

Overstory influences on herb and shrub communities in mature forests of western Washington, U.S.A.

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Abstract: Understanding the relationships between forest overstory and understory communities is essential for predicting changes in the abundance and distribution of understory plants through successional time and in response to forest management. We used correlation analysis, multiple regression, and nonparametric models to explore the relationships between overstory characteristics (canopy cover, stand density, and tree-size distributions) and the abundance of species in the herb and shrub layers in mature forests of western Washington. Overstory variables explained >50% of the variation in the mean response of total shrub cover and ca. 50% of the variation in cover of *Acer circinatum* Pursh (the most common shrub species) and late-seral herbs (species reaching their greatest abundance in late-successional forests). Stronger relationships (80–90% variance explained) were found between overstory variables and the maximum cover of total shrubs, *A. circinatum*, total herbs, and each of three functional groups of herbaceous species. These empirical relationships represent both direct resource limitations and time-dependent responses for which overstory characteristics may be surrogates. Models of maximum abundance yielded the most consistent results, suggesting the relative importance of different overstory variables as limiting factors for understory response, although these limiting factors have different effects on plants with different life-history strategies.

Résumé : Pour prédire les changements dans l'abondance et la distribution des plantes du sous-bois au cours de la succession et en réponse à l'aménagement forestier, il est essentiel de comprendre les relations entre l'étage forestier dominant et les communautés du sous-bois. Les auteurs ont utilisé l'analyse de corrélation, la régression multiple et les modèles non paramétriques pour explorer les relations entre les caractéristiques de l'étage dominant (recouvrement de la canopée, densité du peuplement, distributions de la dimension des arbres) et l'abondance des espèces dans les strates herbacée et arbustive des forêts mûres de l'ouest de l'État de Washington. Les variables de l'étage dominant expliquaient plus de 50% de la variation de la réponse moyenne du recouvrement total du couvert arbustif et environ 50% de la variation du couvert de l'arbuste le plus commun : *Acer circinatum* Pursh et des espèces herbacées de la fin de la succession, qui atteignent leur plus grande abondance dans les forêts de ce stade successional tardif. Une relation plus forte, qui explique 80 à 90% de la variation, a été trouvée entre les variables de l'étage dominant et le recouvrement maximum du total des arbustes, d'*A. circinatum*, du total des herbes et de chacun des trois groupes fonctionnels des espèces herbacées. Ces relations empiriques reflètent à la fois la limitation directe des ressources et les réponses qui sont fonction du temps, pour lesquelles les caractéristiques de l'étage dominant peuvent être des substituts. Les modèles de l'abondance maximale fournissent les résultats les plus consistants, suggérant l'importance relative des différentes variables de l'étage dominant en tant que facteurs limitatifs de la réponse du sous-bois, bien que ces facteurs aient des effets différents sur les plantes possédant différentes stratégies de cycle vital.

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Introduction

To what extent biotic interactions shape the spatial and temporal distributions of species remains among the most fundamental questions in ecology (Tilman 1982; Grace and Tilman 1990; Goldberg and Barton 1992). In terrestrial ecosystems, and in forests in particular, it is often assumed that the competitive effects of taller vegetation layers (e.g.,

overstory trees) determine, in large part, the distribution and abundance of subordinate layers (e.g., subcanopy trees, shrubs and herbs). However, the existence or strength of such interactions can vary at different points during forest development, particularly if there are large changes in the vertical structure of vegetation through time.

In temperate coniferous forests of the Pacific Northwest, strong and predictable relationships between herbaceous and woody plant layers have been described during early succession (Halpern and Franklin 1990) and during stand closure when severe light limitation can lead to dramatic loss of understory plants (Alaback 1982; Klinka et al. 1996; Lezberg 1998). Similar relationships have been inferred from increases in understory cover and biomass following silvicultural thinning of young stands (e.g., Bailey et al. 1998; Thomas et al. 1999). In contrast, there have been few

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Table 1. General environmental features and structural and compositional characteristics of the four study locations.

Location	Elevation (m)	Slope (%)	Aspect	Stand age (years)	Tree density (no./ha) ^a	Basal area (m ² /ha)	Site index ^b (m)	Major (minor) overstory species ^c	Major shrubs and herbs ^d
Gifford Pinchot National Forest									
Butte	975–1280	40–53	E–SE	70–80	759–1781	48–65	27–32	Psme (Tshe, Thpl)	Acci, Vame, Vapa, Bene, Ptaq
Little White Salmon	825–975	40–66	NW–NE	140–170	182–335	61–77	30	Psme (Abgr, Conu)	Acci, Acgl, Coco, Actr, Smst, Bene
Paradise Hills	850–1035	9–33	varied	110–140	512–1005	59–87	26–33	Psme (Tshe, Thpl, Abam)	Acci, Vacc, Vame, Vapa, Gash, Xete, Coca
Department of Natural Resources Lands									
Capitol Forest	210–275	28–52	varied	65	221–562	54–73	37–41	Psme (Tshe, Thpl, Alru)	Acci, Vapa, Pomu, Gash

Note: Ranges are based on mean values for each of the six treatment units within each location (adapted from Halpern et al. 1999).

^aTrees ≥ 5.0 cm DBH.

^bDouglas-fir 50-year site index.

