissected stream breaklands (478) to as high as 92 plots for weakly weathered northern aspects (462), (Table 2).

We had a significant interaction between geological feature and landtype (Table 4, equations D6 and H6) when estimating basal diameter and height; Table 3 shows the sampling density of these combinations. The basal diameter estimates for five geological features were significantly different from the estimate for the St. Regis formation (Ysr). They were the Burke (Ybk), Revett (Yr), Striped Peak (Ysp), middle and lower Wallace (Ywml), and Upper Wallace (Ywu) formations. The height estimates for three geologies were significantly different from the estimate for the St. Regis formation (Ysr). They were the Burke (Ybk), Revett (Yr), and Upper Wallace (Ywu) formations. The Striped Peak (Ysp) and St. Regis (Ysr) formations were the most represented geological features and contained the majority of the landtypes (Table 3). The Striped Peak (Ysp) formation occurred in Jordan Creek while most of the observations of the St. Regis (Ysr) formation occurred in Deception Creek, with both of these geological features being represented in Beaver Creek (Table 2).

Linkages (interactions) among spatial scales

Clearly, multiple spatial scales can be linked to a site-specific response because there was a significant interaction among the spatial scales, which explained the variation in western white pine growth (Table 4, equations D6, D7, H6, and H7). For estimating western white pine basal diameter, the model explained 73% of the variation; and for estimating height, the model explained 70% of the variation (Table 4, equations D7, and H7). Although the relationships are complex (Tables 6 and 7) each spatial scale contributes toward understanding vegetation response. For estimating height, 13 landtypes were significant at $p \leq 0.10$ when compared to ridge tops on northern aspects (490). In contrast, for basal diameter estimates, only seven landtypes were significant when compared to ridge tops on northern aspects. However, for estimating basal diameter, the landtype spatial scale was no longer significant in the partial sum of squares when the interaction term was added to the model. This provides some evidence that the landtype spatial scale plays a stronger role in integrating biophysical factors that dictate height rather than basal diameter. In contrast, when estimating both variables, geological feature was always significant in the partial sum of squares.

When height and basal diameter were estimated, several interactions between geological feature and landtype were significant (Table 6 and 7). Some of these included the Revett (Yr) formation combined with southern aspects dissected with stream breaklands

(479), the upper Wallace (Yml) formation combined with southern aspects with toe slopes (468), and northern aspects with non-dissected stream breaklands (477). In addition, many interactions occurred within the St. Regis (Ysr) formation. The monzonites (Kms), alluvials (Qa), and old gravels (Qts) did not have any significant interactions. However, the sample size was rather small, which could explain the lack of interactions (Table 3).

Multiple spatial scales and silvicultural applications

We examined three western white pine thresholds: occupancy, competitive advantage, and free to grow (Jain et al. Appendix B), to see if using a multiple spatial scale approach could be potentially useful in silvicultural applications. There was a significant relationship between mean annual height increment and visible sky, landtype and geological feature when added to (Table 4). But for landtype, although the partial sum of squares was significant for landtype ($p \leq 0.03$), there were no significant T-values when compared to ridge tops on northern aspects (490). Therefore, we used only geological features to determine how relative mean annual height increment varied and how they may influence the competitive advantage and free to grow thresholds. Occupancy was related to visible sky, weathering, and geological features (Table 5, equation O5, Fig. 3a and 3b). However, when geology and landtype were combined, the overall model was significant, but landtype was not (Table 5, equation O4). Therefore, we used weathering and geological feature to illustrate how occupancy varies over a landscape (Fig. 3c).

Settings occurring on alluvials (Qa), old gravels (Qts), and the St Regis (Ysr) geological features must be fairly productive because western white pine is able to obtain a competitive advantage over western hemlock in relatively small canopy openings, with opening size ranging from 35% to 50% visible sky (Fig. 3a). In contrast, for western white pine to gain a competitive advantage, openings greater than 90% were required on the Revett (Yr), Burke (Ybk), Monzonites (Kms), and Striped Peak (Ysp) geological features. Also, to achieve free to grow on these geological features required opening sizes greater than 100% visible sky (Fig. 3b). According to Jain et al. (Appendix B), visible sky at 100% were greater than 0.7 ha.

Western white pine occupancy occurred on the Striped Peak (Ysp) formation in small openings, compared to sites on the Revett (Yr) formation and Monzonites (Kms). Jain et al. (Appendix B) hypothesized that occupancy may be a good indicator of seed source. Our results tend to verify this hypothesis. For example, in Jordan Creek, where most of the sampling occurred within the Striped Peak (Ysp) formation, two wildfires consumed a large portion of the seed and seed source in the 1930's. After these wildfires, the area was artificially regenerated with western white pine. Although many trees have died from blister rust (*Cronartium ribicola* J.C. Fisch.), there is still a substantial amount of western white pine seed and a limited amount of seed from other species. In contrast, the Revett (Yr) formation, which primarily occurs in Deception Creek and Beaver Creek, was at one time dominated by western white pine. Over time, western white pine abundance has decreased substantially because of blister rust, thus decreasing the available seed. Other species such as western hemlock and grand fir have increased in abundance and now dominate these watersheds. The difference in species composition between Jordan and the other two watersheds and their respective disturbance histories may be contributing to these results. Weathering was also related to occupancy. Slightly weathered soils had western white pine occupancy in openings smaller than those occurring on moderately weathered soils. We assume this occurred as a artifact of sampling. Because these soils were abundant, settings with large numbers of samples had a greater potential to support western white pine.

Discussion

Validation of hierarchical concepts

Weathering, geological features, landtypes, and canopy openings were an imperfect but effective hierarchy. 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 extents. In some cases, lower levels within our hierarchy had different weathering classes (Fig. 2). The levels were not perfectly nested, and landtypes were not unique to the geological features with 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 the response in vegetation (Spomer 1973; Jackson and Spomer 1979). Growth of western white pine seedlings and saplings were directly or indirectly influenced by our spatial hierarchy: 73% of the variation in western white pine basal diameter and 70% of the variation in height was explained by our spatial hierarchy (Table 4, equations D7 and H7).

We hypothesized that as we added progressively broader levels to our spatial hierarchy we would add explanatory power to the models, the broadest levels would explain less variation in growth than the finer levels. As we expected, visible sky had the highest R^2. However, landtype did not always explain the next greatest proportion of variation in growth. Landtype was significant when added to visible sky and age. But for estimating western white pine basal diameter, it only explained an additional 6% of the variation, and for estimating height it only explained an additional 4% of the variation (Table 4, equations D2 and H2). In contrast, an additional 9% of the variation in basal diameter and an additional 7% of the variation in height were explained by geological features (Table 4, equations D3 and H3). Therefore, the broader scale (geological features) explained more of the variation in growth than the finer scale (landtype).

