Modeling landscape patterns of understory tree regeneration in the Pacific Northwest, USA

Wimberly, Michael C.[1,2*] & Spies, Thomas A.[3]

[1]*Department of Forest Science, Oregon State University, Corvallis OR 97331, USA;* [2]*Current Address: University of Georgia, Warnell School of Forest Resources, Athens, GA 30602-2152, USA;* [3]*USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA;*
*Corresponding Author; E-mail wimberly@smokey.forestry.uga.edu

Abstract. Vegetation maps serve as the basis for spatial analysis of forest ecosystems and provide initial information for simulations of forest landscape change. Because of the limitations of current remote sensing technology, it is not possible to directly measure forest understory attributes across large spatial extents. Instead we used a predictive vegetation mapping approach to model *Tsuga heterophylla* and *Picea sitchensis* seedling patterns in a 3900-ha landscape in the Oregon Coast Range, USA, as a function of Landsat TM imagery, aerial photographs, digital elevation models, and stream maps. Because the models explained only moderate amounts of variability (R^2 values of 0.24 - 0.56), we interpreted the predicted patterns as qualitative spatial trends rather than precise maps.

   P. sitchensis seedling patterns were tightly linked to the riparian network, with highest densities in coastal riparian areas. *T. heterophylla* seedlings exhibited complex patterns related to topography and overstory forest cover, and were also spatially clustered around patches of old-growth forest. We hypothesize that the old growth served as refugia for this fire-sensitive species following wildfires in the late 19th and early 20th centuries. Low levels of *T. heterophylla* regeneration in hardwood-dominated forests suggest that these patches may succeed to shrublands rather than to conifer forest.

   Predictive models of seedling patterns could be developed for other landscapes where georeferenced inventory plots, remote sensing data, digital elevation models, and climate maps are available.

Keywords: Disturbance; Environmental gradient; *Picea sitchensis*; Predictive vegetation mapping; Remote sensing; Seed-source limitation; Spatial model; Tree seedling; *Tsuga heterophylla*.

Introduction

Forest vegetation maps are used to assess landscape pattern changes resulting from human land use (Mladenoff et al. 1993; Spies et al. 1994), analyse wildlife responses to landscape patterns (McGarigal & McComb 1995; Ripple et al. 1997), and initialize spatial simulations of forest landscape change (He & Mladenoff 1999). Maps of forest cover are typically derived from either aerial photographs or satellite images and classify forest patches by community type (Wolter et al. 1995) or successional stage (Cohen et al. 1995). Although emerging remote sensing technologies such as lidar (light detection and ranging) hold promise for mapping multiple canopy layers (Lefsky et al. 1999), it is not yet possible to directly measure most forest understory attributes across large spatial extents. Mapping forests based on overstory characteristics is sufficient for many applications, but information about specific understory attributes such as subcanopy trees, dead wood, and tree regeneration is often necessary for making ecological assessments and initializing landscape models (Moeur & Stage 1995; He et al. 1998). Thus, alternative approaches to mapping forest understory characteristics are needed.

A lack of knowledge about understory tree regeneration patterns, which influence rates and pathways of forest succession, currently limits our ability to predict landscape dynamics in coastal forests of the Pacific Northwest, USA. Such forest dynamics are complex. Overstory canopy gaps are created in young *Pseudotsuga menzeisii* (Douglas-fir) and *Alnus rubra* (red alder) stands by suppression mortality or by disturbances such as wind, disease, or insects (Spies et al. 1990; Taylor 1990). Gaps are gradually filled in by the establishment of conifers such as *Tsuga heterophylla* (western hemlock) and *Picea sitchensis* (Sitka spruce), or by the release of understory saplings that were present prior to the disturbance. The presence of multiple gaps in a range of sizes and developmental stages leads to the development of a multilayered canopy that is a distinctive structural characteristic of Pacific Northwest old-growth forests (Franklin & Spies 1991) and an important component of *Strix occidentalis* (Northern spotted owl) habitat (Mills et al. 1993). In stands where tree regeneration is sparse or absent in the forest understory, competition from shrubs may limit seedling establishment in canopy gaps

(Tappeiner et al. 1991) and multilayered structure will develop slowly if at all.

Previous research has shown that understory conifer regeneration has a patchy distribution throughout much of the Coast Range of Oregon, USA (Schrader 1998). Knowing the spatial pattern of tree regeneration across the landscape would enhance our ability to identify areas where development of late-successional forest structure might be limited by the absence of shade-tolerant tree regeneration. This spatial information is currently unavailable at the landscape scale because measurements of understory vegetation are taken in small, dispersed field plots. If plot data can be associated with variables for which spatial data are available, it may be possible to use these spatial variables to interpolate between the isolated plots – the 'predictive vegetation mapping' approach outlined by Franklin (1995). Although this method has been used successfully to map individual species (Sperduto & Congalton 1996; Iverson et al. 1997; Guisan et al. 1998) and plant communities (Frank 1988; Davis & Goetz 1990; Lees & Ritman 1991; Brown 1994) in a number of ecosystems, it has not been widely applied to predicting patterns of regeneration in the forest understory (but see Baker & Weisberg 1997).

