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Evaluation and prediction of shrub cover in coastal Oregon forests (USA)

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Abstract

We used data from regional forest inventories and research programs, coupled with mapped climatic and topographic information, to explore relationships and develop multiple linear regression (MLR) and regression tree models for total and deciduous shrub cover in the Oregon coastal province. Results from both types of models indicate that forest structure variables were most important for explaining both total and deciduous shrub cover. Four relationships were noted: (1) shrub cover was negatively associated with *Tsuga heterophylla* basal area and density of shade-tolerant trees; (2) shrub cover was negatively associated with variables that characteristically peak during stem exclusion and mid-succession; (3) shrub cover was positively associated with variables that characterize later successional stages; and (4) higher total and especially deciduous shrub cover were positively associated with hardwood stands. Environmental variables were more important for explaining deciduous shrub cover compared to total shrub cover, but they have an indirect effect on total shrub cover by influencing tree composition. However, because of land ownership patterns, it was difficult to decouple environmental from disturbance factors associated with management strategies across multiple ownerships.

Tree models performed similarly (PRD = 0.17–0.27) or better compared to MLR models (PRD = 0.17–0.23) although they contained more (2) predictor variables. Our results indicate that response variable transformation can greatly improve regression tree model performance. While interpretation of MLR and tree models were somewhat similar, the tree models allowed a more explicit understanding of relationships and provided thresholds for anticipating shifts in shrub cover. Such thresholds are useful to forest managers who are monitoring and evaluating critical amounts of shrub cover necessary for different ecosystem components such as bird habitat. Lack of strong predictive power in both types of models may be because many common shrubs can persist and maintain consistent cover under a variety of stand and environmental conditions or there may be a lag time between disturbance events and shrub response. The stochastic nature of disturbance and their interactions with site conditions also makes prediction at this scale in this highly managed landscape inherently problematic. Yet, our models provide both a predictive and conceptual tool for understanding shrub cover patterns across the region.

Keywords: Forest understory; Linear regression; Pacific Northwest; Predictive models; Regression trees; Shrubs

1. Introduction

In the Pacific Northwest of the US (Oregon and Washington), development of forest policies to sustain biological diversity and ecological function while providing for other social and economic values is a major

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challenge for decision makers and managers. Conflict over the appropriate balance between ecological, economic and social goals led to major controversies regarding forest management in the 1980s and 1990s and development of new forest polices in the region. In Oregon's Coast Range, separate new policies for federal, state, and private lands have been initiated in the last few years (Spies et al., 2002b). These policies are based on current scientific information, but it is unclear how effective they will be in meeting ecological, economic and social goals. Monitoring, modeling, and evaluation of ecological indicators at the landscape scale can provide important feedback on the effectiveness and outcomes of land management policies and programs and focus attention on the status and trends of biosocial systems.

Shrub cover is a good candidate for an ecological indicator because shrubs form a distinct structural layer or layers in the subcanopy of most Pacific Northwest forests, cover data are relatively easy to obtain in the field and are widely available from forest inventory data and research plots, and shrub cover can be used as an indicator of forest health and is directly linked to ecological function. Measures of understory cover are included in a suite of forest health indicators that are monitored nationally in the US (Stolte et al., 2002). The meaningful ecological significance of some general measures of vegetation structure is not always clear (Cole, 2002), but shrub cover has been directly and significantly linked to habitat quality and a number of interconnected, complex ecological processes (Carey, 1995; Hagar et al., 1996; Muir et al., 2002). Shrubs provide shelter, substrate, and food for forest organisms and provide important organic matter inputs to soils, play a major role in nutrient cycling, contribute substantially to compositional and structural diversity, help protect watersheds from erosion and enhance the aesthetics of forest ecosystems (Alaback and Herman, 1988; Halpern and Spies, 1995; Muir et al., 2002). For example, the cover and distribution of shrubs influence the variety and abundance of mycorrhizal fungi, which are critical food for small mammals that are important prey for avian and terrestrial predators (Carey, 1995; Carey et al., 1999). Shrub stems, particularly deciduous shrubs, provide substrates for many mat-forming bryophytes and macrolichens, which serve as nitrogen fixers, function as hydrological buffers, and provide food for flying squirrels, deer, elk and arthropods (Rosso, 2000; Peck and McCune, 1998). Arthropods have important functions in forest ecosystems as they serve as defoliators, decomposers, and prey or hosts to carnivores, and pollinators (Miller, 1993; Muir et al., 2002). Arthropods are also an important part of the diet of most neotropical migratory birds that breed in Pacific Northwest forests. Many shrubs are also key resources for humans, providing food, medicinal and floral products, and recreational opportunities (Carroll et al., 2003; Blatner and Alexander, 1998). Although these ecological and social benefits are widely recognized, little is known about distribution and abundance patterns of shrubs across the landscape.

In this paper, we report on our efforts to develop quantitative models for total and deciduous shrub cover in the Oregon coastal province and to evaluate these patterns in the context of ecological theory and the environmental and social dynamics of the regional ecosystem. We used ground plot data, coupled with mapped data on climate, topography and forest structure, to develop quantitative models using multiple linear regression (MLR) and regression tree analysis. Classification and regression trees are a powerful, relatively new statistical technique ideally suited for analysis of complex ecological data (De'Ath and Fabricius, 2000). Although typically viewed as exploratory, trees have been used in ecological modeling and predictive mapping (Franklin, 1995, 1998; Aaron and Meentemeyer, 2001; Thuiller et al., 2003). Our models are part of a larger interdisciplinary effort to provide a framework for analyzing the ecological consequences of different forest policies and strategies across multiple ownerships in the Oregon Coast Range (Spies et al., 2002a, 2002b). We selected total and deciduous shrub cover because these variables are key indicators for wildlife habitat and results from our analysis are being applied to habitat suitability models for black-throated gray warblers in the Oregon Coast Range. Studies have found black-throated gray warblers to be associated with shrub cover, particularly deciduous cover, and it is thought that shrub cover is the vegetative cue to which populations respond (Morrison, 1982; Chambers, 1996; Hagar et al., 1996; Guzy and Lowther, 1997). For black-throated gray warblers, habitat suitability peaks when deciduous shrub cover ranges from 65 to 85% (Michael

McGrath, USDA Forest Service Pacific Northwest Research Station, unpublished data).