Sampling density and spatial scale definition probably did not affect the hierarchy. Although, there were different sampling densities (two to five fold, Table 2) across the 19 landtypes, the standard error for height and diameter were similar for all landtypes discounting this problem. Some may argue that potential vegetation type is a more appropriate variable to use in spatial scale definition. Potential vegetation type is a classification system that partitions the physical environment identified through the use of indicator species (Pfister 1989; Fassnatcht and Gower 1998). Neither Ferguson et al. (1986) nor Jain et al. (Appendix B), were able to find a significant relationship between western white pine growth 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 growth, supporting the use of landtype rather than potential vegetation type to define our spatial scales. It is possible that we had too many landtypes, adding noise to western white pine growth 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, are grouping landtypes as a function of the biophysical factors operating at this broader spatial scale. A significant interaction between geological features and landtype explained an additional 16% of the variation in western white pine basal diameter and an additional 14% of the variation in height (Table 4, equations D6 and H6). This indicates that the variation in western white pine growth was better explained when landtypes were linked to a higher level within our spatial hierarchy. When Fassnatcht and Gower (1998) linked forest potential vegetation types to a broader spatial scale defined on soil nutrition and moisture, 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 verify the hierarchical concept that 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 multi-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). Jain et al. (Appendix B) concluded that canopy opening, as measured by percent visible sky, in addition to light, 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 growth was explained by this fine spatial scale. In Jain et al. (Appendix B), and in our study, 55% of the variation in basal diameter and 53% of the variation in height were explained by visible sky and age (Table 4, equations D1 and H1). For estimating mean annual height increment, 26% of the variation was explained by visible sky. Therefore, it appears that canopy opening, as defined by visible sky, does a good job of integrating the microsite environment that influences site specific responses.

Canopy opening does not, however, reflect differences in the operational environment constrained by geomorphology. An additional spatial scale was needed to account for this mid-scale variation. The results from this study showed that western white pine growth was 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, were derived from volcanic ash, and were located adjacent to streams. Landtype 467 was dominated by northern aspects and southern aspects prevailed in landtype 470. The 19 landtypes we used in this study integrated the mid-scale environment and were useful in predicting western white pine growth responses (0.06 R^2 improvement, Table 4).

Geological feature was intended to reflect geological and geomorphological characteristics that change slowly over time (Klijn 1994). We intended this spatial scale to also reflect soil nutrition, water holding capacity, below ground waterflow, 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. We found trees at 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, the location of these geological features also represent different moisture regimes (Fig. 1). Deception Creek averages 127 to 135 cm of precipitation annually and Beaver Creek 84 to 95 cm.

This was also verified by observing the weathering classes in this geologic formation. In Beaver Creek, all the observations on the St. Regis formation fell within the slightly weathered classification identified in our broadest scale. In Deception Creek, 45 of the 132 observations for the St. Regis formation were within the moderately weathered class. We did find a significant relationship with growth when only weathering was added to visible sky (Table 4, equations D4 and H4). Western white pines on moderately weathered soils grew better than pines growing on slightly weathered soils. As defined, moderately weathered soils have more clay, tend to be more nutritious, and hold more water (Brady 1974). This variation in climate subsequently influences soil development. Therefore, the significant relation between western white pine basal diameter and geological feature may not totally be related to geological feature. It also may be related to other environmental factors occurring at this spatial scale.

When the geological feature and landtype scales were included with weathering in predicting western white pine basal diameter and height, weathering was no longer significant (Table 4). There are a couple reasons why this occurred. We intended weathering to reflect weathering state, but geological feature also reflected this attribute (as was shown in previous example). Moreover, our data did not occur across all weathering classes. Jordan Creek only had weakly weathered soils. Two plots were sampled on moderately weathered soils in Beaver Creek, and both weakly and moderately weathered soils were relatively evenly distributed in Deception Creek. This variation in sampling density could be another reason why more of the variation in western white pine growth was not explained by weathering when the entire spatial hierarchy was used in the analysis.

Applying a spatial hierarchy

In this study, the spatial scales do not represent the classification system (e.g., landtype) or variable name (Striped Peak) alone, but they incorporate climate, soil formation, disturbance, and other biophysical factors that operate within each spatial scale. Hierarchies defined this way provide more insight into the processes and structures occurring in the scales than do hierarchies defined on geography (stand, subwatershed, watershed, river basin, region) or political boundaries (counties). Western white pine growth is dependent upon factors not represented in these other types of hierarchies since, their boundary delineation do not reflect biophysical factors (variation in climate, light, topographic position) within and across watersheds or counties that influence vegetation growth (Jackson and Spomer 1979; Crawley 1986; Pfister 1989; Aber and Mellilo 1991; Cooper et al. 1991). From this perspective inferences using a spatial hierarchy based on biophysical factors can be more robust because they directly or indirectly identify environments unique to a "place."

We were able to identify the indirect contribution each spatial scale made toward explaining the variation in western white pine growth. More importantly, we determined that linkages among spatial scales better described vegetation response then 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 added knowledge from our hierarchy could be used to design and apply silvicultural treatments across a landscape. For example, when we applied our spatial scales to the free to grow threshold (Fig. 3b). The free to grow threshold was achieved in small openings (approximately 0.3 ha) when they occurred on the St. Regis (Ysr) formation, Alluvials (Qa), and old gravels (Qts). In contrast, for western white pine to achieve free to grow on the Striped Peak formation, a canopy opening with 100% visible sky (0.7 ha) was required. Silvicultural treatments can now be adjusted to reflect the variation in biophysical factors represented by our spatial hierarchy thus linking site specific from silvicultural activities to the landscape.

The same example that showed how geological feature integrated mid-scale factors, also showed how our scales reflect "place." Western white pine (same age) growing in Deception Creek, on the St. Regis formation, had larger basal diameters than the pines growing on the St. Regis formation occurring in Beaver Creek (Ysr) (Fig. 6). Deception Creek receives more moisture and has better developed soils than Beaver Creek, resulting in taller and larger western white pines. Taking into account the spatial variation from this study, we would never assume that western white pines growing on the St. Regis formation in the St. Joe River Basin (adjoining 200,000 ha basin) would behave similarly as they did in the Deception Creek within the Coeur d'Alene River Basin. We extrapolate that the results are tied to the location where they occur, but this is inherent in all spatial hierarchies and not only to those defined on soil forming processes.

Limitations

As with all studies, this study has some limitations. Because the sampling densities varied among the categories within each spatial scale, we had an unbalanced experimental design, making this study 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. Therefore, we cannot infer cause and effect. There are several ways a hierarchy can be defined. We did not evaluate other spatial hierarchies that could have been defined using a different set of biophysical criteria (e.g., climate, disturbance), therefore, we cannot say our hierarchy was the most effective. Our choice was limited by available data and by our requirement to define our hierarchy on factors related to soil development. The explanatory power of the hierarchy is significant but not remarkable and although it is imperfect it nevertheless is 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 are limitations to our study, we were able to relate our landscape spatial scales to a site specific response. Moreover, the interactions among the spatial scales provides evidence that spatial scales are linked, thus multiple spatial scales describe vegetation response better than using a single scale.

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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	Resolution (cell size)	Data source
Site	620	$\leq$ 2 ha	1 m	Jain et al.[a]
Landtypes	19 to 45	$\leq$ 650 ha	30 m	IPNF[b]
Geological feature	3 to 15	$\leq$ 2,425 ha	30 m	USGS[c,d]
Weathering class	2 to 3	$\leq$ 14,029 ha	30 m	IPNF[b]

[a] Data sources: Site data supplied by Jain et al. (Appendix B).

[b]Weathering class and landtypes were provided by United States Department of Agriculture, Forest Service, Idaho Panhandle National Forests (IPNF).

[c] Geological features were supplied by the United States Geological Survey (USGS) with the classification based on individual geologic reports of study area and digital data (Coeur d'Alene Quadrangle 2000; Harrison and Jobin 1963; 1965; Hobbs et al. 1965; Hosterman 1956; Thompson Falls Quadrangle 1999; Wallace Quadrangle 1999.

[d] St. Maries Quadrangle [unpublished digital data], Derkey, P.D. Available: United States Geological Survey, Spokane, WA .