Physiographic variables can be used to map regeneration patterns along environmental gradients. Digital elevation models can be used to derive estimates of soil moisture (Beven & Kirby 1979) and solar radiation (Bonan 1989; Nikolov & Zeller 1992), as well as slope, aspect, and other topographic indices. Overstory trees can utilize large portions of available light and moisture, thereby limiting resource availability in the understory (Christy 1986). Consequently, the abundance of understory seedlings and saplings is often sensitive to variation in overstory cover (Collins & Good 1987; Russell-Smith 1996; Schrader 1998) and can be particularly high in canopy gaps (Gray & Spies 1996). Maps of tree crown size, canopy cover, and stand age provide some information about conditions in the forest understory and can be derived from Landsat satellite images (Cohen et al. 1995). It may be also possible to use landscape attributes as indicators of potential seed source areas. In landscapes of mixed forest age classes, for example, old-growth patches represent areas that have either escaped past fires or burned at lower severity than the rest of the landscape. If these patches can be identified using aerial photographs or satellite imagery, they may serve as indicators of refugia for disturbance-sensitive species (Camp et al. 1997).

Our main objective was to assess the potential for developing predictive maps of understory tree regeneration in forests of the Pacific Northwest, USA, through a case study of tree seedling patterns in a coastal Oregon landscape. We developed statistical models of the presence and density of *T. heterophylla* and *P. sitchensis* seedlings in an Oregon Coast Range landscape using predictor variables available in a geographic information system (GIS), and used these models to map seedling patterns. To gain a better understanding of the proximal factors influencing tree regeneration, we also examined the relationships between the GIS variables used in the models and stand composition and structure variables measured in the field.

Study area

The 3900-ha Cummins Creek Wilderness (44° 15' N, 124° 5' W) encompasses three forested watersheds on the central Oregon Coast (Fig. 1). The area is mostly underlain by Yachats basalt, with deeply dissected terrain and steep slopes. Soils are mostly well-drained Andisols and Inceptisols. Elevation ranges from ca. 10 m near the coast to over 800 m at the eastern boundary of the study area. Climate is characterized by abundant precipitation (1800 mm/yr near the coast) with the majority falling during the winter months (November-March). Temperatures typically range from 10 - 20 °C during the growing season, and rarely fall below freezing in the winter. Low-lying fog is common near the coast, and may extend several km inland along river valleys (Franklin & Dyrness 1988). *P. menziesii* and *A. rubra* are the dominant tree species in young, post-fire stands,
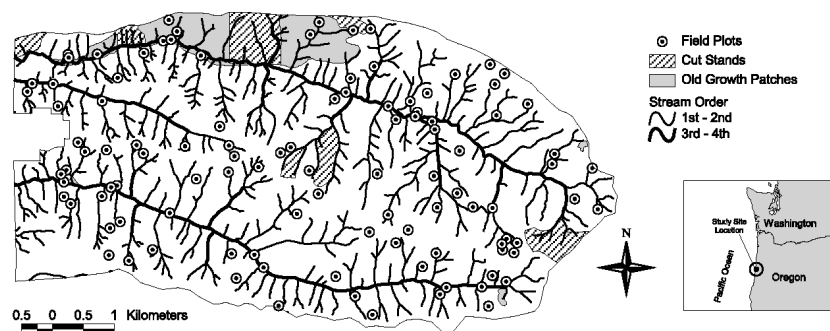

Fig. 1. Map of the Cummins Creek Wilderness, including the stream network and field plot locations. Cut stands were excluded from the analysis. Old-growth patches were delineated using aerial photographs.

whereas *T. heterophylla* and *P. sitchensis* are the most common species of understory regeneration. *T. heterophylla* can establish under closed forest canopies (Harmon 1987) and can survive for decades in suppressed form until it is released by canopy gap formation (Spies et al. 1990). *P. sitchensis* is less shade-tolerant than *T. heterophylla*, requiring higher light levels for establishment (Harmon 1987) and larger gaps to reach the forest canopy (Taylor 1990).

Cummins Creek, like most of the Oregon Coast Range, was affected by a series of large fires occurring between the mid-19th and the early 20th centuries. These burns have created a landscape mosaic dominated by even-aged forests from 70 to 150 yr in age. Remnant trees (defined as trees greater than 200 yr in age that survived those wildfires) are rare, and are concentrated in a few old-growth patches (defined as patches with > 3 remnant trees/ha) scattered throughout the wilderness (Fig. 1). Less than 5% of the study area has been logged, mostly around the perimeters – these harvested areas were excluded from the study.

Methods

Field data collection

In 1997 we divided the landscape into two geographic zones (< 5 km from the coast and > 5 km from the coast), as well as three hillslope (lower, middle, and upper) and two riparian topographic zones (high-order riparian areas encompassing third- and fourth-order streams, low-order riparian areas encompassing first- and second-order streams). Hillslopes were further subdivided into two aspect zones (north and south aspects). We created a map of these zones using a GIS and randomly selected four sites in each of the 12 hillslope strata (two geographic zones × three topographic zones × two aspect zones) and six sites in each of four riparian strata (two geographic zones × two topographic zones) giving 72 sites. Because valley floors were typically narrow in the first- and second-order streams (< 10 m in width), the low-order riparian sites mostly encompassed the adjacent footslopes. Most of the high-order riparian sites were located entirely on the broad valley floors (20 - 140 m in width) of third- and fourth-order streams, although some also overlapped the adjacent footslopes.