^cTree species codes: Abam, *Abies amabilis*; Abgr, *Abies grandis*; Alru, *Alnus rubra*; Conu, *Cornus nuttallii*; Psme, *Pseudotsuga menziesii*; Thpl, *Thuja plicata*; Tshe, *Tsuga heterophylla*.

^dBased on cover. Species codes in addition to those above: Acci, *Acer circinatum*; Acgl, *Acer glabrum*; Actr, *Achlys triphylla*; Bene, *Berberis nervosa*; Coca, *Cornus canadensis*; Coco, *Corylus cornuta*; Gash, *Gaultheria shallon*; Pomu, *Polystichum munitum*; Ptaq, *Pteridium aquilinum*; Vacc, *Vaccinium ovalifolium* – *V. alaskaense*; Vame, *V. membranaceum*; Vapa, *V. parvifolium*; Xete, *Xerophyllum tenax*.

attempts to describe or model these empirical relationships in mature or late-seral forests (but see McKenzie and Halpern 1999), forests that are, by comparison, less dynamic but more complex structurally. We suspect that in these older forests, strong direct effects may be masked or confounded by myriad possible interactions among vegetation layers, by legacies of past disturbance, or simply by the passage of time.

In this paper, we employ correlation analysis, multiple regression, and nonparametric models to explore the relationships between overstory characteristics and the abundance of herbs and shrubs in mature forests of western Washington. In conventional analyses of “mean” response, direct interactions between overstory and understory may not be detectable through the variation induced by other factors. Thus, we employ an additional approach, in which we estimate “maximum” responses (Thompson et al. 1996; Guo et al. 1998; Scharf et al. 1998; Cade et al. 1999). This approach is analogous to that used to describe biomass–density relationships in pure, even-aged forests (Yoda et al. 1963) or tree density maxima in uneven-aged, mixed-species stands (Sterba and Monserud 1993). Models of maximum response are useful for quantifying thresholds or limits, and the extent to which a predictor (e.g., tree cover) constrains a response variable (e.g., herb cover) within the context of other influences that comprise the operational environment.

Our goal is to identify those dependent and independent variables that have strong and predictable relationships and to interpret these relationships in light of our understanding of species’ life histories, environmental influences, and successional development. We examine an array of analytical approaches, including correlation and regression analysis, regression trees, and linear and nonlinear models of maximum response. Given the large number of species-level comparisons possible, we restrict our analyses to the responses of broad groups of plants that occupy distinct vegetation layers (i.e., shrub and herb layers), or that share common successional patterns or responses to disturbance (Halpern 1989; Spies 1991; Halpern and Spies 1995). In addition to reducing the number of comparisons to a manageable level, this approach facilitates comparison with other forest types in which vegetation may differ floristically but is similar structurally or functionally.

Methods

Study areas

The data used in this analysis comprise a subset of the baseline measurements of forest vegetation collected as part of the Demonstration of Ecosystem Management Options (DEMO) study. DEMO is a large-scale experiment that examines the effects of level and spatial pattern of green-tree retention on various components of mature coniferous forests in the Pacific Northwest; these include vegetation, wildlife, invertebrates, and fungi (Aubry et al. 1999; Halpern et al. 1999). Here we restrict our analyses to pre-treatment data from four study locations in southwestern Washington: three in the Cascade Range in the Gifford Pinchot National Forest and one in Capitol State Forest in the Black Hills, south and west of Olympia. These represent a diversity of forest types, stand ages, and environmental conditions (Table 1). Elevations range from ca. 200 to 1700 m, slopes are gentle to steep, and aspects vary considerably. Three forest zones are represented: *Tsuga*

Table 2. Three groups of species in the herb layer based on successional dynamics and responses to disturbance (Halpern 1989; Spies 1991; Halpern and Spies 1995).

Dominant herbs	Release herbs	Late-seral herbs
<i>Berberis nervosa</i> Pursh	<i>Galium triflorum</i> Michx.	<i>Achlys triphylla</i> (Smith) DC.
<i>Gaultheria shallon</i> Pursh	<i>Hieracium albiflorum</i> Hook.	<i>Adenocaulon bicolor</i> Hook.
<i>Polystichum munitum</i> (Kaulf.) Presl	<i>Linnaea borealis</i> L.	<i>Chimaphila menziesii</i> (R.Br.) Spreng.
<i>Xerophyllum tenax</i> (Pursh) Nutt.	<i>Pteridium aquilinum</i> (L.) Kuhn.	<i>Chimaphila umbellata</i> (L.) Bart.
	<i>Rubus ursinus</i> Cham. & Schlecht.	<i>Clintonia uniflora</i> (Schult.) Kunth.
	<i>Trientalis latifolia</i> Hook.	<i>Cornus canadensis</i> L.
		<i>Disporum hookeri</i> (Torr.) Nicholson
		<i>Goodyera oblongifolia</i> Raf.
		<i>Pyrola asarifolia</i> Michx.
		<i>Pyrola picta</i> Smith
		<i>Pyrola secunda</i> L.
		<i>Smilacina racemosa</i> (L.) Desf.
		<i>Smilacina stellata</i> (L.) Desf.
		<i>Tiarella trifoliata</i> L.
		<i>Trillium ovatum</i> Pursh
		<i>Vancouveria hexandra</i> (Hook.) Morr. & Dec.