Table 2. Number of canopy opening plots provided by Jain et al. (Appendix B) occurring within each weathering, geological feature, and landtype class within each watershed.

	Spatial scale	Watershed: Deceptio n Creek	Watershed: Jordan Creek	Watershed: 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, & silt above modern stream channels	--	--	2	2
Ybk	Burke formation; metamorphosed mudrock siltite/quartzite	7	--	16	23
Ypl	Lower member of Prichard formation; siltitge/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; sillciclastics/argillite/carbonate rocks	–	–	54	54
Ywu	Wallace formation; siltite/argillite/doomitic siliciclastics	--	2	47	49

Table 2 continued. Number of canopy opening plots provided by Jain et al. (Appendix B) occurring within each weathering, geological feature, and landtype class within each watershed.

		Watershed			
	Spatial scale	Deception Creek	Jordan Creek	Beaver Creek	Total
	Landtype				
130	Stream bottoms and meadows	5	14	2	21
131	Toe slopes on benches above stream flood plains	12	15	--	27
133	Alluvial & 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 non-dissected stream breaklands	6	12	7	25
480	North aspects dissected stream breaklands	8	35	48	91
490	Norh aspect ridge tops - moderately weathered	--	50	6	56
491	North aspect ridge tops - weakly weathered	--	--	3	3
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 non-dissected stream breaklands with rock outcrops and shallow soils	--	2	7	9
483	South aspects non-dissected stream breaklands	6	9	19	34
488	South aspects dissected stream breaklands with rock outcrops and shallow soils	--	8	2	10
479	479 - South aspects dissected stream breaklands	27	--	9	36
468	Basins on south aspects	--	8	10	18

Table 3. Number of canopy opening plots occurring in the combinations of landtype and geological features. See Table 2 for an explanation of the geological features and landtypes.

	Geological feature										
Landtype	Kms	Qa	Qts	Ybk	Ypl	Yr	Ysp	**Ysr**	Ywml	Ywu	Total
130	–	2	--	--	--	--	14	5	--	--	19
131	--	7	--	--	--	--	8	12	--	--	20
133	--	6	--	--	--	--	8	2	--	2	12
462	--	--	--	1	--	7	--	38	--	--	46
466	1	--	2	4	11	--	38	17	13	6	78
477	--	--	--	--	--	--	12	6	4	3	25
480	4	--	--	--	--	4	37	10	14	22	87
490	--	--	--	--	--	2	48	--	6	--	56
467	--	--	--	--	2	8	12	21	--	--	41
464	--	--	--	--	--	17	--	4	--	--	21
470	--	--	--	8	2	2	8	10	7	--	35
446	--	--	--	2	--	26	--	2	--	--	30
465	--	--	--	--	--	1	--	--	--	--	1
478	--	--	--	--	--	2	2	--	--	5	9
483	--	--	--	6	--	4	9	2	9	9	39
488	--	--	--	--	--	--	8	2	--	--	10
479	--	--	--	10	1	5	--	16	4	--	35
468	--	--	--	8	--	--	6	--	2	2	18
Total	--	--	--	39	--	78	210	144	59	47	582

Table 4. Evaluation of spatial scales in explaining variation in western white pine growth (basal diameter, height, relative mean annual height increment) in different canopy openings (as defined by visible sky) using the full versus reduced model hypothesis testing. (R^2 and P-value belong to model. F-value is result of full versus reduced model hypothesis test.)

Eq. No.	Model	Adj. R^2	P-value	Full Model[a] SSE	Full Model[a] DF	Reduced[a] Model SSE	Reduced[a] Model DF	F^b
				Ln basal diameter				
D1	Visible sky + age (N = 613)	0.55	0.0001	138.1	611	--	--	--
D2	**Visible sky + age** + landtype[a]	0.61	0.0001	120.5	594	138.1	611	5.1*
D3	**Visible sky + age** + geological feature (geo. feat.)	0.64	0.0001	112.5	602	138.1	611	15.2*
D4	**Visible sky + age** + weathering	0.57	0.0001	131.5	610	138.1	611	30.6*
D5	Visible sky + age + weathering + geo. feat. + (weathering x geo. feat.)	0.64	0.0001	--	--	--	--	--
D6a	**Visible sky + age** + geo. feat. + landtype + (geo. feat. x landtype)	0.71	0.0001	89.3	541	138.1	611	4.2*
D6b	**Visible sky + age + geo. feat.** + landtype + (geo. feat. x landtype)	0.71	0.0001	89.3	541	112.5	602	2.3*
D6c	**Visible sky + age + landtype** + geo. feat. + (geo. feat. x landtype)	0.71	0.0001	89.3	541	120.5	594	3.6*
D7	**Visible sky + age + geo. feat.+ landtype** + (**geo. feat. x landtype** x visible sky)	0.73	0.0001	83.2	516	89.3	541	2.9*
				Ln height				
H1	Visible sky + age (N = 618)	0.53	0.0001	112.8	616			
H2	**Visible sky + age** + landtype	0.59	0.0001	98.9	599	112.8	616	4.9*
H3	**Visible sky + age** + geo. feat.	0.60	0.0001	95.7	607	112.8	616	12.0*
H4	**Visible sky + age** + weathering	0.55	0.0001	108.8	615	112.8	616	22.6*
H5	Visible sky + age + weathering + geo. feat. + (weathering x geo. feat.)	0.60	0.0001	--	--	--	--	--
H6a	**Visible sky + age** + geo. feat. + landtype + (geo. feat. x landtype)	0.67	0.0001	79.2	546	112.8	616	3.3*
H6b	**Visible sky + age + geo. feat.** + landtype + (geo. feat. x landtype)	0.67	0.0001	79.2	546	95.7	607	1.9*
H6c	**Visible sky + age + landtype** + geo. feat. + (geo. feat. x landtype)	0.67	0.0001	79.2	546	98.9	599	2.6*
H7	**Visible sky +age+ geo. feat. + landtype** + (**geo. feat. x landtype** x visible sky)	0.70	0.0001	98.9	599	72.2	521	2.5*

Table 4 continued. Evaluation of spatial scales in explaining variation in western white pine growth (basal diameter, height, relative mean annual height increment) and occupancy in different canopy openings (as defined by visible sky) using the full versus reduced model hypothesis testing.

	Model			Full model[1]		Reduced model[1]		
Eq. No.		R^2	P-value	SSE	DF	SSE	DF	F[2]
				Relative mean annual height increment[c]				
R1	Visible sky (N = 142)	0.26	0.0001	4140	141			--
R2	**Visible sky** + landtype[1]	0.39	0.0001	3382	126	4140	141	1.9*
R3	**Visible sky** + geo. feat.	0.41	0.0001	3289	132	4140	141	3.8*
R4	**Visible sky** + weathering	0.26	0.0001	--	--	--	--	--
R5	Visible sky + weathering + geo. feat. + (weathering x geo. feat.)	0.41	0.0001	--	--	--	--	--
R6	Visible sky + geo. feat. + landtype + (geo. feat. x landtype)	0.54	0.0001	--	--	--	--	--

[a] Variables in bold are included in the reduced model and all variables are included in the full model.

[b] The F statistic tests the variable addition from the reduced to the full model with * indicating significance ($p \leq .05$).

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

Table 5. Evaluation of spatial scales in explaining variation occupancy in different canopy openings (as defined by visible sky) using logistic regression. Occupancy of a site occurs when three or more western white pines occupy a 60 cm radius microplot.