Each of the 72 sample sites encompassed approximately 0.25 ha, and was subsampled using three systematically located sets of nested circular plots. We recorded diameter at breast height (DBH) and species of trees (≥ 5 cm DBH) in 333-m^2 plots (10.3 m radius), and seedlings (≥ 10 cm in height and < 5 cm DBH) by species in 167-m^2 plots (7.3 m radius). Within each set

of nested plots, we measured dead down wood volume along a 20 m transect using the line intercept method. We measured percent tall shrub cover (≥ 1.5 m height) at three points along each transect. All measurements were corrected for slope angle based on the projected horizontal area of each plot. We obtained increment cores from several dominant, shade-intolerant trees at each site and determined tree ages by counting annual rings under a dissecting microscope.

In 1998, we sampled seedling density at 33 additional sites concentrated in geographic areas that had been sparsely sampled in 1997. These locations were chosen subjectively using topographic maps. We used this selection method because it allowed us to choose sites spanning the range of topographic strata mentioned above while considering efficient travel paths through the wilderness. Although these sites did not comprise a truly random sample, they were not overtly biased because we did not take vegetation characteristics into account when selecting their locations.

GIS data layers

Sample site coordinates measured with a global position system (GPS) were converted into a GIS point data layer. Site locations were then overlaid on a series of GIS layers to obtain a set of predictor variables for each site. Elevation and slope (Fig. 2a) were computed using a U.S. Geological Survey 30-m digital elevation model (DEM). We computed a slope curvature index in ArcInfo GRID to distinguish convex land forms (high index values) from concave landforms (low index values). Slope position (Fig. 2b) was computed using an algorithm that interpolated between valley bottoms and ridges – values ranged from 0 (valley bottoms) to 100 (ridge tops). Total solar radiation input during the growing season (May-September) was calculated using algorithms developed by Bonan (1989) and Nikolov & Zeller (1992). Distance from the ocean to each site was computed in ArcInfo GRID. We used a detailed stream layer provided by the Siuslaw National Forest to classify streams by stream order.

Overstory vegetation GIS layers were created from cloud-free 1988 Landsat TM imagery. The image was resampled to 25 m resolution for consistency with previous remote sensing maps, and the reflectance bands were transformed into brightness, greenness, and wetness indices using the TM Tasseled Cap transformation. Data for model building came from over 200 aerial photo points on which vegetation cover, conifer cover, broad-leaf cover and crown diameter were measured using a zoom stereoscope. Both unsupervised classification (Wilkie and Finn 1996) and regression modeling approaches (Cohen et al. 1995) were used to estimate
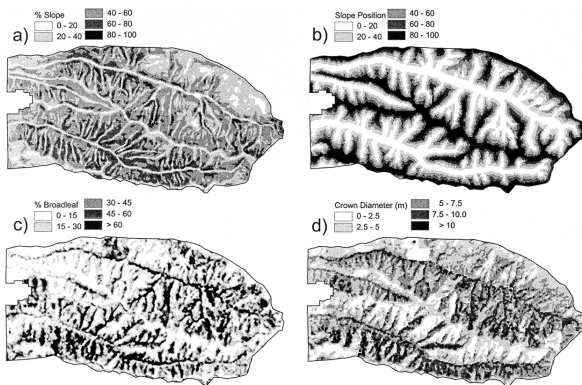
Fig. 2. Maps of independent variables used to develop the predictive maps: **a.** percent slope; **b.** slope position; **c.** percent broadleaf cover; and **d.** crown diameter.

Fig. 3. Maps of predicted seedling patterns: **a.** *P. sitchensis* deterministic map; **b.** *P. sitchensis* probabilistic map; **c.** *T. heterophylla* deterministic map; and **d.** *T. heterophylla* probabilistic map. Individual grid cells are 30 m × 30 m (0.09 ha) in size. Hatched areas represent cut stands that were excluded from the analysis.

open areas (< 70% vegetation cover), percent conifer cover, percent broadleaf cover (Fig. 2c), and crown diameter (Fig. 2d). Remote sensing methods are described in more detail by Cohen et al. (2001). Although there was a 9-yr (1988-1997) lag between image acquisition and ground data collection, a comparison of the vegetation layers with recent aerial photographs indicated that current landscape patterns were similar to those in 1988. Because the size of the field sites (0.25 ha) was larger than the individual Landsat pixels (0.0625 ha) we smoothed the continuous vegetation layers by taking the mean values from a 3 × 3 pixel (0.56 ha) moving window (Wilkie & Finn 1996). This smoothing also helped to reduce sensitivity to potential errors in the vegetation layers and in the location of the ground plots.

Old-growth patches could not be accurately identified using the satellite imagery because many remnant trees had broken tops and were intermixed with smaller trees. We were able to identify four remnant old-growth patches (defined as patches with > 3 trees/ha > 200 yr old) using 1:12 000 scale 1995 color aerial photographs viewed through a mirror stereoscope. Old-growth patches were distinguished based on the presence of emergent tree crowns, dead tops, and multilayered structure characteristics of old-growth canopies. Patch boundaries were delimited using acetate overlays on 1:25 000 scale orthophotos, and were verified in the field at several locations. The patch maps were digitized and converted to 30-m grids, and the distance to each site from the nearest old-growth patch was computed using ArcInfo GRID.
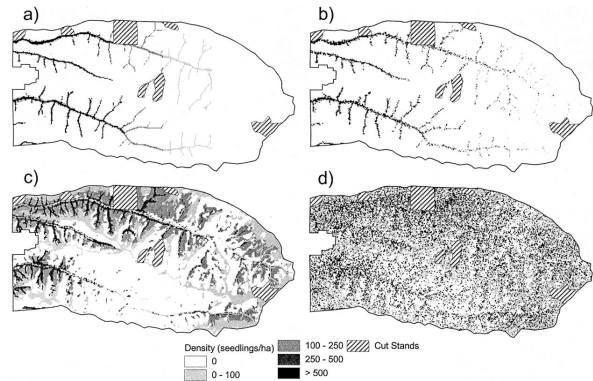
Statistical models of regeneration