Studies of forest understory composition and cover are frequently conducted at small scales, or within a limited or controlled range of environmental and disturbance characteristics (e.g. Alaback, 1982; Halpern, 1989; Bailey et al., 1998; McKenzie and Halpern, 1999; McKenzie et al., 2000). We present a landscape-scale study and explore a wide range of explanatory variables including: overstory stand structure, natural and anthropomorphic disturbance history (e.g. land management, ownership, timber harvest history), and environment (topography, climate, geography and geology). Numerous studies have shown the importance of environmental variables such as temperature and moisture (Zobel et al., 1976; Spies, 1991; Franklin and Spies, 1991; Ohmann and Spies, 1998), topography (Pabst and Spies, 1998; Wimberly and Spies, 2001), and soil chemistry (Whittaker, 1960) in structuring forest communities. However, in forested environments it is frequently assumed that overstory stand structure strongly influences understory species cover by altering microsites, resources, and environmental conditions (Halls and Schuster, 1965; Ford and Newbould, 1977; Alaback, 1982; Oliver and Larson, 1996; Stone and Wolfe, 1996).

Our objectives are to identify and quantify multiple ecological and anthropomorphic factors associated with shrub cover in coastal Oregon forests and develop descriptive and predictive models. Specifically, we address the following questions: (1) Is shrub cover more tightly linked to environmental, forest structure, or natural and anthropomorphic disturbance factors? (2) Are different variables important for explaining shrub cover across different landowners and can these differences be interpreted in relation to forest policy?

2. Methods

2.1. Study area

Our study area was the approximately 2.5 million ha multi-ownership Oregon coastal province (Fig. 1). The terrain consists of the rugged Oregon Coast Range, with sharp ridges and steep slopes that are dissected by major river drainages with undulating hills and flat valley bottoms. Elevations range from sea level, to 450–750 m at main ridge summits, with a high of 1249 m. The mild maritime climate is strongly influenced by cyclonic storms that approach from the Pacific Ocean on dominant westerlies. Annual precipitation ranges from 150 to 350 cm, with most moisture falling as rain between 1 October and 31 March. The coastal mountains block winter storms from the interior valleys, creating a gradient of decreasing precipitation and increasing temperature from west to east. In summer, storm tracks shift to the north, and summers are relatively cool and dry, but a narrow fog belt along the coast can contribute to precipitation. A general latitudinal decrease in precipitation and increase in temperature occurs from the north to south.

Two major vegetation zones dominate the study area, *Picea sitchensis*, and *Tsuga heterophylla*, but small areas of *Abies amabilis* are also present (Franklin and Dyrness, 1988). The *P. sitchensis* zone only exists within several kilometers of the coast, in a zone of frequent summer fog. *Pseudotsuga menziesii* is an extremely important species for commercial timber production and dominates the study area and the more extensive *T. heterophylla* zone. Throughout the study area, major hardwoods are deciduous and frequently limited to recently disturbed and riparian areas (Franklin and Dyrness, 1988). See Franklin and Dyrness (1988) and Ohmann and Spies (1998) for more detailed descriptions of vegetation and environment.

Fire is a critical disturbance process in the study area. Impara (1997) found that a mixture of high- and low-severity fires with an estimated natural fire rotation interval of 271 years distinguished fire episodes in the central Coast Range. Historical fires in the drier and warmer eastern and southern portions of the study area were smaller and more frequent (Impara, 1997). Large, high severity fires characteristic of the settlement period (1846–1909) have initiated or influenced much of the forest lands in Oregon coastal province (Impara, 1997; Wimberly and Spies, 2001). Other natural disturbance caused by geomorphic instability, windstorms, and pathogens are also important in this landscape. Today, timber management and fire suppression have largely replaced natural disturbance regimes. Timber management in western Oregon was historically focused on even-aged management, which consists of clear-cut logging, intensive site-preparation, and tree re-planting (Hansen

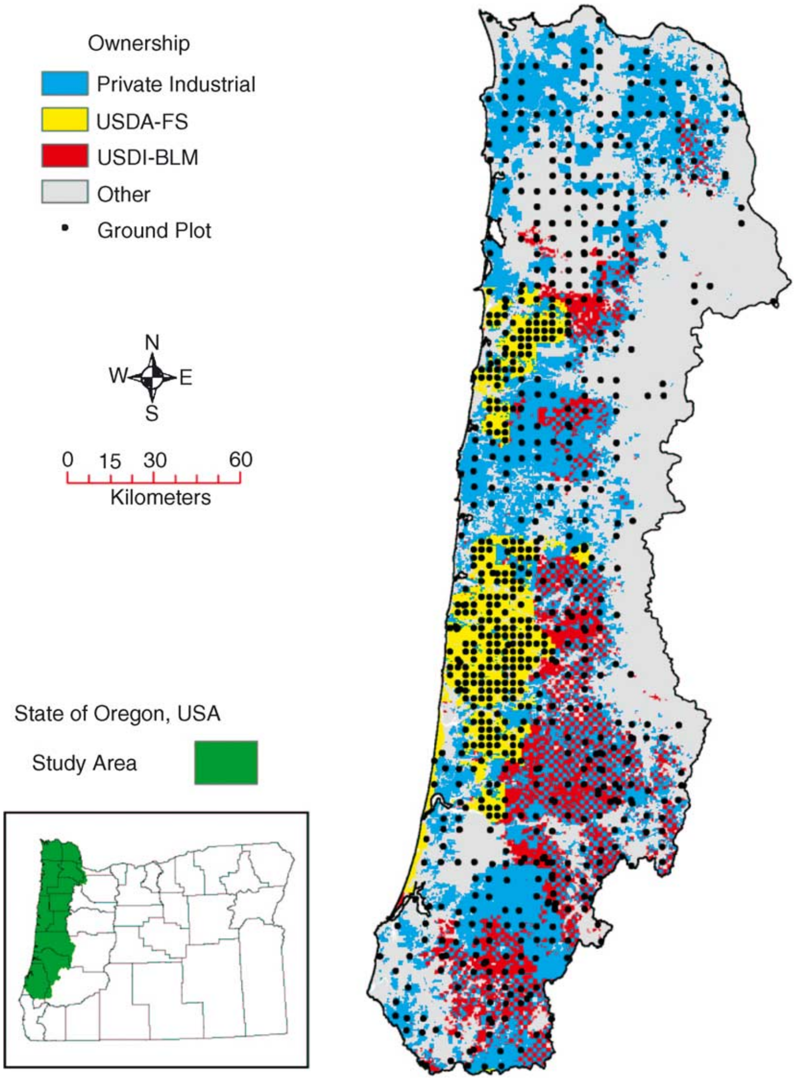

Fig. 1. Study area showing plot locations and land ownership. Boundaries on state map are counties.