		Occupancy				
		Likelihood Ratio - Chi-Square Statistic				
Eq. No.	Model	Model P-Value	Canopy Opening	Second Variable	Third Variable	Fourth Variable
O1	Visible sky	0.0005	0.006			
O2	Visible sky + weathering	0.0001	0.006	0.0003		
O3	Visible sky + geological feature (geo. feat.)	0.0001	0.008	0.006		
O4	Visible sky + landtype	0.0001	0.005	0.140		
O5	Visible sky + weathering + geo. feat.	0.0001	0.010	0.003	0.05	
O6	Visible sky + geo. feat. + weathering + geo. feat. * weathering	0.0001	0.010	0.020	0.06	0.20
O6	Visible sky + geo. feat. + landtype	0.0001	0.010	0.820	0.56	

Table 6. The interaction among canopy opening (CO) (as defined by visible sky), geological feature, and landtypes for estimating the ln of basal diameter (cm) of western white pine seedlings and saplings. For geological feature and landtype definitions refer to Table 2.

Parameter	Est.	Std. Err.	t value	Pr > |t|	Parameter	Est.	Std. Err.	t value	Pr>|t|	Parameter	Est.	Std. Err.	t value	Pr>|t|
Intercept	**-1.88**	**0.32**	**-5.79**	**<.0001**	CO * Qa * 133	0.75	0.64	1.17	0.24	**CO * Ysp * 483**	**1.03**	**0.58**	**1.80**	**0.07**
Canopy opening	**0.77**	**0.45**	**1.72**	**0.09**	CO * Qts * 466	11.53	8.22	1.40	0.16	CO * Ysp * 488	0.53	0.33	1.59	0.11
Kms	-1.39	1.44	-0.96	0.34	CO * Qts * 446	0.41	0.63	0.65	0.52	**CO * Ysp * 490**	**1.47**	**0.53**	**2.78**	**0.01**
Qa	-0.49	0.45	-1.08	0.28	CO * Qts * 462	-0.43	0.59	-0.73	0.47	CO * Ywml * 466	0.83	0.65	1.28	0.20
Qts	-11.39	8.71	-1.31	0.19	CO * Qts * 466	-0.14	0.57	-0.24	0.81	CO * Ywml * 468	1.05	1.00	1.05	0.29
Ybk	**0.70**	**0.35**	**1.98**	**0.05**	CO * Qts * 468	0.15	0.63	0.25	0.81	CO * Ywml * 470	0.68	0.56	1.22	0.22
Ypl	-0.51	0.68	-0.75	0.46	CO * Ybk * 470	-0.29	0.63	-0.45	0.65	CO * Ywml * 477	1.06	0.87	1.22	0.22
Yr	0.12	0.30	0.39	0.70	CO * Ybk * 479	0.10	0.57	0.18	0.86	CO * Ywml * 479	0.90	0.62	1.45	0.15
Ysp	**-0.51**	**0.21**	**-2.39**	**0.02**	CO * Ybk * 483	-0.56	0.62	-0.90	0.37	CO * Ywml * 480	-0.04	0.58	-0.07	0.94
Ywml	-0.54	0.34	-1.58	0.11	CO * Ypl * 466	0.74	0.66	1.13	0.26	**CO * Ywml * 483**	**1.00**	**0.61**	**1.65**	**0.10**
Ywu	**-0.69**	**0.42**	**-1.64**	**0.10**	CO * Ypl * 467	0.99	0.71	1.38	0.17	**CO * Ywml * 490**	**1.70**	**0.65**	**2.64**	**0.01**
Ysr	0.00	--	--	--	CO * Ypl * 470	0.86	0.71	1.20	0.23	CO * Ywu * 133	0.87	0.92	0.94	0.35
130	**1.22**	**0.42**	**2.90**	**0.004**	CO * Ypl * 479	1.35	1.22	1.10	0.27	CO * Ywu * 466	1.02	0.73	1.39	0.16
131	**0.81**	**0.41**	**1.99**	**0.05**	CO * Yr * 446	0.82	0.52	1.58	0.11	**CO * Ywu * 468**	**1.25**	**0.64**	**1.96**	**0.05**
133	**1.13**	**0.61**	**1.85**	**0.07**	CO * Yr * 462	0.22	0.55	0.40	0.69	**CO * Ywu * 477**	**1.69**	**0.81**	**2.08**	**0.04**
446	0.12	0.46	0.27	0.79	CO * Yr * 464	0.73	0.60	1.21	0.23	CO * Ywu * 478	-0.46	0.83	-0.56	0.58
462	**0.83**	**0.38**	**2.20**	**0.03**	CO * Yr * 465	0.93	1.03	0.90	0.37	CO * Ywu * 480	0.52	0.63	0.82	0.41
464	0.39	0.53	0.73	0.46	CO * Yr * 467	0.51	0.58	0.89	0.38	CO * Ywu * 483	0.85	0.86	0.99	0.32
465	0.24	0.56	0.43	0.67	CO * Yr * 470	0.12	0.56	0.21	0.83	CO * Ysr * 130	-0.10	0.56	-0.18	0.85
466	0.37	0.35	1.07	0.29	CO * Yr * 478	-1.37	1.03	-1.33	0.18	CO * Ysr * 131	0.52	0.52	1.01	0.31
467	0.29	0.37	0.78	0.44	**CO * Yr * 479**	**1.22**	**0.66**	**1.84**	**0.07**	CO * Ysr * 133	0.11	0.99	0.11	0.91
468	0.45	0.53	0.85	0.39	CO * Yr * 480	-0.33	0.61	-0.55	0.58	CO * Ysr * 446	0.80	0.81	0.99	0.32
470	0.55	0.40	1.38	0.17	CO * Yr * 483	0.53	0.71	0.74	0.46	CO * Ysr * 462	0.60	0.49	1.21	0.23
477	0.44	0.46	0.96	0.34	CO * Yr * 490	0.59	0.56	1.05	0.29	CO * Ysr * 464	0.21	0.92	0.23	0.82
478	1.76	0.79	2.24	0.03	CO * Ysp * 130	-0.04	0.64	-0.07	0.95	CO * Ysr * 465	0.00	--	--	--
479	0.22	0.41	0.53	0.60	CO * Ysp * 131	0.38	0.58	0.65	0.52	**CO * Ysr * 466**	**0.95**	**0.48**	**2.01**	**0.05**
480	**1.00**	**0.32**	**3.10**	**0.002**	CO * Ysp * 133	-0.22	0.91	-0.24	0.81	**CO * Ysr * 467**	**1.18**	**0.52**	**2.28**	**0.02**
483	0.57	0.42	1.35	0.18	CO * Ysp * 466	0.86	0.55	1.57	0.12	CO * Ysr * 470	0.43	0.51	0.85	0.40
488	**1.16**	**0.51**	**2.30**	**0.02**	**CO * Ysp * 467**	**1.01**	**0.55**	**1.84**	**0.07**	**CO * Ysr * 477**	**0.92**	**0.55**	**1.68**	**0.09**
490	0.00	--	--	--	CO * Ysp * 468	0.83	0.72	1.16	0.25	**CO * Ysr * 479**	**1.06**	**0.55**	**1.92**	**0.06**
CO * Kms * 466	0.32	1.06	0.30	0.77	CO * Ysp * 470	0.55	0.59	0.93	0.35	CO * Ysr * 480	-0.20	0.47	-0.44	0.66
CO * Kms * 480	1.39	1.89	0.73	0.46	CO * Ysp * 477	0.83	0.61	1.36	0.17	**CO * Ysr * 483**	**1.14**	**0.65**	**1.76**	**0.08**
CO * Qa * 130	0.49	0.67	0.73	0.46	CO * Ysp * 478	-0.22	0.97	-0.23	0.82	CO * Ysr * 488	0.00	--	--	--
CO * Qa * 131	0.52	0.64	0.81	0.42	CO * Ysp * 480	0.28	0.50	0.56	0.58	**age**	**0.07**	**0**	**21.75**	**<.0001**

Table 7. The interaction among canopy opening (CO)(as defined by visible sky), geological feature, and landtypes for estimating the ln of height (cm) of western white pine seedlings and saplings. For geological feature and landtpe definitions refer to Table 2.