Note: Herbs included were present on >10% of plots, with >1% cover (see text). Nomenclature follows Hitchcock and Cronquist (1973).

heterophylla (Raf.) Sarg. (western hemlock); *Abies grandis* (Dougl.) Forbes (grand fir); and *Abies amabilis* (Dougl.) Forbes (silver fir) (Franklin and Dyrness 1988). *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) dominates the canopy at all locations, but associated canopy and subcanopy species vary. Stand basal area, density, and understory composition also vary within and among locations, reflecting differences in disturbance history, regeneration patterns, and physical environments. Stands are considerably older at Little White Salmon and Paradise Hills and considerably denser at Paradise Hills and Butte (Table 1). Despite this heterogeneity, many of the same taxa dominate the understory (e.g., *Acer circinatum* Pursh (vine maple), *Berberis nervosa* Pursh (Oregongrape), and *Vaccinium* spp. (huckleberry)).

Data collection

A complete description of the vegetation sampling design is presented in Halpern et al. (1999). Here we describe only those components pertinent to the current analysis. At each of six, 13-ha treatment units within each study location, permanent vegetation plots were established across a systematic grid (40-m spacing), although the number and spatial distribution of plots vary by treatment (Halpern et al. 1999). A total of 32–37 plots were sampled per treatment unit yielding a grand total of 818 plots. Distances among the treatment units within each location vary considerably because of constraints of local topography and past management activity (e.g., harvest units and roads). Treatment units are adjacent at some locations but are separated by as much as 9–10 km at others.

At each grid point sampled, overstory and understory attributes were measured using a series of nested plots and transects. Trees 5–15 cm diameter at breast height (DBH) were identified to species and measured for diameter in a circular, 0.01-ha plot; trees >15 cm DBH were measured in a circular, 0.04 ha plot. Saplings (trees >10 cm tall, <5 cm DBH) were tallied in four 1 × 6 m quadrats, arranged along perpendicular radii within each circular tree plot. Cover of species in the shrub layer was estimated with the line-intercept method along the line defining one side of each sapling quadrat. Cover of all species in the herb layer (including graminoids, ferns, herbs, subshrubs, and low shrubs) was visually estimated in a series of twenty-four 0.10-m² microplots per plot (six along each intercept line). Overstory canopy cover (cover of trees >5 cm DBH) was estimated with a moosehorn densiometer.

Readings were made at eight points within each tree plot (at both ends of each intercept line).

Data analysis

We calculated plot-level means for tree basal area and density (total and by species), overstory canopy cover, sapling density, and shrub- and herb-layer cover (summed totals and by species), in each of the 818 plots. In addition, we grouped herbaceous species into three categories based on species classifications in Halpern (1989): (i) “dominant” herbs, or “successional generalists,” species that are ubiquitous and abundant during most stages of forest development (equivalent to “R3” species of Halpern (1989)); (ii) “release” herbs, typically subordinate, forest species that respond positively to canopy removal or other disturbance (“R1” and “R2” species); and (iii) “late-seral” herbs, those that reach maximum development in old-growth forests (Halpern and Spies 1995) and that are sensitive to canopy removal and disturbance (“R5” species) (Table 2). Plot-level measurements were integrated into a model data base, and SPLUS for Windows version 4.5 (Mathsoft 1997) was used for all analyses. Correlation analyses were performed and predictive models were developed for the shrub and herb layers.

Correlation analysis

To examine the pairwise relationships among all variables, and to assess the strength and possible confounding effects of same-layer interactions, we computed a matrix of Pearson product-moment correlations. The relative strength of relationships in the correlation matrix suggested initial choices of variables for the mean response and maximum abundance models (see below). Because of the large sample size (producing correlations as low as ±0.08 that were significant at $\alpha = 0.05$) and possible confusion over significance levels with multiple tests (Wright 1992), inferences from the correlation analysis were based on the relative strengths of relationships and their signs rather than on levels of significance.

Predictive models of mean response

To develop predictive models for components of the shrub and herb layers as functions of components of taller strata, we used a combination of linear models and two nonparametric methods, locally weighted regression (LOESS; Cleveland and Devlin 1988; Trexler and Travis 1993) and classification and regression trees (CART; Breiman et al. 1984). Overstory variables and sapling

Table 3. Plot-level means and ranges (in parentheses) by location for predictor variables used in the models.

Location	Stand density index (SDI)	Canopy cover (CANOPY) (%)	Quadratic mean diameter (QMD) (cm)	Coefficient of variation in tree diameters (CVD)	Sapling density (SAPL) (no./m ²)
Gifford Pinchot National Forest					
Butte	240.2 (82.7–487.4)	80.0 (32.4–97.6)	30.0 (17.6–59.5)	0.39 (0.21–1.03)	0.14 (0.00–0.92)
Little White Salmon	122.6 (3.5–316.7)	64.8 (0.0–93.3)	74.4 (16.0–123.0)	0.47 (0.00–1.84)	0.06 (0.00–0.67)
Paradise Hills	227.3 (79.9–370.9)	83.3 (34.9–98.1)	40.1 (26.5–56.2)	0.50 (0.30–1.11)	0.58 (0.00–8.46)
Department of Natural Resources Lands					
Capitol Forest	148.1 (38.3–357.7)	77.3 (30.6–97.5)	53.0 (17.2–82.4)	0.38 (0.04–0.94)	0.02 (0.00–0.42)

Table 4. Proportion of plots present, and means and ranges in percent cover for the response variables.