et al., 1991). Therefore, both fire and human disturbance processes have created a landscape dominated by relatively young, even-aged, dense stands of *P. menziesii*. However, forest management practices vary among landowners, creating marked differences in disturbance history and stand age (Table 1). USDA Forest Service National Forests retain landscape patterns created by decades of staggering small harvest units in space. Lands managed by the USDI Bureau of Land Management (USDI-BLM) occur in a “checkerboard” pattern interspersed with private lands, and contain a mix of old and young forest (Table 1 and Fig. 1). Most remaining old growth in the Pacific Northwest is concentrated on federal lands (Bolsinger and Waddell, 1993). Forest industry lands typically occur in large blocks that are still intensively managed for timber production. Virtually all private forest lands have been harvested at least once and most stands are less than 80 years old.

Table 1
Stand characterization and disturbance history by landowner (old-growth study plots are not included in age calculations)

Landowner	*n*	Stand age in years (Mean ± S.E., range)	Landowner characterization, management, and disturbance history
USDA Forest Service (USDA-FS)	312	80.9 (3.3) 0–718	Past management of small (40 acre) clear-cut harvest units; currently managed under the Northwest Forest Plan, with a combination of land allocations managed primarily to protect and enhance habitat for late-successional and old-growth forest related species
USDI Bureau of Land Management (USDI-BLM)	111	71.3 (5.3) 0–341	Lands interspersed with private lands ("checkerboard" pattern, see Fig. 1); located predominantly on the east side of the Coast Range; management history similar to USDA Forest Service
Private forest industry	272	33.8 (1.5) 0–256	Virtually all land has been harvested at least once. Generally intensively managed for timber production with regulation under the Forest Practice Act; rotation lengths 40–70 years; 120 acres maximum clear-cuts.
Other	203	40.0 (1.6) 0–122	Miscellaneous private, farm, state, country, municipal and tribal lands with variable management and disturbance histories reflecting individual landowner goals; generally less intensively managed than forest industry lands

2.2. Data sources and variables

The data used in this study included measures of forest tree and shrub composition and structure, disturbance history recorded on field plots, and mapped environmental variables (Table 2). All variables listed in Table 2 are in GIS and are spatially complete and can be applied across the landscape. The dataset spans a range of stand ages, land ownerships, land management regimes, disturbance histories, and environmental gradients across Oregon coastal forests (Fig. 1). Vegetation and other ground-based data were obtained and summarized from field plots established by regional forest inventories and research studies described in Table 3. Approximate field plot locations are shown in Fig. 1. Only forested plots with complete understory vegetation data were included ($n = 936$). We obtained map layers for climatic, topographic, and geologic variables (Table 2) that are available in digital format and that have been shown to be associated with patterns of forest vegetation in Oregon (Ohmann and Spies, 1998; Ohmann and Gregory, 2002). Climate data were derived from mean annual and mean monthly precipitation and temperature surfaces generated by the Precipitation–Elevation Regressions on Independent Slopes Model (PRISM) (Daly et al., 1994). PRISM uses DEMs to account for topographic effects in interpolating weather measurements from an irregular network of weather stations to a uniform grid. Detailed descriptions of the creation of other variables are provided in Ohmann and Gregory (2002).

Shrub cover was calculated by adding ocularly estimated percent cover values recorded (recorded to the nearest percent, not as a cover class) on small fixed-radius plots (Table 3) for either all shrub species or all deciduous shrub species. A species was categorized as a shrub if it is a perennial woody plant less than 3 m in height when mature (although some shrubs can occasionally attain tree height) (USDA Forest Service, 1995; USDA and USDI, 2000). A list of deciduous shrubs was developed form the National Plants Database (USDA and USDI, 2000). Seventy-nine species of shrubs were recorded on the plots, but most of these species (50.4%) occurred on less than 1% of the plots (Table 4). Only 14 species, or 17.8% of the total species found, occurred on 10% or more of the plots in the study area. Because the cover of any two species may overlap, this shrub cover value can exceed 100% (e.g. range for total shrub cover: 1.2–208).

2.3. Data analysis

We reduced a large number of possible predictor variables available to us to the final list of 36 in Table 2 by examining correlation coefficients. For variables that were highly correlated with each other ($r > 0.8$), we selected the variable that was more general. For example, we selected the basal area of all hardwood trees rather than the basal area of individual hardwood species. The only exception to this general approach was inclusion of *T. heterophylla* based on results from previous work (Rogers, 1980; Alaback, 1982; Alaback