Parameter	Est.	Std. Err.	t value	Pr > |t|	Parameter	Est.	Std. Err.	t value	Pr>|t|	Parameter	Est.	Std. Err.	t value	Pr>|t|
Intercept	**2.29**	**0.30**	**7.73**	**<.0001**	CO * Qa * 133	0.16	0.59	0.27	0.79	CO * Ysp * 483	0.59	0.53	1.10	0.27
Canopy opening	**0.30**	**0.42**	**0.71**	**0.48**	CO * Qts * 466	10.18	7.62	1.34	0.18	CO * Ysp * 488	0.30	0.31	0.96	0.34
Kms	-1.04	1.34	-0.78	0.44	CO * Qts * 446	0.43	0.59	0.74	0.46	**CO * Ysp * 490**	**1.61**	**0.48**	**3.32**	**0.001**
Qa	0.24	0.42	0.58	0.56	CO * Qts * 462	0.20	0.55	0.36	0.72	CO * Ywml * 466	0.88	0.61	1.45	0.15
Qts	-9.80	8.07	-1.21	0.23	CO * Qts * 466	0.07	0.52	0.14	0.89	CO * Ywml * 468	1.24	0.86	1.45	0.15
Ybk	0.31	0.33	0.95	0.34	CO * Qts * 468	0.76	0.58	1.31	0.19	CO * Ywml * 470	0.64	0.52	1.23	0.22
Ypl	0.22	0.63	0.35	0.73	CO * Ybk * 470	0.09	0.59	0.16	0.88	CO * Ywml * 477	0.94	0.80	1.17	0.24
Yr	0.01	0.28	0.04	0.97	CO * Ybk * 479	0.39	0.52	0.75	0.46	CO * Ywml * 479	0.86	0.57	1.51	0.13
Ysp	**-0.37**	**0.20**	**-1.85**	**0.06**	CO * Ybk * 483	-0.57	0.57	-0.99	0.32	CO * Ywml * 480	-0.02	0.54	-0.03	0.97
Ywml	**-0.54**	**0.32**	**-1.71**	**0.09**	CO * Ypl * 466	0.28	0.61	0.47	0.64	CO * Ywml * 483	0.74	0.56	1.31	0.19
Ywu	**-0.70**	**0.39**	**-1.81**	**0.07**	CO * Ypl * 467	0.61	0.66	0.93	0.35	**CO * Ywml * 490**	**2.10**	**0.60**	**3.53**	**0.001**
Ysr	0.00	--	--	--	CO * Ypl * 470	0.16	0.66	0.24	0.81	CO * Ywu * 133	1.12	0.85	1.31	0.19
130	1.26	0.39	3.28	0.001	CO * Ypl * 479	0.45	1.13	0.39	0.69	**CO * Ywu * 466**	**1.17**	**0.68**	**1.72**	**0.09**
131	**0.90**	**0.37**	**2.41**	**0.02**	CO * Yr * 446	0.49	0.48	1.03	0.30	**CO * Ywu * 468**	**1.28**	**0.59**	**2.16**	**0.03**
133	**1.35**	**0.57**	**2.39**	**0.02**	CO * Yr * 462	0.46	0.51	0.89	0.37	**CO * Ywu * 477**	**1.78**	**0.75**	**2.37**	**0.02**
446	**0.79**	**0.42**	**1.85**	**0.06**	CO * Yr * 464	0.54	0.53	1.02	0.31	CO * Ywu * 478	-0.51	0.77	-0.67	0.50
462	**0.83**	**0.34**	**2.40**	**0.02**	CO * Yr * 465	0.49	0.96	0.51	0.61	CO * Ywu * 480	0.61	0.58	1.05	0.29
464	**0.85**	**0.47**	**1.80**	**0.07**	CO * Yr * 467	0.65	0.54	1.22	0.22	CO * Ywu * 483	0.57	0.79	0.72	0.47
465	0.76	0.52	1.48	0.14	CO * Yr * 470	0.19	0.52	0.36	0.72	CO * Ysr * 130	0.14	0.52	0.27	0.79
466	**0.59**	**0.32**	**1.87**	**0.06**	CO * Yr * 478	-1.18	0.95	-1.24	0.22	CO * Ysr * 131	0.71	0.48	1.47	0.14
467	**0.63**	**0.34**	**1.86**	**0.06**	CO * Yr * 479	1.16	0.61	1.89	0.06	CO * Ysr * 133	-0.06	0.92	-0.06	0.95
468	0.32	0.49	0.65	0.51	CO * Yr * 480	-0.20	0.56	-0.36	0.72	CO * Ysr * 446	0.12	0.75	0.16	0.87
470	**0.91**	**0.37**	**2.48**	**0.01**	CO * Yr * 483	0.17	0.66	0.26	0.79	**CO * Ysr * 462**	**0.83**	**0.46**	**1.83**	**0.07**
477	**0.52**	**0.42**	**1.25**	**0.21**	CO * Yr * 490	0.79	0.52	1.54	0.13	CO * Ysr * 464	-0.00	0.82	0.00	1.00
478	**2.09**	**0.73**	**2.87**	**0.004**	CO * Ysp * 130	0.20	0.60	0.33	0.74	CO * Ysr * 465	0.00	--	--	--
479	0.45	0.38	1.19	0.23	CO * Ysp * 131	0.56	0.54	1.03	0.31	**CO * Ysr * 466**	**0.86**	**0.44**	**1.95**	**0.05**
480	**1.31**	**0.29**	**4.46**	**<.0001**	CO * Ysp * 133	0.02	0.84	0.02	0.98	**CO * Ysr * 467**	**1.06**	**0.48**	**2.21**	**0.03**
483	**1.18**	**0.39**	**3.04**	**0.002**	**CO * Ysp * 466**	**0.82**	**0.51**	**1.62**	**0.10**	CO * Ysr * 470	0.37	0.47	0.78	0.44
488	**1.61**	**0.47**	**3.45**	**0.001**	CO * Ysp * 467	0.82	0.51	1.61	0.11	**CO * Ysr * 477**	**0.94**	**0.51**	**1.86**	**0.06**
490	0.00	--	--	--	CO * Ysp * 468	1.04	0.67	1.57	0.12	**CO * Ysr * 479**	**0.96**	**0.51**	**1.87**	**0.06**
CO * Kms * 466	0.73	0.98	0.74	0.46	CO * Ysp * 470	0.42	0.54	0.76	0.44	CO * Ysr * 480	-0.23	0.43	-0.52	0.60
CO * Kms * 480	0.91	1.76	0.52	0.61	**CO * Ysp * 477**	**0.98**	**0.57**	**1.72**	**0.09**	CO * Ysr * 483	0.62	0.60	1.04	0.30
CO * Qa * 130	0.12	0.62	0.19	0.85	CO * Ysp * 478	-0.47	0.89	-0.53	0.60	CO * Ysr * 488	0.00	--	--	--
CO * Qa * 131	0.10	0.60	0.16	0.87	CO * Ysp * 480	0.15	0.46	0.33	0.74	**Age**	**0.07**	**0.00**	**23.01**	**<.0001**

Figure Captions

Fig. 1. The Coeur d'Alene River Basin in northern Idaho. Jain et. al. (submitted) conducted a study relating the growth of western white pine (*Pinus monticola*) to different sized openings in the Deception Creek, Jordan Creek, and Beaver Creek Drainages.