We developed separate statistical models for *T. heterophylla* and *P. sitchensis* seedling density using the GIS layers. Since both species were absent at a high proportion of sites (63% for *P. sitchensis* and 45% for *T. heterophylla*) we used a two-phase modeling approach (Hamilton & Brickell 1983; Guisan et al. 1998). The two-phase method allowed for the possibility that a different set of factors might affect the presence of a particular understory species as opposed to its abundance. First, logistic regression models (Hosmer & Lemeshow 1989) were used to predict seedling presence using the function

$$\text{logit}(p) = b_0 + \Sigma\, b_i\, x_i \qquad (1)$$

where p is the probability of seedling presence, b_0 and b_i are the regression coefficients, and x_i are the independent variables. Standard least-squares linear regression was used to model density at the sites where seedlings were present using the function

$$\log(y) = b_0 + \Sigma\, b_i\, x_i \qquad (2)$$

where y is seedling density. Backward stepwise regression was used to reduce the initial pools of independent variables to more parsimonious subsets. Interactions among the independent variables were also explored. All of the coefficients in the final models were statistically significant at the $p < 0.05$ level.

The models were applied to maps of the independent variables to generate maps of predicted seedling patterns. We examined two different methods for generating these maps. First, the deterministic approach used the logistic regression equations to classify seedlings as either present

or absent. The predicted probability in each grid cell was computed as

$$p = 1/(1 + e^{-\text{logit}(p)}) \tag{3}$$

Seedlings were predicted to be present when p was higher than the proportion of sampled sites with seedlings present (0.37 for *P. sitchensis* and 0.55 for *T. heterophylla*) and absent otherwise (Neter et al. 1989). Where seedlings were predicted to be present, the linear regression models were then applied to predict seedling density.

Second, we generated a set of maps using a probabilistic approach to predict seedling patterns. Instead of using a fixed cutoff to predict presence/absence, we generated a random number between 0 and 1 for each site and modeled understory conifers as present where this random variable was less than p. Stochastic variation in the predicted density response was incorporated into the predictions as follows

$$y = \exp(b_0 + \Sigma\, b_i\, x_i + \text{N}(0, \sigma)) \tag{4}$$

where N is a normal random variable and Σ is equivalent to the square root of the mean squared error of the regression equation (Neter et al. 1989).

Correlation of GIS variables with habitat features

The GIS variables used in predictive vegetation mapping typically serve as surrogates for more detailed, ground-based measurements of site condition (Franklin 1995). We used Pearson product-moment correlations to examine the relationships between GIS variables that were included in the final models and a number of stand composition and structure variables computed from field data. Variation in stand structure and composition across three topographic classes (hillslopes, low-order riparian areas, and high-order riparian areas) was also evaluated using one-way analysis of variance. Where the overall F-test was statistically significant, multiple comparisons were obtained using Tukey's studentized

range test. Where necessary, we transformed the data using root or logarithmic functions in order to meet the assumptions of the statistical tests. These analyses included only the 72 sites sampled in 1997 because they were the only sites where we obtained detailed measurements of stand structure. Stand structure variables included *P. sitchensis* basal area, *T. heterophylla* basal area, percent hardwood basal area, shrub cover, down wood volume, and stand age. Crown competition factor (Krajicek et al. 1961) was also computed as an index of overstory canopy closure.

Results

Seedling Models

The probability of *P. sitchensis* seedling presence decreased with distance from the coast and was greater on lower hillslopes than on upper hillslopes (Table 1). *P. sitchensis* seedling density also decreased with distance from the coast, and was higher in riparian areas than on hillslopes (Table 2). The logistic regression model correctly predicted presence or absence 82% of the time, and the linear regression model explained 56% of the variation in seedling density. The deterministic map showed *P. sitchensis* seedlings occurring only in riparian areas and on lower hillslopes, with highest densities near the coast (Fig. 3a). The abrupt termination of the *P. sitchensis* distribution approximately seven km inland reflected the fixed cutoff value used to predict seedling presence. Similar patterns were evident in the probabilistic map of *P. sitchensis* seedlings (Fig. 3b), though fine-scale variability in *P. sitchensis* density was more evident in the probabilistic map, and the predicted range extended further inland than in the deterministic map.

The probability of *T. heterophylla* seedling presence increased with crown diameter and decreased with percent hardwood cover, slope angle, and distance from remnant patches (Table 1). Density of *T. heterophylla*

Table 1. Logistic regression models predicting presence and absence of tree seedlings.