Table 2
Explanatory variables used for data analysis and model development

Variable class and code	Description
Land ownership	
OWN	Four land ownerships based on plot data: USDA-FS, USDI-BLM, private forest industry, other
Overstory tree variables (all trees >2.5 cm diameter at breast height or dbh)	
SDI	Stand density index = (basal area of all trees × TPH of all trees)$^{0.5}$
QMDHAL	Quadratic mean diameter (QMD) of all hardwoods (cm)
QMDALL	QMD of all trees (cm)
TPHVS	Trees per hectare (TPH) of very small trees (2.5–12.7 cm dbh)
TPHSM	TPH of small trees (2.5–25.4 cm dbh)
TPHMD	TPH of medium trees (25.5–50.4 cm dbh)
TPHS_MD	Sum of TPHSM and TPHMD
TPHLG	TPH of large trees (50.5–75.4 cm dbh)
TPHVL	TPH of very large trees (75.5–100.4 cm dbh)
TPH_TOL	TPH of all shade-tolerant trees[a]
TSHE	Basal area of *Tsuga heterophylla* (m^2/ha)
BAHALL	Basal area of all hardwoods (m^2/ha)
BAALL	Basal area of all trees (m^2/ha)
BA100	Basal area of trees >100 cm dbh (m^2/ha)
Mapped topographic variables	
ELEVATION	Elevation (m), from 30 m digital elevation model (DEM)
ASPECT	Cosine transformation of aspect (degrees) (Beers et al., 1966), 0.0 (southwest)
SLOPE	Slope (%), from 30 m DEM
SLOPOS	Slope positions(%), 0 = bottom of drainage, 100 = ridge top, from 30 m DEM
RIPARIAN	Indicates whether plot is within 100 m of stream, from GIS overlay
SOLAR	Solar radiation (cal/cm^2), from program SolarImg (Harmon and Marks, 1995) and 100 m DEM
Mapped climatic variables (from approximately 4.7 km resolution PRISM grids)	
ANNPRE	Mean annual precipitation (natural logarithm, mm)
CONTPRE	Percentage of mean annual precipitation falling in June–August, a measure of seasonality
ANNTMP	Mean annual temperature (°C)
AUGMAXT	Mean August maximum temperature, hottest month (°C)
Disturbance variables	
AGE	Stand age (years) from plot data, mean total age of dominant and co-dominant trees
HARVEST	Three timber harvest classes recorded on plot: clear-cut, partial cut, never cut
DISTURBANCE	Years since major disturbance (assigned from 1996, usually clear-cutting) computed from GIS overlay
Geology and geography	
ECOREG	Ecoregion: coastal, interior, foothill and valley, computed from GIS overlay
GEOLOGY	Indicators of lithology and age, generalized from Walker and MacLeod (1991)
VOLC	Volcanic and intrusive rocks
MAFO	Mafic rocks (basalt, basaltic andesite, andesite, gabbro), Miocene and older
SEDR	Siltstones, sandstones, mudstones, conglomerates (sedimentary)
TUFO	Tuffaceous rocks and tuffs, pumicites, silicic flows; Miocene and older
DEPO	Depositional (dune sand, alluvial, glacial, glaciofluvial, loess, etc.)
MIXR	Mixed rocks (unspecified)

[a] Shade-tolerant species are: *Abies amabilis*, *Abies grandis*, *Abies concolor*, *Chamaecyparis lawsoniana*, *Picea sitchensis*, *Thuja plicata*, *Taxus brevifolia*, *Tsuga heterophylla*, *Acer macrophyllum*, *Cornus nuttallii*, *Lithocarpus densiflorus*, *Rhamnus purshiana*, *Umbellularia californica* (USDA Forest Service, 1990; Minore, 1979).

Table 3
Sources of vegetation data and sampling designs

Ownership	Source of data	Data collection methods
USDA-FS USDI-BLM	Current vegetation survey (CVS) Forest inventory and analysis (FIA)	Plots established on a 2.7 km systematic grid (FS wilderness area plots and BLM plots use a 5.5 km grid). Tree data were summarized from a series of fixed-radius subplots (0.004–1 ha); cover by shrub species was recorded on five 170 m^2 fixed-radius subplots
All non-federal (state, private, etc.)	FIA	Plots established on a 5.5 km systematic grid. Tree data were summarized from variable-radius plots; cover by shrub species (>3%) was recorded on five 826 m^2 fixed-radius subplots
USDA-FS USDI-BLM	Spies (1991)	Plots were selected in late-successional stands ranging from 4 to 20 ha. Tree data were collected on a 0.1 and 0.05 ha fixed-radius plot; cover of short shrubs were recorded by species on a 20 m^2 subplot and tall shrubs on a 500 m^2 subplot

and Herman, 1988; Stewart, 1988; Franklin and Spies, 1991).

The issue of the best approach for vegetative modeling has been the subject of much discussion in the literature and many new types of statistical approaches are gaining popularity (Franklin, 1995; Guisan and Zimmerman, 2000; Thuiller et al., 2003). We used two types of models: (1) Gaussian GLM model with an identity link (equivalent to ordinary least-squares multiple linear regression or MLR (Guisan and Zimmerman, 2000)); and (2) regression trees (Breiman et al., 1984). We used MLR because our dependent variable was continuous (not binomial or ordinal), theoretically unbounded, and our error terms were approximately normal after transformation (total and deciduous shrub cover − natural log and natural log + 1) (Franklin, 1995; Guisan and Zimmerman, 2000).

Table 4
Common shrub species found in the study area

Latin name	Common name	Frequency
Vaccinium parvifolium	Red huckleberry	70.1
Acer circinatum	Vine maple	65.5
*Gaultheria shallon**	Salal	64.3
Rubus spectabilis	Salmonberry	60.0
*Berberis nervosa**	Dull Oregon grape	53.4
Rubus ursinus	Trailing blackberry	52.9
Holodiscus discolor	Oceanspray	38.9
Rubus parviflorus	Thimbleberry	38.7
*Vaccinium ovatum**	Evergreen huckleberry	29.5
Sambucus racemosa	Red elderberry	27.3
Rosa gymnocarpa	Baldhip rose	25.0
Corylus cornuta	Beaked hazelnut	22.4
*Rhododendron macrophyllum**	Pacific rhododendron	15.7
Menziesia ferruginea	False azalea	11.0

Non-deciduous species are marked with an asterisk.

Because current methods for variable selection in MLR analysis exhibit considerable bias, we initially used a modified bootstrap method (1000 bootstrap replicates with subsample size $= N/2$) to select predictors from our set of 26 independent variables (Olden and Jackson, 2000). However, this criterion resulted in the inclusion of too many variables, as many coefficients were statistically significantly different from zero ($P < 0.01$). Therefore, we used a conservative forward stepwise procedure (0.01 alpha-to-enter and 0.05 alpha-to-remove). Final models were selected when the increase in r^2 with additional variables flattened. Outliers were removed if studentized residuals exceeded 3 (the largest number of outliers removed was 3). We also developed different MLR models for each landowner (Table 1) to assess whether or not variables that were important for explaining shrub cover varied across land ownership.

Rather than splitting our data into training and test sets, we used a cross-validation procedure called error optimism to calculate an improved estimate of prediction error (Efron and Tibshirani, 1993) for the MLR models. This procedure uses 100 bootstrap replicates to generate a separate error that is then added to the mean residual square error (the apparent error calculated from the model-building dataset). The resultant value reflects the increase in residual square error expected if the model was extrapolated to other data. While our sample size of 936 seems large, given the extent of our study area and the environmental variability between sites, withholding data would result in too large of a loss of information for model calibration, resulting in greater uncertainty in parameter estimates and less stability in the validation estimate of the prediction error (Olden and Jackson, 2000). Data splitting would also be especially impractical for the different landowner models. The bootstrap procedure we used aids in reducing problems associated with obtaining representative samples for model validation and provides for greater sample size for model construction (Olden and Jackson, 2000).