	Total shrubs	Vine maple	Total herbs	Dominant herbs	Release herbs	Late-seral herbs
Proportion of plots	0.96	0.59	1.00	0.93	0.94	0.89
Mean	40.0	45.3	38.5	20.1	3.5	15.0
Range	0.1–160.4	0.1–100.0	<0.1–118.6	<0.1–105.8	<0.1–41.8	<0.1–90.1

density were predictors for shrub-layer responses and these plus shrub-layer variables were predictors for herb-layer responses. Response variables in the shrub layer were (i) summed shrub cover, hereafter total shrub cover (the summed cover of the individual species, which can exceed 100%), and (ii) cover of any species present on more than 10% of the plots. Response variables in the herb layer were (i) summed herb cover (as calculated above), hereafter total herb cover, and (ii) for species with $\geq 1\%$ cover in at least 10% of the plots, the summed cover of individual species within each of the three functional groups described above (see Table 2).

We then built a separate multiple linear regression model for each response variable, using only those plots in which the response variable was not zero (because the abundance of a plant group or species is conditional on its presence). Potential predictors for shrub models were as follows:

- (1) tree basal area (BA) in m²/ha;
- (2) stem density (TPH) in trees/ha;
- (3) a simple stand density index (SDI), where $SDI = (BA \times TPH)^{0.5}$;
- (4) overstory canopy cover (CANOPY) in percent;
- (5) two variables representing tree-size distributions: (i) quadratic mean diameter of trees (QMD): $QMD = (\sum DBH_i^2 / n)^{0.5}$ where DBH_i is the diameter of tree i and n is the number of trees/plot; and (ii) coefficient of variation of diameter (CVD) for all trees on a plot; and
- (6) sapling density (SAPL) in saplings/m².

These same predictors, plus total shrub cover (SHRUB) were used for all herb models. Predictors are summarized in Table 3 and response variables in Table 4.

We used backward elimination (Neter et al. 1990) to select subsets from the full set of predictors that were most strongly correlated with each response variable. The final model was that which minimized the mean-squared error of residuals, while retaining only those predictors whose coefficients were significantly different from zero at $\alpha = 0.05$. Standard diagnostics were applied to check for normality and constant variance of residuals, and a Cook's distance plot was used to identify and remove significant outliers. Where appropriate, we transformed the response variables to meet the assumptions of regression.

Although the influence of location in our data base represents a "random effect" and cannot be interpreted as a factor in a predictive regression model, we added a "location variable" to each of the optimal models to identify those that might be distinctly differ-

ent if built using data from a single location. A large number of "significant" coefficients for the location variable would suggest that many model predictions would be sensitive to location. Conversely, a dearth of "significant" coefficients would suggest that the models were insensitive to location and, therefore, more robust to extrapolation across their geographic range (western Washington).

For each optimal linear model, we checked for possible nonlinear relationships using (i) scatterplots of each predictor versus the response and (ii) LOESS models (Cleveland and Devlin 1988). Where strong nonlinear relationships were apparent, we attempted to fit nonlinear models using partially linear least squares (Bates and Lindstrom 1986). To validate the models and estimate their predictive power, we used a refined bootstrap estimate of prediction error (Efron and Tibshirani 1993), based on 100 replicates for each model. The resulting statistic, "error optimism," reflects the percent increase in residual squared error expected if the model were extrapolated to other data from a similar population (Efron and Tibshirani 1993).

After selecting each final model, we fit a nonparametric, tree-based model (CART; Breiman et al. 1984; Clark and Pregibon 1992) using the same variables. Tree-based modeling uses binary recursive partitioning based on reduction in deviance to split the data into increasingly homogeneous subsets. We used this method for exploratory purposes to suggest whether incorporating complex nonadditive interactions into models could increase the proportion of variance explained (Clark and Pregibon 1992) and to assess the possibility of threshold responses. We used an adaptive estimation method (Breiman et al. 1984) to minimize the complexity of each model (number of branches and nodes) without sacrificing goodness of fit. This method first fits an overly large tree, then uses a cost-complexity criterion to "prune" branches that do not contribute significantly to the reduction in deviance (Breiman et al. 1984).

Models of maximum response

Because the constraints or limitations that arise from biotic interactions may be more evident from maximum than from mean responses (see above), we used a method outlined by Scharf et al. (1998) to model the maximum abundance of one variable as a function of another. Using two-dimensional scatterplots of our six response variables on potential predictors, we identified the predictor that produced the scatterplot with the clearest "edge" at maximum levels of the response. We identified and removed outliers that were clearly isolated in the scatterplots, then divided the

Table 5. Correlation matrix for selected overstory and understory variables (density of saplings, cover of shrubs and herbs).

	BA	TPH	CANOPY	QMD	SDI	CVD	Sapling density	Total shrubs	Vine maple	Total herbs	Dominant herbs	Release herbs	Late-seral herbs
BA	1.00												
TPH	-0.01	1.00											
CANOPY	0.41	0.37	1.00										
QMD	0.28	-0.71	-0.34	1.00									
SDI	0.42	0.86	0.57	-0.63	1.00								
CVD	-0.05	0.12	0.01	-0.14	0.15	1.00							
Sapling density	-0.01	0.10	0.02	-0.13	0.11	0.14	1.00						
Total shrubs	-0.08	-0.53	-0.57	0.66	-0.60	-0.02	-0.17	1.00					
Vine maple	0.00	-0.49	-0.45	0.55	-0.50	-0.06	-0.23	0.89	1.00				
Total herbs	-0.13	-0.47	-0.30	0.48	-0.55	-0.06	-0.23	0.35	0.03	1.00			
Dominant herbs	-0.13	-0.24	0.05	0.02	-0.25	-0.14	-0.17	-0.09	-0.18	0.56	1.00		
Release herbs	-0.22	0.27	-0.05	-0.39	0.18	-0.09	-0.02	-0.28	-0.39	0.03	-0.13	1.00	
Late-seral herbs	0.08	-0.35	-0.36	0.63	-0.38	0.12	-0.08	0.55	0.31	0.48	-0.39	-0.11	1.00