Fig. 2. Diversity of weathering geological feature, and landtype for each sampled watershed (Beaver Creek, Deception Creek, Jordan Creek).

Fig. 3. The relation between visible sky and geological features for the three thresholds Jain et al. (submitted) identified. Competitive advantage is when relative mean annual height increment between western white pine and western hemlock is positive. Free to grow is when relative mean annual height increment between western white pine and western hemlock no longer increases. Occupancy is when three or more western white pine are established and occur on a 60 cm circular plot. Significant p-values for t-test is shown in relation to the St. Regis formation (Ysr) for competitive advantage and free to grow. Definitions for other geological features are located in Table 2.

Fig. 4. The relationship between basal diameter of 10-year-old western white pine and size of canopy opening (as defined by visible sky) varies with landtype and geological feature (Table 4, equation D6). Landtype 467 (north aspects adjacent to streams) and landtpe 470 (south aspects) are shown within the St. Regis (Ysr) formation.

Fig. 5. The difference between locations within a geological formation. The equation: ln(basal diameter) = visible sky + age, + location (Beaver and Deception) using only plots occurring on the St. Regis formation (Ysr).

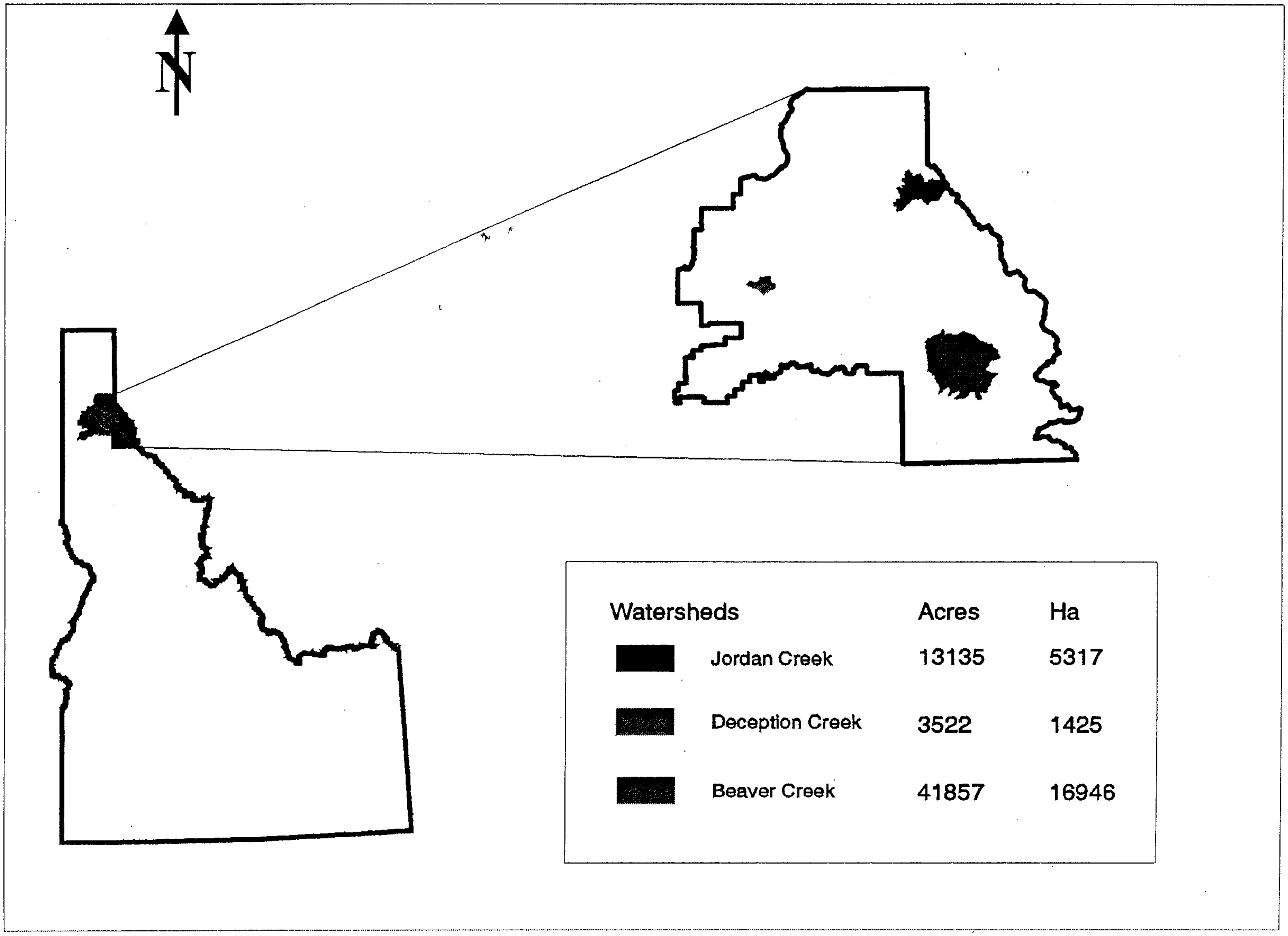

N
Watersheds
Acres
Ha
Jordan Creek
13135
5317
Deception Creek
3522
1425
Beaver Creek
41857
16946