Classification and regression trees are a very different approach to prediction developed by Breiman et al. (1984) that have gained recent popularity for vegetation modeling (Franklin, 1995; Aaron and Meentemeyer, 2001; Thuiller et al., 2003). Part of this popularity stems from the fact that it is not necessary to deal with the issue of the form of the relationship between response and explanatory variables (De'Ath and Fabricius, 2000). Classification and regression trees are constructed by binary recursive partitioning of data into homogenous subunits (sums of squares) defined by prediction variables (Breiman et al., 1984). The result is a binary decision tree that permits the classification of new cases. Classification trees are used for binary and categorical dependent variables and regression trees are used for continuous dependent variables. To avoid confusion, we will refer to our regression tree models simply as trees.

To develop our trees, we used the same prediction variables as those used for the MLR models, except total and deciduous shrub cover were not transformed (De'Ath and Fabricius, 2000) and additional categorical variables were included (OWN, HARVEST, ECOREG, GEOLOGY; Table 2). We developed full trees using default settings in S-PLUS 2000 (stopping criteria = 0.01, minimum node size = 10, minimum split = 5) and pruned the models back using a cost-complexity parameter (Breiman et al., 1984). Ten-fold cross-validation was applied to determine optimum tree size with the smallest deviance and to assess model stability (Clark and Pregibon, 1993). We used cross-validation, rather than splitting our data into training and test sets because of issues concerning loss of information as discussed above. Using all available data may be even more important in these instances because tree models are so strongly data driven. Because the size of a selected tree will vary under repeated cross-validations, this procedure was repeated 10 times (De'Ath and Fabricius, 2000). We did not develop different models for each landowner because we hypothesized that landowner would emerge as an explanatory variable.

2.4. Model comparison

MLR and tree models were compared based on proportional reduction in deviance (PRD): (SSTO − SSE)/SSTO, where SSTO is the sums of squares total and SSE the sums of squares error. Use of PRD as a metric for comparison is appropriate because normal error function is assumed in both types of models (Franklin, 1998). For comparative purposes, we pruned our tree models to contain as many variables as the MLR models to assess how additional variables in the tree models change the proportional reduction in deviance. We also transformed the response variables to assess the effect of variable transformation on tree model performance.

3. Results

3.1. MLR models

For the entire Oregon coastal province, three predictor variables were selected for total shrub cover: basal area of *T. heterophylla* (TSHE); density of medium sized trees (TPHMD); and density of very large trees (TPHVL) (Table 5). MLR models developed for the different landowners show different predictor variables were selected for each, although the negative relationship between shrub cover and the basal area of *T. heterophylla* was always selected first in the stepwise procedures and explained more variability than any other variable. A positive relationship between total shrub cover and either density of very large trees or stand age was also present in all of the models. A positive relationship between shrub cover and very small trees was detected for USDI-BLM lands. Quadratic mean diameter of all hardwoods (QMDHAL) appeared as a predictor variable for USDI-BLM and other lands, although the sign of this relationship was not consistent between these landowners. Except for USDI-BLM lands, MLR models for individual landowners had better predictive power than the entire landscape model. None of the MLR models for total

Table 5
Multiple regression models for total and deciduous shrub cover in the Oregon coastal province

	Intercept	Coefficients				r^2	MRSE[a]	IEPE[b]
ln(total shrub cover)								
Coastal province ($n = 934$)	3.94282	−0.03451 (TSHE)	−0.00094 (TPHMD)	0.00837 (TPHVL)		0.23	0.49	0.98
USDA-FS lands ($n = 318$)	4.24142	−0.05173 (TSHE)	−0.00156 (TPHS_MD)	0.00676 (TPHVL)		0.49	0.38	0.77
USDI-BLM lands ($n = 139$)[c]	3.17480	−0.02700 (TSHE)	0.00050 (TPHVS)	0.01190 (TPHVL)	0.01120 (QMDHAL)	0.14	0.50	0.99
Private industrial ($n = 272$)	3.73415	−0.03251 (TSHE)	0.00574 (AGE)			0.25	0.41	0.82
Other ($n = 201$)	3.81515	−0.03443 (TSHE)	0.00948 (AGE)	−0.012889 (QMDHAL)		0.30	0.28	0.57
ln(deciduous shrub cover + 1)								
Coastal province ($n = 936$)	3.35577	−0.02409 (TSHE)	0.017346 (QMDHAL)	−0.00853 (BAALL)		0.17	0.77	1.50
USDA-FS lands ($n = 320$)	−8.60771	−0.03568 (TSHE)	−0.00273 (TPHMD)	0.01983 (QMDHAL)	1.52709 (ANNPRE)	0.35	0.71	1.36
USDI-BLM lands ($n = 139$)	4.08035	−0.00548 (SDI)	−0.01902 (Slope)			0.18	0.81	1.62
Private industrial ($n = 273$)	5.44584	−0.03089 (TSHE)	0.01367 (QMDALL)	−0.00711 (Solar)		0.17	0.60	1.20
Other ($n = 201$)	3.5448	−0.02399 (TSHE)	−0.00161 (TPHMD)	0.00871 (AGE)		0.23	0.39	0.77

Sample sizes (n) reflect model-building datasets after removal of outliers.

[a] Mean residual squared error, the apparent error estimate calculated using the model-building dataset.

[b] Improved estimate of prediction error, based on error optimism, a bias correction factor calculated from 100 bootstraps replicates.

[c] Alpha-to-enter and alpha-to-remove for stepwise procedure was 0.15.

shrub cover contained environmental or topographic mapped variables as predictors.

The MLR models for deciduous shrub cover showed similar trends in predictor variables as the total shrub cover models. In contrast to total shrub cover MLR models, several mapped environmental and topographic variables appear in deciduous shrub models for the different landowners, including annual precipitation (ANNPRE), slope (SLOPE) and solar radiation (SOLAR). For the entire Oregon coastal province, three predictor variables were selected: basal area of *T. heterophylla*; quadratic mean diameter of all hardwoods; and basal area of all trees (BAALL) (Table 5). Basal area of *T. heterophylla* was again the most important predictor variable for all of the models, except for USDI-BLM lands. A positive relationship was detected between quadratic mean diameter of all hardwoods and deciduous shrub cover, as well as quadratic mean diameter of all trees, stand age, and annual precipitation. Models for the different landowners had better predictive power than the overall model, except for private industrial lands.