Model	R^{2*}	% Error**	Variable	Coefficient	X^2	p value
P. sitchensis	0.54	18	Intercept	3.61	18.60	< 0.001
			Distance from coast	-5.53×10^{-4}	19.41	< 0.001
			Slope position	-0.0416	16.36	< 0.001
T. heterophylla	0.24	33	Intercept	1.791	3.89	0.049
			(% Hardwood cover)$^{1/2}$	-0.0226	4.13	0.042
			Crown diameter	0.0212	5.22	0.022
			Slope angle	-0.0254	4.20	0.041
			(Distance from Old-growth)$^{1/2}$	-0.0355	5.03	0.025

* R^2 was computed using the method of Nagelkerke (1991).
**   Percentage of sites that were incorrectly classified as having regeneration present or absent.

Table 2. Linear regression models predicting the natural logarithm of seedling density at sites where seedlings were present.

Model	R^2	Variable	Coefficient	t-statistic	P value
P. sitchensis	0.56	Intercept	5.27	9.99	< 0.001
		Riparian areas	3.20	4.23	< 0.001
		Distance from coast	-2.28×10^{-4}	-1.75	0.090
		Riparian areas × Distance from coast	-5.25×10^{-4}	-2.34	0.025
T. heterophylla	0.35	Intercept	5.87	11.04	< 0.001
		Slope position	-0.0194	-2.86	0.006
		High-order riparian areas	-1.19	-2.05	0.045
		Low-order riparian areas	2.03	2.49	0.016
		Distance from coast	2.77×10^{-5}	-0.40	0.693
		Low-order riparian areas ×Distance from coast	3.76×10^{-3}	-2.23	0.030

seedlings was lower in high-order riparian areas than in other parts of the landscape (Table 2). *T. heterophylla* seedling density in low-order riparian areas decreased with distance from the coast. *T. heterophylla* seedling density was also greater on lower than upper hillslopes. These models did not fit the data as well as the *P. sitchensis* models. The logistic regression model correctly predicted seedling presence or absence 67% of the time, and the linear regression model explained 35% of the variability in seedling density. The mapped distribution of *T. heterophylla* regeneration showed large-scale patterns related to the locations of remnant old-growth patches, as well as finer-scale patterns reflecting variation in overstory vegetation and topography (Fig. 3c). Predicted patterns changed considerably in the probabilistic map (Fig. 3d). Although large-scale trends related to the patterns of old-growth patches were still discernible, residual variability obscured much of the finer-scale pattern related to topography and overstory vegetation.

Correlation of GIS variables with Habitat Features

Remotely sensed measures of forest overstory vegetation were correlated with several stand structure variables, including crown competition factor, hardwood basal area, shrub cover, down wood volume, and overstory age (Table 3). Distance from the coast and distance from old growth remnants had negative correlations with overstory basal area of *P. sitchensis* and *T. heterophylla* basal area. Lower hillslopes tended to have older stands with a high proportion of hardwoods, high shrub cover, and high volumes of down wood. Slope angle was negatively correlated with down wood volume. Riparian sites were older and had higher down wood volumes and lower crown competition factors than hillslope sites (Table 4). High-order riparian sites had higher hardwood basal area than low-order riparian areas and hillslopes. Low-order riparian areas had higher shrub cover than hillslopes.

Table 3. Pearson product-moment correlation ($n = 72$) between GIS variables used in the predictive models and stand attributes measured in the field plots.

Stand variables	GIS Variables					
	Distance from coast	Slope angle	Slope position	Percent hardwood cover	Crown diameter	Distance from old growth
P. sitchensis basal area	-0.74**	-0.14	-0.21	-0.24	0.09	-0.35**
'*T. heterophylla* basal area	-0.37**	-0.01	-0.20	-0.27	0.07	-0.49**
Crown competition factor	0.05	0.20	0.48**	-0.37**	-0.34**	-0.09
% hardwood basal area	0.10	-0.16	-0.34**	0.71**	0.31**	0.22
Percent high shrub cover	0.18*	-0.01	-0.32**	0.41**	0.14	0.13
Down wood volume	0.08	-0.31**	-0.41**	0.12	0.27**	-0.21
Overstory age	0.09	-0.16	-0.57**	0.23	0.34**	0.15

* $p < 0.05$; ** $p < 0.01$.

Discussion

Seedling Patterns and Successional Pathways

Climatic and topographic gradients were the dominant factors influencing landscape patterns of *P. sitchensis* seedlings. Several factors may account for the abundance of *P. sitchensis* seedlings in coastal riparian areas. The first is the coastal fog zone, which extends further inland along river valleys than on hillslopes (Franklin & Dyrness 1988). *P. sitchensis* seedlings are intolerant of moisture stress (Minore 1979), and low-lying coastal fog during the dry summer months both reduces evaporative demand and contributes precipitation in the form of fog drip. *P. sitchensis* seedlings are also relatively shade-intolerant, typically establishing in relatively large gaps or under sparse overstory canopies. The open canopied riparian and lower-hillslope forests probably provide a more favorable environment for *P. sitchensis* regeneration than the comparatively dense upper-hillslope forests. The importance of dead wood as a regeneration substrate for *P. sitchensis* has been well established (Harmon & Franklin 1989; Gray & Spies 1996) and the high volume of down wood in riparian areas may provide more opportunities for establishment than on hillslopes.