Note: Abbreviations for overstory variables are as follows: BA, tree basal area; TPH, trees per hectare; CANOPY, percent canopy cover; QMD, quadratic mean diameter; SDI, stand density index; CVD, coefficient of variation of tree diameters.

paired observations of the predictor and response variables into “bins” containing equal numbers of observations. Within each bin, we identified the maximum level of the response variable and paired that observation with the corresponding observation of the predictor. We then regressed these maxima on their predictors (where n is the number of bins) to obtain a “maximum density line” made up of the fitted values, using both linear and LOESS techniques. Choice of bin size involves a trade-off between sample size for the regression (number of bins) and the number of observations within each bin. Thus we adjusted bin size iteratively during the modeling process to optimize the fit (Scharf et al. 1998), with the constraint that it remained a constant proportion of total observations for each of the six models.

We extended this method to three dimensions (maximum abundance of one variable in response to two others), to estimate maximum abundance surfaces. From the scatterplots we identified the two predictors showing the clearest “edges.” We tested several pairs of variables for each model, however, to accommodate interactions not evident from visual examination, and selected the pair that minimized the residual squared error. Because pairs of numbers cannot be ordered, we did not generate bins with equal numbers of observations, as in the two-dimensional models, but instead created equal-sized rectangular bins in the space of the two predictors, where the dimensions of the rectangles were equal proportions of the range of predictors 1 and 2, respectively (creating equal numbers of bins in X and Y directions). Within each bin, we selected response and predictor observations in the same manner as for the two-dimensional model, with the constraint that bins with fewer than 10 observations were excluded. Once again, bin size was adjusted iteratively during the modeling process.

Results

Correlation analysis

Total shrub cover displayed the strongest relationship to individual overstory variables of any of the response variables considered (Table 5). Pearson correlations were strongly negative with SDI ($R = -0.60$), CANOPY ($R = -0.57$), and tree density ($R = -0.53$) and strongly positive with QMD ($R = 0.66$). Correlations for *Acer circinatum* cover (which comprised 76% of shrub cover on plots in which it was present) were very similar to those for total shrub cover. Total herb and late-seral herb cover had slightly weaker correlations with overstory variables than did shrub variables; dominant herbs and release herbs had significantly weaker correlations (Table 5). In addition, correlations for release herbs were mostly opposite in sign from those of dominant and late-seral herbs.

Models of mean response

Six predictor variables appeared in one or more of the regression models of understory abundance, with each model using a subset of three to five predictors (Table 6). The model of total shrub cover had the best explanatory power, while the late-seral herb model was the best among the herb models. In contrast, models of dominant and release herbs were considerably weaker (Table 6). QMD appeared as a predictor in every model, CANOPY in five of six, and SAPL and SDI in four (these latter two always had a negative coefficient). Overstory variables with the strongest simple correlations to the response variables were not always the best predictors, or even significant, in the multiple regression models. For example, late-seral herb cover was more

Table 6. Predictive models for understory cover.

Model	Coefficients for predictors							Summary statistics			
	Intercept	SDI	QMD	CANOPY	SHRUB	SAPL	CVD	R ²	% error optimism ^a	PRD ^b (tree)	
Total shrubs ^c	0.689 379 (0.048 532)	-0.000 420 (0.000 124)	0.006 469 (0.000 430)	-0.005906 (0.000 537)		-0.056 234 (0.012 281)		0.57	6	0.67	
Vine maple ^d	0.972 278 (0.089 511)	-0.000 485 (0.000 246)	0.006 467 (0.000 767)	-0.006 935 (0.001 004)		-0.376 521 (0.102 426)		0.41	0	0.52	
Total herbs ^e	7.326 848 (0.330 175)	-0.011 361 (0.000 945)	0.016 303 (0.003759)			-0.768 489 (0.115 298)		0.36	29	0.49	
Dominant herbs ^c	0.708 947 (0.067 142)	-0.001 870 (0.000 162)	-0.001 779 (0.000 639)	0.002 863 (0.000 763)	-0.001 899 (0.000 371)	-0.106 525 (0.017 356)		0.20	0	0.62	
Release herbs ^c	4.876 471 (0.273 084)		-0.022 923 (0.002 407)	-0.021 953 (0.002 854)	-0.006 204 (0.001 538)		-0.878 130 (0.195 504)	0.25	3	0.53	
Late-seral herbs ^d	-0.016 808 (0.056 333)		0.006 229 (0.000 500)	-0.001 826 (0.000 590)	0.001 366 (0.000 319)		0.282 699 (0.040 738)	0.45	4	0.80	

Note: See Table 3 for definitions of predictors. Standard errors are given in parentheses.

^aPercent error optimism, which is the increased prediction error expected (from 100 bootstrap replicates).

^bPRD (tree) is the percent reduction in deviance in corresponding tree-based model, roughly equivalent to R².