3.2. Tree models

For the total shrub cover tree model, 10 sets of 10-fold cross-validation showed that deviance was minimized at 3–10 nodes (mean = 5.9, median = 6; most frequent node size = 6 and 7) and the final tree was pruned to six nodes (Fig. 2). The tree shows primary partitions using five predictor variables: basal area of *T. heterophylla*, quadratic mean diameter of all trees (QMDALL); density of very small trees; density of shade-tolerant trees (TPH_TOL); and elevation (ELEVATION). Shrub cover is the lowest in stands with basal area of *T. heterophylla* greater than 8.3 m^2/ha (node 1) and highest in stands with less basal area of *T. heterophylla*, larger trees, and low densities of shade-tolerant trees (node 4). Elevation is important for stands with little *T. heterophylla*, larger

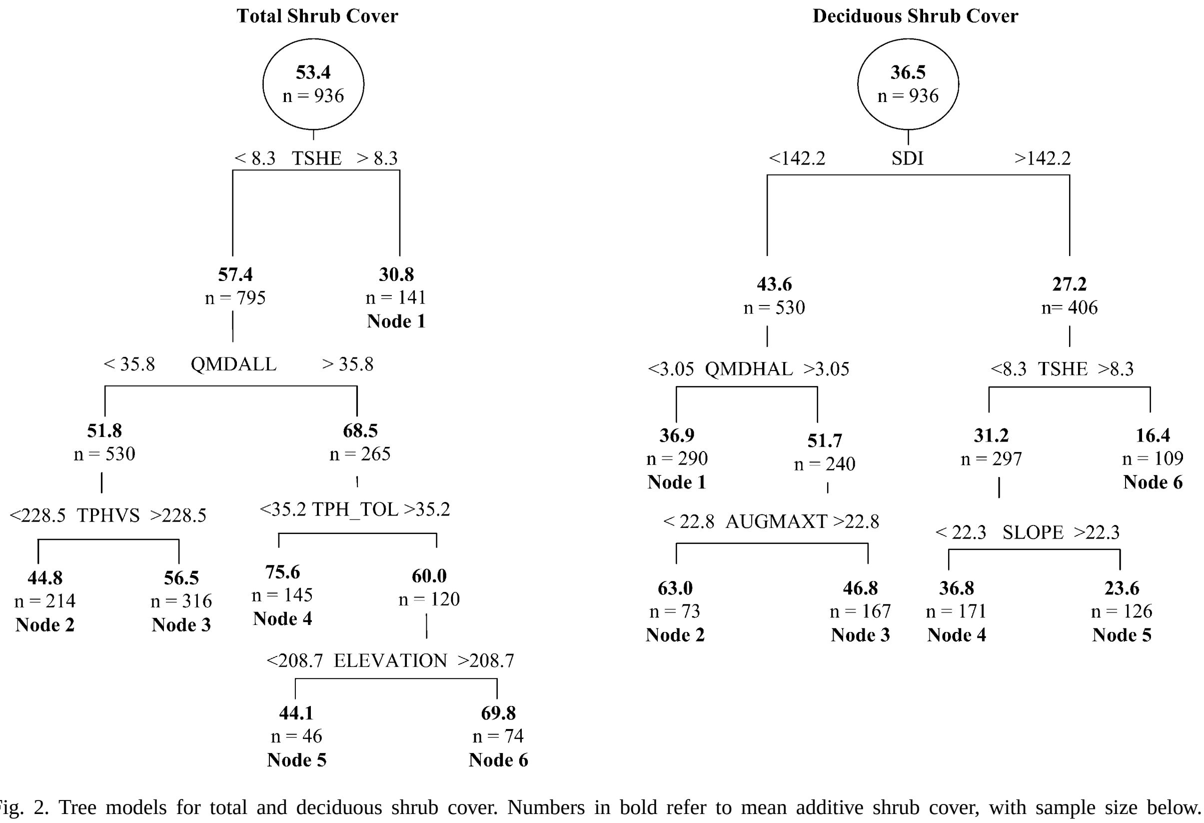

Fig. 2. Tree models for total and deciduous shrub cover. Numbers in bold refer to mean additive shrub cover, with sample size below. Node numbers are for reference to discussions in the text only.

Table 6
Comparison of MLR and tree models of total and deciduous shrub cover for the Oregon Coast Range

Response variable	Model type	Number of variables	Variables selected	Reduction in deviance (PRD) %
ln(total shrub cover)	MLR	3	TSHE, TPHMD, TPHVL	23
Total shrub cover	Tree	5	TSHE, QMDALL, TPHVS, TPH_TOL, ELEVATION	21
Total shrub cover	Tree	3	TSHE, QMDALL, TPHVS	17
ln(total shrub cover)	Tree	3	TSHE, BAALL, TPHMD	27
ln(deciduous shrub cover + 1)	MLR	3	TSHE, QMDHAL, BAALL	17
Deciduous shrub cover	Tree	5	SDI, QMDHAL, TSHE, AUGMAX, SLOPE	22
Deciduous shrub cover	Tree	3	SDI, BAHALL, TSHE	18
ln(deciduous shrub cover + 1)	Tree	3	SDI, BAHALL, QMDALL	18

trees, and higher densities of shade-tolerant trees (nodes 5 and 6).

For the deciduous shrub cover tree model, 10 sets of 10-fold cross-validation revealed that deviance was minimized at 4–10 nodes (mean = 6, median = 6.2; 4, 6, and 8 nodes were most frequent) and the final tree was pruned to 6 nodes (Fig. 2). The tree shows primary partitions using five predictor variables: stand density index (SDI), quadratic mean diameter of all hardwoods, mean August maximum temperature (AUGMAX), basal area of *T. heterophylla*; and slope. Deciduous shrub cover was highest in plots with a stand density index less than 142.2, quadratic mean diameter of all hardwoods greater than 3.05 cm and mean August maximum temperatures less than 22.8 °C (node 2). Very low deciduous cover is noted for plots with a stand density index greater than 142.2, and basal area of *T. heterophylla* greater than 8.3 m^2/ha (node 6). Interestingly, 8.3 m^2/ha basal area for *T. heterophylla* appears as an important threshold in both tree models.