T. heterophylla seedlings were distributed more widely across the landscape than *P. sitchensis*, and were related to forest overstory variables as well as climate and topography. Increasing probability of *T. heterophylla* seedling occurrence with crown diameter may reflect structural changes that occur with increasing stand age such as larger tree sizes, decreasing canopy cover, and increasing down wood volume (Spies & Franklin 1991). Most of the hardwood- (primarily *A. rubra*) dominated stands within the Cummins Creek Wilderness lack *T. heterophylla* in their understories. Of the 30 sample sites with more than 40% hardwood cover, only 33% had *T. heterophylla* regeneration present. This relationship may reflect low seed availability and competition from tall, dense shrubs in the understory of hardwood-dominated stands. Because of high *P. sitchensis* regeneration in many riparian areas near the coast, some of the hardwood patches along coastal streams may eventually develop into conifer stands. The surrounding conifer matrix may subsume relatively small hardwood patches (< 0.1 ha) as adjacent tree crowns expand into the area formerly occupied by hardwoods. It seems unlikely, however, that most large hardwood patches in riparian areas farther from the coast and on hillslopes will have sufficient understory seedling densities to succeed to conifer stands over the next several decades. In many cases, these stands may instead succeed to stable, shrub-dominated communities as the overstory hardwoods senesce (Tappeiner 1991). Although studies have explored the ecology and dynamics of transient canopy gaps in Pacific Northwest forests (Spies et al. 1990; Taylor 1990), little work has been done on the ecology of persistent canopy gaps. More research is needed to provide a scientific basis for managing this vegetation type.

Disturbance and historical legacies

Biological legacies, such as remnant old-growth trees, are known to influence the pathways and rates of succession within forest stands (Swanson & Franklin 1992). Our results suggest a landscape-scale relationship between *T. heterophylla* regeneration and old-growth patches, at the scale of hundreds to thousands of meters. *T. heterophylla* has thin bark, shallow roots, and relatively inflammable foliage that make it extremely fire-sensitive (Agee 1993). Old-growth patches represent areas where fires were less severe and more *T. heterophylla* survived

Table 4. Mean values of stand attributes measured in the field plots for each of three landscape categories used in the predictive models. Standard errors are given in parentheses. Values for each variable with different letters were significantly different at the $p < 0.05$ level based on multiple comparisons using Tukey's studentized range test.

Stand variables	Landscape unit					
	High-order riparian area ($n = 14$)		Low-order riparian area ($n = 18$)		Hillslope ($n = 74$)	
P. sitchensis basal area (m²/ha)	14.8	(6.4)	9.0	(3.3)	11.1	(3.6)
T. heterophylla basal area (m²/ha)	3.2	(1.8)	8.9	(4.2)	5.2 (	1.2)
Crown competition factor	116.6[a]	(18.4)	133.5[a]	(16.2)	226.6[b]	(9.5)
Percent hardwood basal area	51.5[a]	(10.8)	21.0[b]	(5.5)	13.2[b]	(3.0)
Percent high shrub cover	18.8[ab]	(18.8)	34.8[a]	(5.7)	14.3[b]	(2.6)
Down wood volume (m³/ha)	1566.6[a]	(389.7)	1848.8[a]	(295.6)	747.8[b]	(142.1)
Overstory age (yr)	116.0[a]	(4.4)	114.8[a]	(3.9)	99.2[b]	(2.6)

than in other portions of the landscape. Higher seed availability following fire may account for the higher basal areas of *T. heterophylla* currently found in and near old-growth patches. Because most seed dispersal distances for *T. heterophylla* beneath closed canopies are very short, on the order of tens of meters (Schrader 1998), the current seedling pattern is still linked to the overstory trees that established after fire.

Other factors besides seed source availability, such as shading by the remnant tree patches and variation in soil characteristics or substrate availability might have also influenced the spatial pattern of *T. heterophylla*. In addition, the old-growth trees found on the landscape today do not represent all of the seed sources present following the fires. Trees are often damaged but not killed outright and may survive long enough to disperse seeds, only to succumb within a few years to pathogens and disease (Franklin et al. 1987); some historical patches of remnant trees may no longer exist in the current landscape. Despite these caveats, the spatial association of *T. heterophylla* seedlings with old-growth patches does suggest that the spatial pattern of fires has a persistent influence on the landscape patterns and successional pathways in these forests.

Model evaluation

Although we found statistically significant relationships between understory variables and the mapped explanatory variables, the models explained only low to moderate amounts of the spatial variability in seedling presence and density. Some of the noise arises from the coarse scale of the predictor variables. Seedling establishment and survival are known to be associated with many microsite-scale factors such as environmental suitability (Harmon 1987; Christy 1986), substrate availability (Harmon & Franklin 1989; Gray & Spies 1996), and competition with other plants (Maguire & Forman 1983; Harmon & Franklin 1989). Our choice of predictor variables was limited by the requirement that they be available as GIS layers. Although the environmental indices reflected variation with distance from the coast and physiography, they could not predict finer-scale micro-environmental patterns that can have a strong influence on regeneration. Similarly, although the estimates of overstory vegetation derived from remote sensing were correlated with a number of stand-level variables there was still a large amount of structural variability that could not be predicted from these measures. Other less predictable factors such as inter-annual variability in the size of seed crops (Pickford 1929) and short-term climate fluctuations (Baker 1990) also limit our ability to predict the occurrence and abundance of regeneration based on habitat alone.