^cArcsine square-root transformation of normalized response variable.

^dArcsine square-root transformation of response variable.

^eSquare-root transformation of response variable.

strongly correlated with SDI (-0.38) than with CVD (0.12), but only CVD proved to be significant within the context of multiple regression (Tables 5 and 6). The "location variable" had minimal effect on most models. Only in the late-seral herb model was there a "significant" coefficient for location (for two of four locations).

Three different transformations of the response variables were used to achieve normality in the residuals (Table 6). Although partially linear models (see above) and extra non-linear parameters were examined, none of these proved superior to ordinary linear models, although some simple relationships (one response, one predictor) were clearly non-linear. The bootstrap validations indicate that only the model of total herb cover substantially underestimated the mean-squared error expected from applying the model to another sample from the same population (Table 6).

Tree-based models

Each tree-based model explained more variation than its corresponding regression model. Comparisons of the percent reduction in deviance (PRD) with R² for regression models show a wide range of increased explanatory power, from a 17% difference for total shrub cover to a threefold increase for dominant herbs (Table 6). Primary partitions were either on QMD (for total shrub cover, *Acer circinatum* cover, release herbs, and late-seral herbs) or SDI (for total herb cover and dominant herbs). For late-seral herbs, the primary partition accounted for more than one half of the total deviance explained (Fig. 1a), but for dominant herbs, it accounted for only one sixth of the total (Fig. 1b). No variables were lost in the pruning process for any of the models, thus variables that were significant in regression models remained significant in tree-based models.

Maximum abundance relationships

Both two-dimensional (one predictor) and three-dimensional (two predictor) models of maximum response suggested tighter relationships than did models of mean response (Table 7). Predictors in two-dimensional models were either SDI or SHRUB, and in three-dimensional models, either SDI and QMD or SDI and SHRUB. In two dimensions, the maximum response was either clearly linear (Fig. 2a) or clearly nonlinear (Fig. 2b). In three dimensions, nonlinear relationships were more evident. For example, the two fits for release herbs and total herb cover were similar in two dimensions but very different in three dimensions (R² values in Table 7), while dominant herb cover was different in both two and three dimensions. For total and dominant herb cover, differences between linear and LOESS models reflected the presence of unimodal responses to overstory conditions (responses reached a peak at intermediate values of the two predictors; Figs. 3a and 3b). In contrast, the abundance of late-seral herbs increased monotonically as SDI decreased and QMD increased (Fig. 3c).

Half of the linear models in three dimensions had only one significant predictor, reducing them to two dimensions. Even where there were two significant predictors, three-dimensional models for responses in the shrub layer showed poorer relationships than did their two-dimensional counterparts (Table 7). This reflects two limitations in the three-dimensional modeling process: the poorer efficiency of the

Table 7. Maximum abundance models for understory cover.

Response	Two dimensions			Three dimensions		
	Predictor	R^2 (linear)	R^2 (LOESS)	Predictors	R^2 (linear)	R^2 (LOESS)
Total shrubs	SDI	0.89	0.93	SDI, QMD	0.80 ^a	0.88
Vine maple	SDI	0.81	0.94	SDI, QMD	0.64 ^b	0.82
Total herbs	SDI	0.61	0.65	SDI, QMD	0.42 ^b	0.89
Dominant herbs	SHRUB	0.41	0.66	SDI, QMD	0.53	0.92
Release herbs	SHRUB	0.68	0.71	QMD, SHRUB	0.63	0.84
Late-seral herbs	SDI	0.83	0.86	SDI, QMD	0.84	0.92

^aSDI (stand density index) nonsignificant.

^bQMD (quadratic mean diameter) nonsignificant.

binning algorithm with respect to the two-dimensional models and the inability to reasonably remove outliers by visual inspection.

Discussion

We expected that understory development (total cover of herbs or shrubs) would be negatively correlated with overstory variables. Moreover, assuming that the inhibitory effects of overstory trees are manifested primarily through reduction in light availability, we expected correlations with canopy cover to be stronger than those with other aspects of stand structure (e.g., stand density or tree size distributions). Herb and shrub cover were indeed negatively correlated with overstory variables; however, correlations with SDI were slightly stronger than with CANOPY. The contributions of sunflecks (Chazdon and Pearcy 1991), or light that penetrates at lower angles of incidence, are not captured by our densiometer readings but instead may be more accurately represented by measures of stand density. Alternatively, light levels may be less limiting for understories in mature stands than in earlier stages of stand development (Alaback 1982; Lezberg 1998; Thomas et al. 1999).

We also expected that understory responses to overstory conditions would be more apparent for taller growth forms that are able to take advantage of openings and ascend into canopy or subcanopy gaps (shrubs) than for growth forms restricted to the ground layer (herbs). Shrub-layer responses in the regression models and correlations were stronger on average than herb-layer responses; however, late-seral herbs were an exception, particularly in the tree-based model.

Our expectations for herb-layer responses varied among groups. Species that exhibit the potential for rapid vegetative expansion ("release" herbs) might be expected to show strong negative correlations with overstory canopy cover. Conversely, if development of late-seral herbs is temporally dependent (increasing with time since disturbance; Halpern and Spies 1995), rather than resource limited, they should show weak correlations with overstory variables. Likewise, correlations for dominant herbs could be expected to be weak, because they are abundant during most stages of stand development. Our expectations proved false for both release and late-seral herbs. Thus, it is likely that herb-layer responses reflect not only the direct effects of the overstory but also indirect effects that change coincidentally with overstory development. We suspect that these are time-dependent responses for which overstory characteristics may serve as surrogates.