3.3. Model evaluation and comparison

MLR models of total and deciduous shrub cover for the entire province contained three variables and PRD values were 23% and 17%, respectively (Table 6). Tree models of total and deciduous shrub cover contained five predictor variables (selected by repeated cross-validation) and PRD values were 21 and 22%, respectively (Fig. 2). The MLR model performed slightly better for predicting total shrub cover but for deciduous cover the tree model performed much better (Table 6). Constraining tree models to three variables reduced PRD by 4% for each model; however, MLR stepwise procedures indicated that performance was only negligibly increased with the inclusion of two additional predictor variables. Response variable transformation resulted in a substantial increase in performance (10%) for the constrained total shrub cover tree model. For both total and deciduous cover, transformations resulted in the selection of slightly different explanatory variables. However, the basal area of *T. heterophylla* was still the most important predictor for total shrub cover and stand density index was still the most important predictor of deciduous cover.

4. Discussion

Results from all of our models suggest that forest structure and stand development, site disturbance history, and environment all interact to influence shrub cover in the Oregon coastal landscape. Overstory forest structure variables emerged as the most important for explaining both total and deciduous shrub cover. Environmental variables were more important for explaining deciduous shrub cover, but they also indirectly explain patterns in total shrub cover by influencing tree composition (e.g. basal area of *T. heterophylla* and hardwoods). Our results are consistent with others who note that regional gradients in species composition are associated primarily with climate, whereas patterns of forest structure vary with disturbance but are not predictable based on physical landscape characteristics (Bormann and Likens, 1979; Ohmann and Spies, 1998; Wimberly and Spies, 2001; Ohmann and Gregory, 2002).

Four major relationships in our results can be summarized as follows: (1) shrub cover was negatively associated with *T. heterophylla* basal area and density of shade-tolerant trees; (2) shrub cover was negatively associated with variables that characteristically peak during stem exclusion (sensu Oliver, 1981) and mid-succession (small and medium tree density, stand density index); (3) shrub cover was positively associated with variables that characterize later successional stages (very large tree density, quadratic mean diameter of all trees, stand age); and (4) higher total and especially deciduous shrub cover was positively associated with hardwood stands. These relationships provide managers with a framework for understanding how management and forest development can potentially impact shrub cover and the ecosystem components that rely on shrubs. We discuss each of these relationships in turn below.

The processes underlying the first three patterns noted above can be described by successional dynamics and competitive dominance of taller vegetation layers (Oliver, 1981; Alaback, 1982; Halpern, 1989; Bormann and Likens, 1979; Tappeiner and Alaback, 1989). Low understory cover is characteristic of stem exclusion and mid-succession, when resources such as light and nutrients are limited. In older stands, tree basal area and densities decline, canopy gaps start to form, resources become more heterogeneous and locally abundant, and more favorable environmental conditions develop for understory species (Alaback, 1982; Spies, 1991; Halpern and Spies, 1995; McKenzie et al., 2000; Carey et al., 1999; Thomas et al., 1999). Understory cover may also increase in older stands because of temporal factors associated with dispersal and growth (McKenzie et al., 2000). With our data it is not possible to separate the effects of forest structure from other time-dependent factors such as dispersal.

The basal area of *T. heterophylla* was a very important variable that appeared in many of the models. *T. heterophylla* and other shade-tolerant trees are typically co-dominant with *P. menziesii* and *P. sitchensis* (in the coastal fog zone) or present in the understory. The proportion of *T. heterophylla* and *P. menziesii* in the overstory or subcanopy influence conditions in the understory environment in stands several ways. *T. heterophylla* canopies have high foliar biomass, producing dense, high leaf area canopies that intercept more light and precipitation and have a sparser understory compared to *P. menziesii* canopies (Alaback, 1982; Stewart, 1986; Alaback and Herman, 1988; Deal, 2001). This pattern has been observed for *Tsuga* forests elsewhere (Rogers, 1980). Successful regeneration of *T. heterophylla* seedlings and saplings can also dramatically decrease shrub production (Alaback, 1982; Alaback and Herman, 1988; Stewart, 1988).

The positive association of shrubs, specifically deciduous shrubs, with hardwoods is most likely due to light conditions on the forest floor in these stands. More light penetrates deciduous tree canopies in the early spring when many shrubs begin growing, and more light probably penetrates these canopies throughout the growing season compared to coniferous tree canopies (Pabst and Spies, 1998). This increased light availability may be particularly important for deciduous shrubs because they are not able to photosynthesize throughout the growing season. Other factors, such as nutrient and moisture conditions, may also play an important role. Hardwood stands are frequently dominated by *Alnus rubra*, and nitrogen accretion in soils associated with *Alnus* stands can be significant (Tarrant and Trappe, 1971; Binkley, 1981). Because hardwood stands are frequently limited to recently disturbed areas, the positive association of shrubs with these stands may also represent an early successional stage.

Conceptually, we expected that very high total and deciduous shrub cover would be strongly associated with very early serial stages (e.g. prior to stem exclusion) and that this would be a dominant pattern in the models. For example, in the Oregon Coast Range, vegetative growth and replacement of *Rubus spectabilis* typically allows this species to maintain a dense canopy that can substantially inhibit regeneration of trees and taller shrubs (Tappeiner et al., 1991; Stein, 1995; Knowe et al., 1997). Once persistent cover of *R. spectabilis* is established, succession to other tree or shrub communities could be unlikely without major disturbance or management intervention. Yet, we did not find strong evidence for this type of pattern at the landscape scale. Interestingly, when we examined plots characterized as “open” (definition based on Ohmann and Gregory, 2002: $<1.5\,m^2$/ha total tree basal area and quadratic mean diameter of all dominant trees less than 50) mean shrub cover was below average ($n = 55$; total shrub mean cover = 37.5, S.E. = 3.4; deciduous = 21.3, S.E. = 2.9). Relatively low shrub cover in these areas is most likely due to forest management practices associated with land ownership. The majority (78%) of these open plots are on non-federally owned private industrial or other lands, where management emphasizes production of commercially valuable conifers and herbicides may be used to control competing vegetation after *P. menziesii* is densely re-planted. In the Oregon Coast Range, shrub and hardwood tree cover declined from 1939 to 1993 (R. Hess, USDA Forest Service, Pacific Northwest Research Station, 2003, unpublished data). Historical declines in shrub cover may be due to intensive timber management on private industrial lands, coupled with conservation priorities focused on providing late-successional habitat on federal lands.