Most predictions made using statistical models ignore the uncertainty that is associated with each predicted response. When models explain only a small amount of the total variability, they will predict a narrower range of variability than is present in the actual landscape. This phenomenon is evident in the comparison between deterministic and probabilistic maps. In the case of *P. sitchensis* seedlings, the statistical models explain more than half of the variation in presence and density and the two maps are quite similar. In contrast, the *T. heterophylla* models account for less of the variability in the response, and the predicted patterns change drastically once uncertainty is introduced. When the presence of *T. heterophylla* regeneration is predicted with a deterministic model, for example, the model predicts a large patch void of regeneration in the central and southern portion of the study area (Fig. 3c). When probabilistic predictions are used, the map instead predicts a gradient from high frequencies in and around old-growth patches to low frequencies in large hardwood patches and in areas far from old growth (Fig. 3d). Although the probabilistic map does not provide an accurate prediction for any given site, the larger-scale pattern may be more representative of the actual landscape than the deterministic map – *T. heterophylla* regeneration is never completely absent from large portions of the landscape, nor does it occur at uniformly high density in others.

The potential for modeling seedling patterns in the forest understory will vary depending on the autecological characteristics and life history traits of the species, as well as the environmental patterns and disturbance history of the landscape. The predictive vegetation mapping technique will be most effective when the regeneration niche of a species is relatively narrow and can be readily measured with GIS variables. This was the case with *P. sitchensis* seedlings, which were largely restricted to coastal riparian areas. When species have a broader regeneration niche that is influence by a large number of environmental factors, predictive vegetation mapping will be more difficult. This was the situation with *T. heterophylla* seedlings, which were distributed across the entire study area in relation to climate, topography, and overstory canopy conditions. Potential effects of historical disturbances and seed source limitations are particularly problematic, because GIS maps of these variables are difficult, if not impossible, to obtain. Predictive vegetation maps should be interpreted cautiously when the underlying models explain only a small proportion of the total variability in the response. In most cases, it is probably more reasonable to interpret these predicted patterns as qualitative trends rather than precise, quantitative predictions.

Conclusions

Despite their limitations, predictive maps of tree seedlings and other understory vegetation attributes can provide valuable spatial information for use in management and conservation as long as they are used appropriately. For example, where the lack of tree regeneration is a management concern, predictive maps of understory seedling patterns could used to identify portions of the landscape where low regeneration levels are most likely to occur. Additional research, monitoring, or management activities could then be focused in these areas. Because the models presented in this study are calibrated to a specific landscape, they should not be directly applied to other areas. However, the plot-based inventories, and GIS data bases needed to develop these models are becoming increasing available in the United States as a result of research and monitoring efforts by federal land management agencies. The general methods outlined here could be linked with these new data sources to model landscape patterns of tree seedlings or other understory plant species in a variety of landscapes.

References

Agee, J. K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, DC.

Baker, W. L. 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *J. Biogeogr.* 17: 59-73.

Baker, W.L. & Weisberg, P.J. 1997. Using GIS to model tree population parameters in the Rocky Mountain National Park forest-tundra ecotone. *J. Biogeogr.* 24: 513-526.

Beven, K.J. & Kirby, M.J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. Bull.* 24: 43-69.

Bonan, G.B. 1989. A computer models of the solar radiation, soil moisture, and their regimes in boreal forests. *Ecol. Model.* 45: 275-306.

Brown, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *J. Veg. Sci.* 5: 641-656.

Camp, A. Oliver, C., Hessburg, P. & Everett, R. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecology and Management* 95: 63-77.

Christy, E.J. 1986. Effect of root competition and shading on growth of suppressed western hemlock. *Vegetatio* 65: 21-28.

Cohen, W.B., Spies T.A. & Fiorella, M. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. *Int. J. Remote Sens.* 16: 721-746.

Cohen, W.B., Maiersperger, T.K., Spies, T.A. & Oetter, D.R. 2001. Modeling forest cover attributes as continuous variables in a regional context with Thematic Mapper data. *Int. J. Remote Sens.* 22: 2279-2310.

Collins, S.L. & Good, R.E. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. *Oikos* 48: 89-98.

Davis, F.W. & Goetz, S. 1990. Modeling vegetation pattern using digital terrain data. *Landscape Ecol.* 4: 69-80.

Frank, T.D. 1988. Mapping dominant vegetation communities in the Colorado Rocky Mountain Front Range with Landsat thematic mapper and digital terrain data. *Photogramm. Eng. Remote Sens.* 54: 1727-1734.

Franklin. J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progr. Phys. Geogr.* 19: 474-499.

Franklin, J.F. & Dyrness, C.T. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR.

Franklin, J.F. & Spies. T.A. 1991. Composition, structure, and function of old-growth Douglas-fir forests. In: Ruggerio, L.F., Aubry, K.B., Carey, A.B. & Huff, M.H. (eds.) *Wildlife and vegetation of unmanaged Douglas-fir forests*, pp. 71-80. General Technical Report PNW-GTR-285, USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Franklin, J.F., Shugart, H.H. & Harmon, M.E. 1987. Tree death as an ecological process. *BioScience* 37: 550-556.

Gray, A.N. & Spies, T.A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84: 635-645.

Guisan, A., Theurillat, J. & Kienast, F. 1998. Predicting the potential distribution of plant species in an alpine environment. *J. Veg. Sci.* 9: 65-74.