Overstory characteristics as surrogates for successional time

Release herbs were positively correlated with variables that peak during early to middle succession (SDI, tree density) and negatively correlated with predictors that peak in stands that have remained undisturbed for substantial periods of time (QMD, CANOPY, SHRUB, CVD). Forest species that respond positively to disturbance should be most abundant in early succession but decline in stands that are undisturbed except for occasional treefall. Thus, the counterintuitive relationship between release herbs and SDI may simply reflect their concurrent decline with successional time rather than a beneficial effect of increased stand density. However, the relatively weak regression relation reinforces our previous assumption that any strong effect of the overstory on release herbs would have occurred earlier in stand development (closer in time to stand-initiating disturbance).

Dominant herb response was correlated with five of the six predictors, but the overall regression relation was also weak, supporting the general observation that these species are able to thrive and dominate the herb layer in a variety of forest conditions (Halpern and Spies 1995). Thus, neither overstory structure nor "successional" time appears to be a major influence on the variability in dominant herb abundance among plots. In contrast, the responses of late-seral herbs, total shrubs, and vine maple can be linked both to changes in available resources and to the passage of time. All were strongly positively correlated with QMD (which typically increases monotonically through succession) and negatively correlated with SDI and CANOPY. As canopy gaps form, tree density declines through natural mortality, and biomass is aggregated in space (increase in QMD), resources become more available for shrub species. Late-seral herbs, on the other hand, may be increasing in response to gradual amelioration of unfavorable environmental conditions or belatedly as a consequence of limited dispersal and slow rates of growth (Matlack 1994; Halpern and Spies 1995; Jules 1998). The resulting positive relationship of late-seral herbs and shrubs may thus reflect their parallel increases over time rather than any strong biotic interactions.

Maximum abundance models

Maximum abundance models exhibited clearer relationships than did mean response models for each of the six understory variables (Tables 6 and 7), suggesting that the role of resource limitation in constraining understory abundance can be modeled empirically, even if the underlying mechanisms are not apparent. For example, the success of

Fig. 1. Tree-based models of (a) late-seral herb cover and (b) dominant herb cover as a function of QMD, CVD, shrub cover, canopy cover, and sapling density. Values at nodes are predicted cover, in percent. Predictions for a plot are obtained by moving down the tree, branching left at a split if the plot meets the rule, or branching right if it does not. The insert shows the proportion of deviance accounted for at each split.