Fig. 1

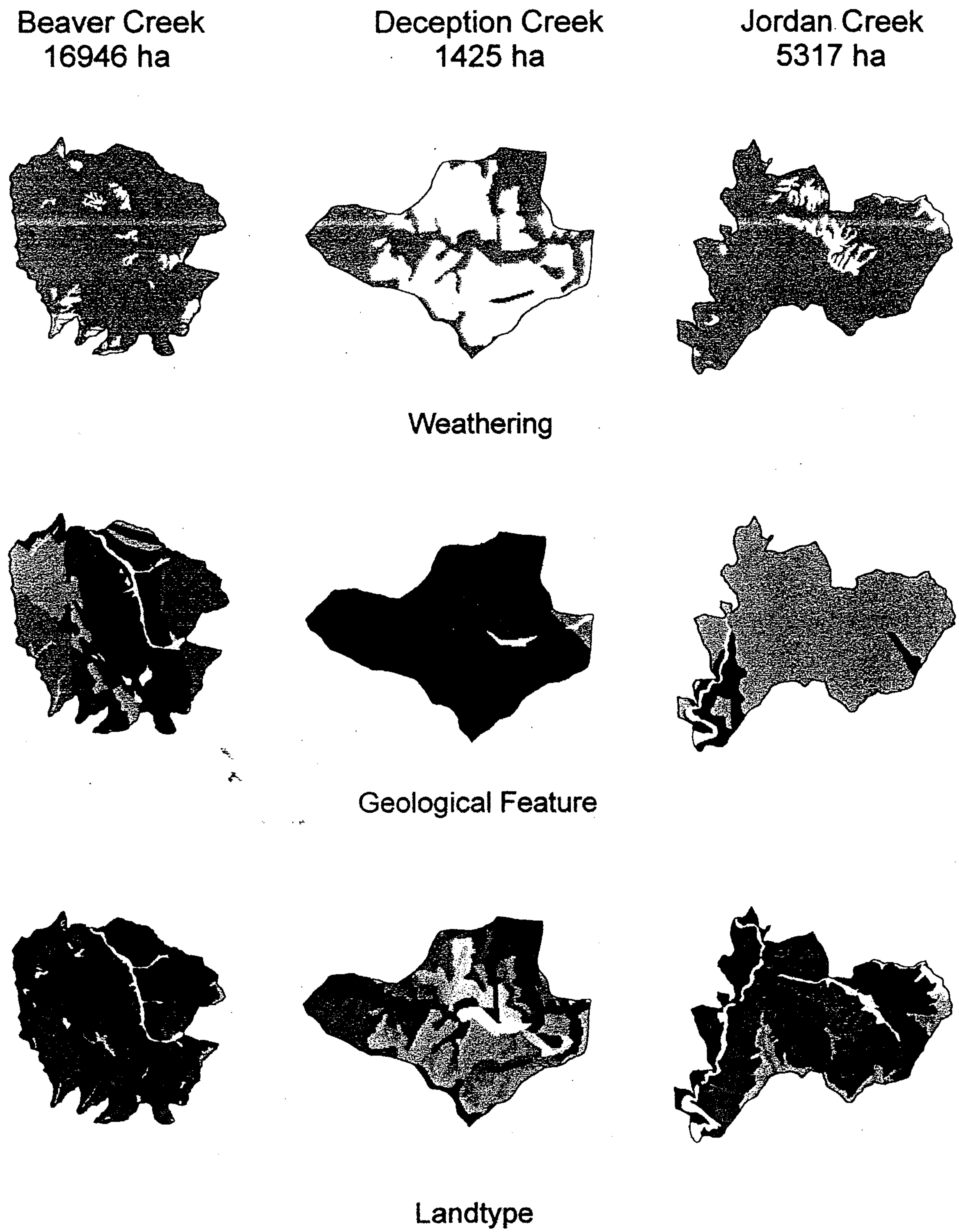
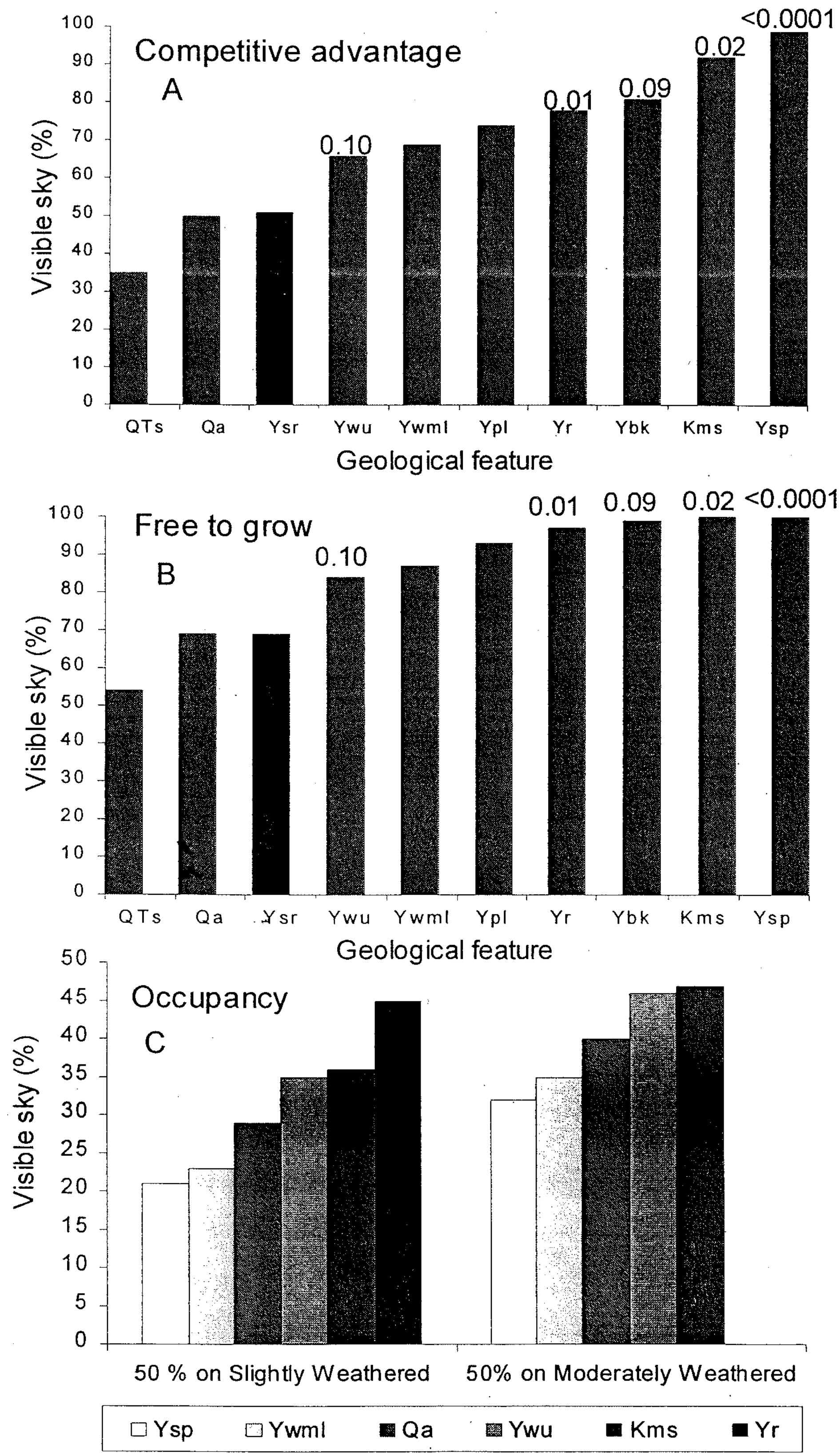
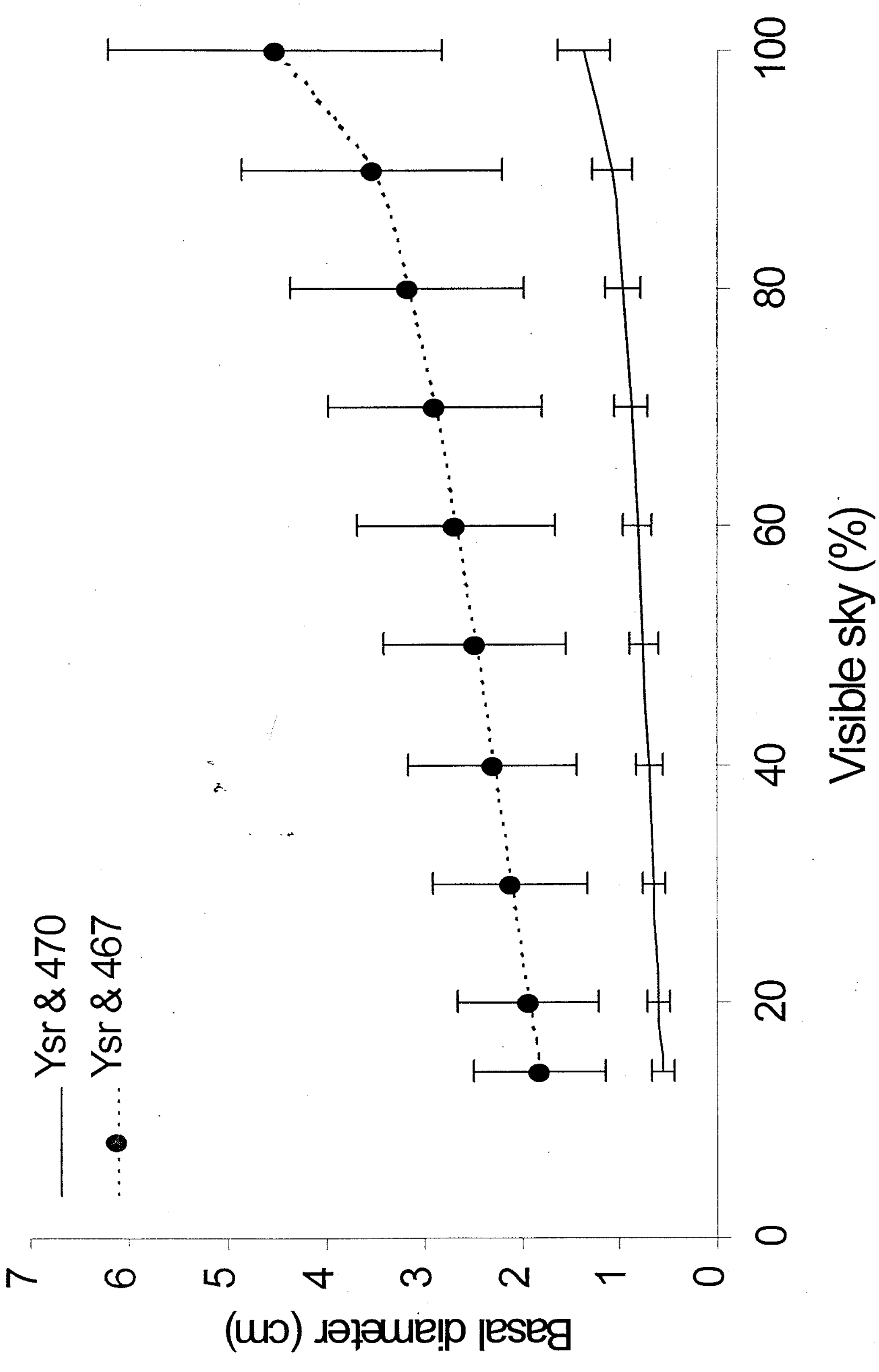