As discussed earlier, environmental variables were more important for explaining deciduous shrub cover, emerging in the model directly and indirectly by affecting tree compositional distribution and abundance. The variables that directly emerged reflect both regional gradients (annual precipitation, mean August maximum temperatures) and local microsite conditions (slope, solar radiation). For example, the only variable important for total shrub cover was elevation (tree model), and the pattern illustrated may reflect dense thickets of shrubs frequently found on ridge tops, where soils are thin and trees are prone to windthrow (Alaback, 1982). Slope, solar radiation, annual precipitation and mean August maximum temperatures were important variables for explaining deciduous shrub cover. Lower shrub cover on slightly steeper slopes (greater than 22.3%, tree model) could reflect the pattern observed by Pabst and Spies (1998), where deciduous shrubs such as *Rubus* sp. and *Acer circinatum* were associated with valley bottoms and lower hillslopes in riparian forests. The negative association between solar radiation and deciduous shrubs on private industrial lands could reflect the observation that evergreen shrub cover tends to be higher on warm and dry sites (Zobel et al., 1976; Franklin and Spies, 1991). Annual precipitation was important for USDA Forest Service (USDA-FS) lands, and reflects a regional west–east and north–south decreasing gradient in precipitation, indicating that deciduous shrubs are more abundant in wetter, western and northern locales compared to drier eastern and southern areas.

However, because of the non-random geographic distribution of landowners across the province (e.g. USDA-FS lands are located in the west and USDI-BLM lands in the east), it is difficult to decouple environmental factors from disturbance factors associated with each landowner. This may explain why ownership did not emerge as an important predictor in our tree models as hypothesized. In the study region, overstory forest structure and composition are not independent of land ownership and their associated management and disturbance histories. That is, ownership, and management and disturbance history are embedded in our other variables. The non-random geographic distribution of federal and non-federal landowners across western Oregon's major environmental gradients has been reported elsewhere (Ohmann and Spies, 1998).

All of our models displayed fairly weak predictive power, and bootstrap validations indicate that prediction errors would double if models were extrapolated to other data. Therefore, we caution against using these models for extrapolation outside conditions represented by our data. Lack of strong empirical relationships may reflect the facts that many shrubs can persist and maintain consistent cover under a variety of forest stand and environmental conditions (Halpern and Spies, 1995). In addition, understory response may lag behind overstory treatments or disturbances. For example, if a stand was thinned, overstory measurements would reflect the event instantaneously, while understory measurements would not (McKenzie et al., 2000). Moreover, grouping all shrub species as a functional group may be problematic and responses to our independent variables could be quite different for individual species. Future research efforts could focus on examination of individual shrub species, life histories and growth patterns.

The stochastic nature of site conditions, history, and disturbance also makes prediction at this large scale in this highly managed variable landscape inherently problematic. The most powerful MLR models were derived for USDA-FS lands, which are probably more homogeneous in terms of site conditions and disturbance history compared to the other landowners. Indeed, most of the MLR models developed for individual landowners for both total and deciduous shrub cover had better predictive power than models developed at the landscape scale and showed different variables were important; yet, we were somewhat surprised by how similar the models were in terms of interpretation.

MLR and tree models were somewhat similar in terms of interpretation yet performance varied. Overall, trees models performed similarly or better except when constrained to contain as many predictor variables as MLR models. Yet, the opposite was not true. That is, inclusion of additional variables in the MLR models did not significantly increase model performance. Additional variables in tree models have a different and more profound effect on model performance compared to the effect of additional variables in MLR models. When we transformed total and deciduous shrub cover, tree model performance improved substantially for total shrub cover but not for deciduous cover. This suggests that variance issues were more serious for total shrub cover compared to deciduous shrub cover. Because it is not necessary to deal with the issue of the form of the relationship between response and explanatory variables, response variables for tree model development are not commonly transformed. Yet, De'Ath and Fabricius (2000) note that non-constant variation will give greater weight to data with higher variation and response variable transformation may be desirable. Our results indicate such transformations can greatly improve regression tree model performance.

We found that using a variety of modeling methods provided important insights into complex relationships among variables and improved our understanding of factors that influence shrub cover. For example, MLR models repeatedly showed the importance of *T. heterophylla* in explaining total and deciduous shrub cover, consistent with prior findings concerning the significance of *Tsuga* in controlling forest understory conditions in other regions (Rogers, 1980; Alaback, 1982; Alaback and Herman, 1988; Stewart, 1988; Franklin and Spies, 1991). But the tree models allowed a more explicit understanding of this relationship by providing a threshold. Such identified thresholds may be similarly useful to forest managers and to understand ecological linkages. Strategies to increase total shrub cover for wildlife or other purposes might include reducing the basal area of *T. heterophylla* in stands ($<8\,m^2$/ha) and promoting stands with large trees (QMD $>$ 36). For deciduous shrubs, low stand density index ($<$142) and retention and promotion of hardwood patches with large trees (QMD $>$ 3) is important. However, we caution that application of tree models to make spatial predictions of vegetation or habitat will result in maps with discontinuous boundaries that are the result of the discrete dependent variable (nodes).

We demonstrated the utility of using widely available and extensive forest inventory and research data to identify, quantify, and analyze ecological and anthropomorphic factors associated with shrub cover in coastal Oregon forests. Shrubs are an important ecological and forest health indicator because they contribute to many ecosystem components. However, defining critical levels of shrub cover for these various attributes is complex and will vary by attribute. Generally, low shrub cover in Pacific Northwest forests indicates a lack of structural and compositional complexity and potentially unhealthy ecosystem conditions. Inclusion of shrub cover in assessments of ecosystem health is important because: (1) shrub cover can be used to indicate habitat quality for wildlife; (2) shrubs play a critical role in ecosystem function; and (3) shrub cover is responsive to disturbance and management practices. Our models predict how shrub cover will change with forest structural development in response to natural disturbance or forest management. Forest managers can use our models to analyze landscape level consequences of forest management practices and the effects of potential shifts in climate on shrub cover.

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