Hamilton, D.A. & Brickell, J.E. 1983. Modeling methods for a two-state system with continuous responses. *Can J. For. Res.* 13: 1117-1121

Harmon, M.E. 1987. The influence of litter and humus accumulations and canopy openness on Picea sitchensis (Bong.) Carr. and Tsuga heterophylla (Raf.) Sarg. seedlings growing on logs. *Can J. For. Res.* 17: 1475-1479.

Harmon, M.E. & Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70: 48-59.

He, H.S. & Mladenoff, D.J. 1999. Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. *Ecology* 80: 81-99.

He, H.S., Mladenoff, D.J., Radeloff, V.C. & Crow, T.R. 1998. Integration of GIS data and classified satellite imagery for regional forest assessment. *Ecol. Appl.* 8: 1072-1083.

Hosmer, D.W. & Lemeshow, S. 1989. *Applied logistic regression*. John Wiley and Sons, New York, NY.

Iverson, L.R., Dale, M.E., Scott, C.T. & Prasad, A. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.). *Landscape Ecol*. 12: 331-348.

Krajicek, J.E., Brinkman, K.A. & Gingrich, S.F. 1961. Crown competition – a measure of density. *Forest Sci*. 7: 35-42.

Lees, B.G. & Ritman, K. 1991. Decision-tree and rule-induction approach to integration and remotely sensed and GIS data in mapping vegetation in disturbed or hilly environments. *Environ. Manage*. 15: 823-831.

Lefsky, M.A., Cohen, W.B., Acker, S.A., Parker, G.G., Spies, T.A. & Harding, D. 1999. Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir and western hemlock forests. *Remote Sense. Environ*. 70: 339-361.

Maguire, D.A. & Forman, R.T.T. 1983. Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecology* 64: 1367-1380.

McGarigal, K. & McComb W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol. Monogr*. 65: 235-260.

Mills, L.S., Fredrickson, R.J. & Moorhead, B.B. 1993. Characteristics of old-growth forests associated with northern spotted owls in Olympic National Park. *J. Wildl. Manage*. 57: 315-321.

Minore, D. 1979. *Comparative autecological characteristics of Northwestern tree species – A literature review*. General Technical Report PNW-GTR-87, USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Mladenoff, D.J., White, M.A., Pastor, J. & Crow, T.R. 1993. Comparing spatial pattern in unaltered and disturbed forest landscapes. *Ecol. Appl*. 3: 294-306.

Moeur, M. & Stage, A.R. 1995. Most similar neighbor: an improved sampling inference procedure for natural resource planning. *For. Sci*. 41: 337-359.

Nagelkerke, N.J.D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78: 691-692.

Neter, J., Wasserman, W. & Kutner, M.H. 1989. *Applied linear regression models*. Richard D. Irwin Inc., Homewood, IL.

Nikolov, N.T. & Zeller, K.F. 1992. A solar radiation algorithm for ecosystem dynamic models. *Ecol. Model*. 61: 149-168.

Pickford, A.E. 1929. Studies of seed dissemination in British Columbia. *For. Chron*. 5: 8-16.

Ripple, W.J., Lattin, P.D., Hershey, K.T., Wagner, F.F. & Meslow, E.C. 1997. Landscape composition and pattern around northern spotted owl nest sites in southwest Oregon. *J. Wildl. Manage*. 61: 152-159.

Russell-Smith, J. 1996. Regeneration of monsoon rain forest in northern Australia: the sapling bank. *J. Veg Sci*. 7: 889-900.

Schrader, B.A. 1998. *Structural development of late successional forests in the central Oregon Coast Range: Abundance, dispersal, and growth of western hemlock (Tsuga heterophylla) regeneration*. Unpublished Ph.D. thesis. Oregon State University, Corvallis, OR.

Spies, T.A. & Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggerio, L.F., Aubry, K.B., Carey, A.B. & Huff, M.H. (eds.) *Wildlife and vegetation of unmanaged Douglas-fir forests*, pp. 91-109. General Technical Report PNW-GTR-285, USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Spies, T.A., Franklin, J.F. & Klopsch, M. 1990. Canopy gaps in Douglas-fir forest of the Cascades Mountains. *Can J. For. Res*. 20: 649-658.

Spies, T.A., Ripple, W.J. & Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecol. Appl*. 4: 555-568.

Sperduto, M.B. & Congalton, R.G. 1996. Predicting rare orchid (small whorled pogonia) habitat using GIS. *Photogramm. Engin. Remote Sens*. 62: 1269-1279.

Swanson, F.J. & Franklin, J.F. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecol. Appl*. 2: 262-274.

Tappeiner, J., Zasada, J., Ryan, P. & Newton, M. 1991. Salmonberry clonal and population structure: The basis for a persistent cover. *Ecology* 72: 609-618.

Taylor, A.H. 1990. Disturbance and persistence of Sitka spruce (*Picea sitchensis* (Bong) Carr.) in coastal forests of the Pacific Northwest, North America. *J. Biogeogr*. 17: 47-58.

Wilkie, D.S. & Finn, J.T. 1996. *Remote sensing imagery for natural resources monitoring*. Columbia University Press, New York, NY.

Wolter, P.T., Mladenoff, D.J., Host, G.E. & Crow, T.R. 1995. Improved forest classification in the Northern Lake States using multi-temporal Landsat imagery. *Photogramm. Engin. Remote Sens*. 61: 1129-1143.