Beaver Creek
16946 ha
Deception Creek
1425 ha
Jordan Creek
5317 ha
Weathering
Geological Feature
Landtype

Fig. 2



Competitive advantage
A
Visible sky (%)
0.10
0.01
0.09
0.02
<0.0001
QTs Qa Ysr Ywu Ywml Ypl Yr Ybk Kms Ysp
Geological feature
Free to grow
B
Visible sky (%)
0.10
0.01 0.09 0.02 <0.0001
QTs Qa Ysr Ywu Ywml Ypl Yr Ybk Kms Ysp
Geological feature
Occupancy
C
Visible sky (%)
50 % on Slightly Weathered
50% on Moderately Weathered
Ysp Ywml Qa Ywu Kms Yr

Fig. 3



Ysr & 470
Ysr & 467
Basal diameter (cm)
Visible sky (%)
0
1
2
3
4
5
6
7
0
20
40
60
80
100

Fig. 4

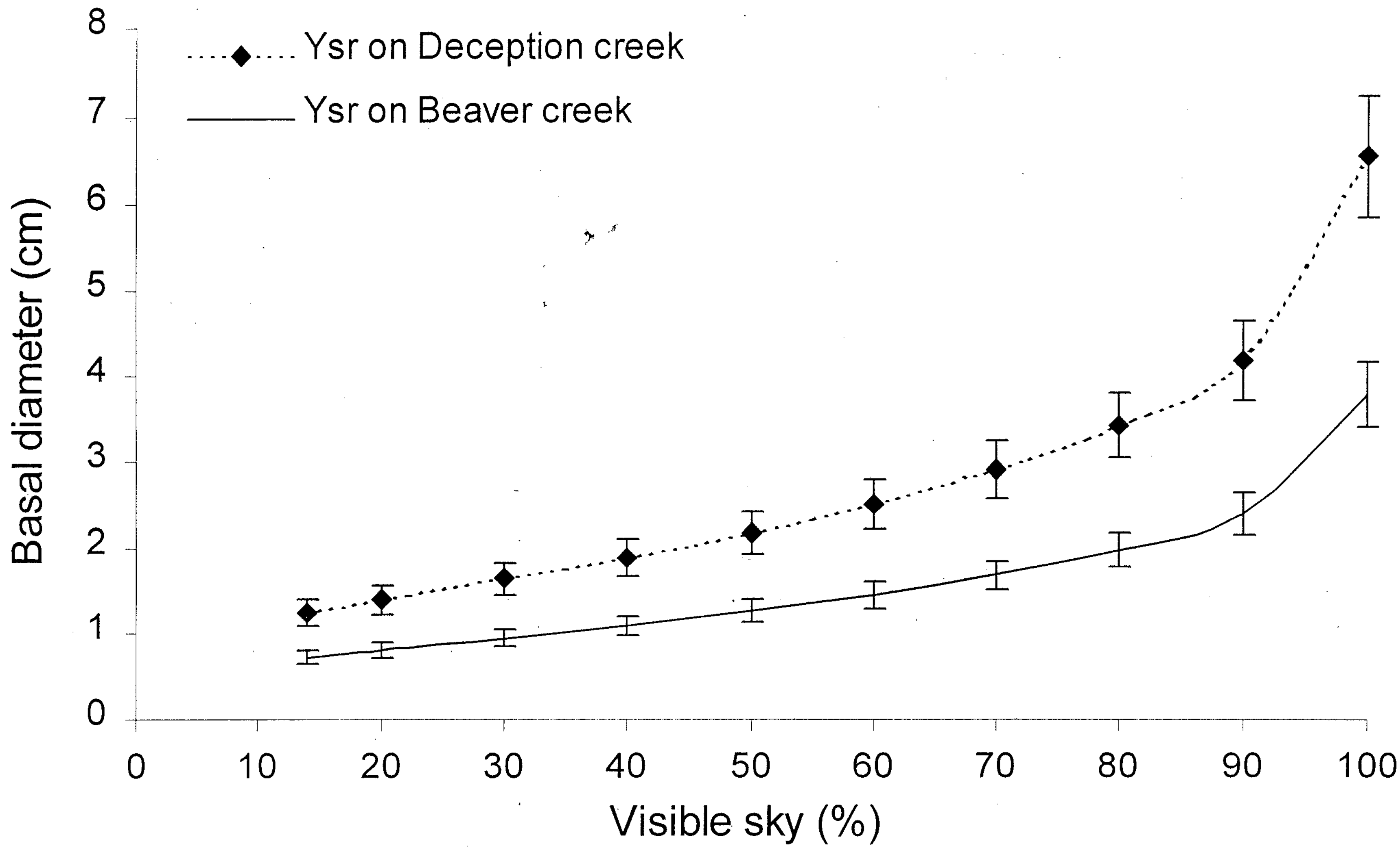

Ysr on Deception creek
Ysr on Beaver creek
Basal diameter (cm)
0
1
2
3
4
5
6
7
8
Visible sky (%)
0
10
20
30
40
50
60
70
80
90
100

Fig. 5