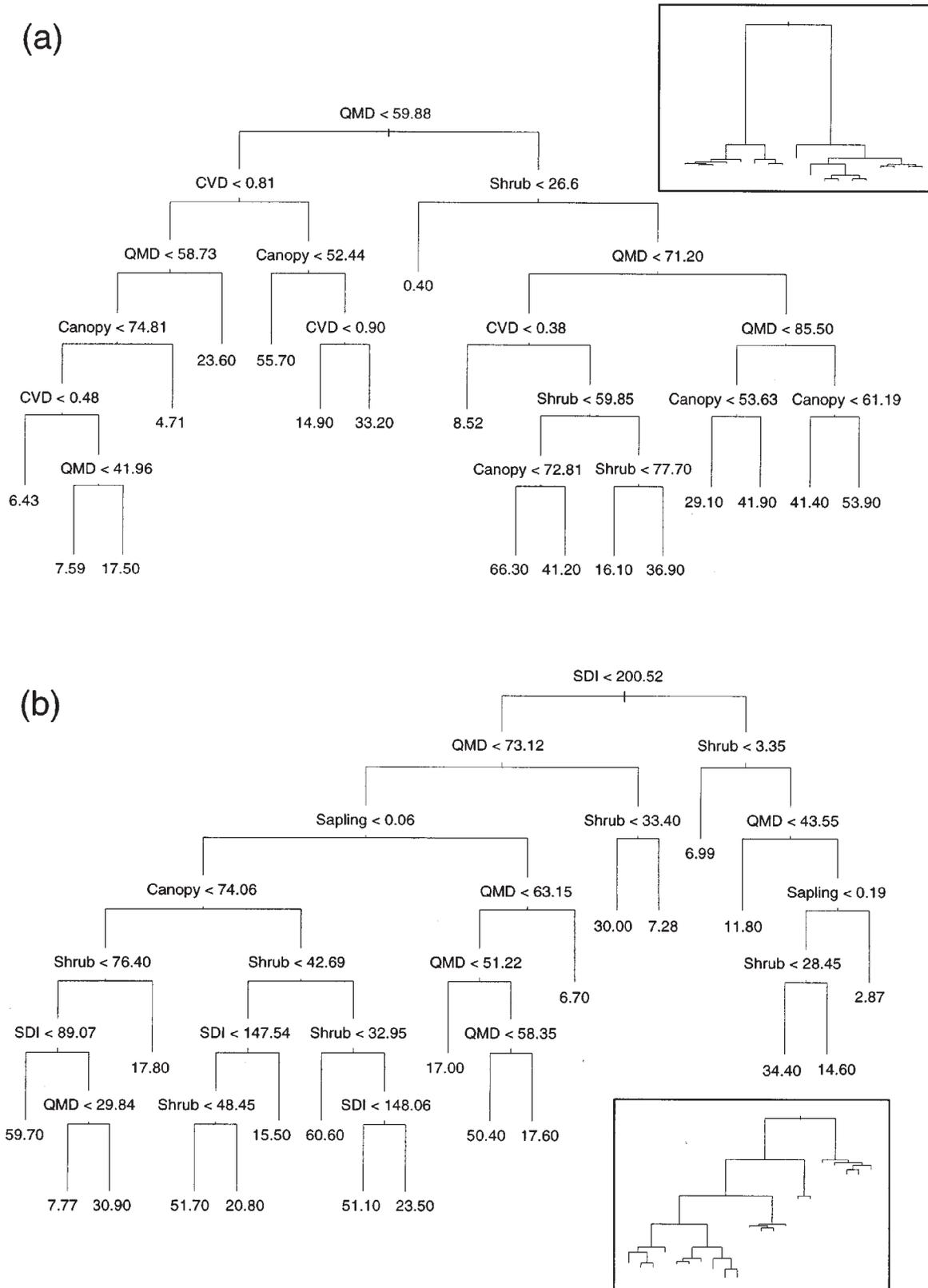
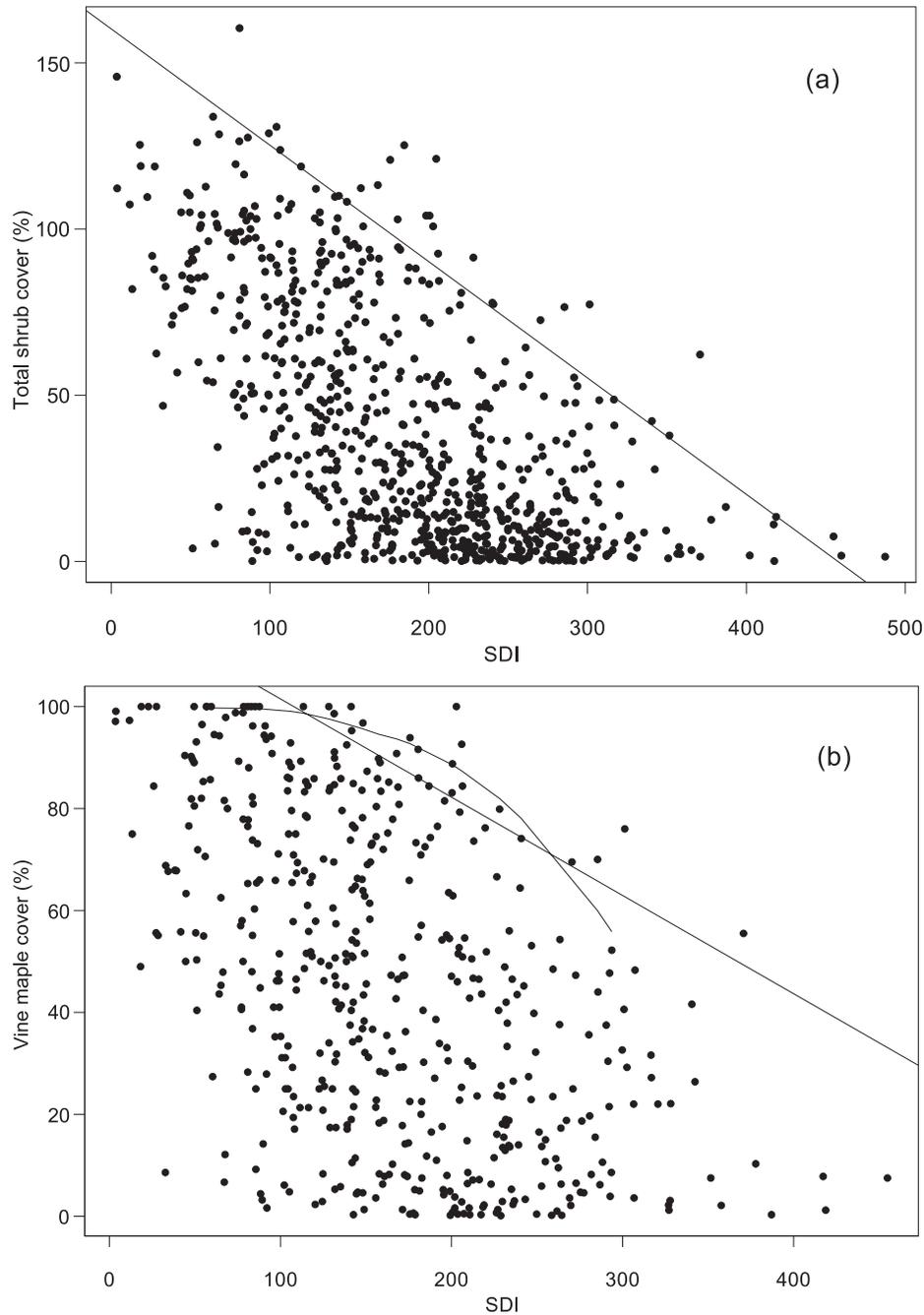


Fig. 2. Maximum abundance models of (a) shrub cover as a linear function of SDI and (b) vine maple cover as functions of SDI. In Fig. 2b, the straight line shows the fitted values of linear regression, and the curved line shows the fitted values of a LOESS model. The latter is truncated at $SDI \approx 300$, because the LOESS algorithm requires a minimum number of data points and fitted values cannot be extrapolated.



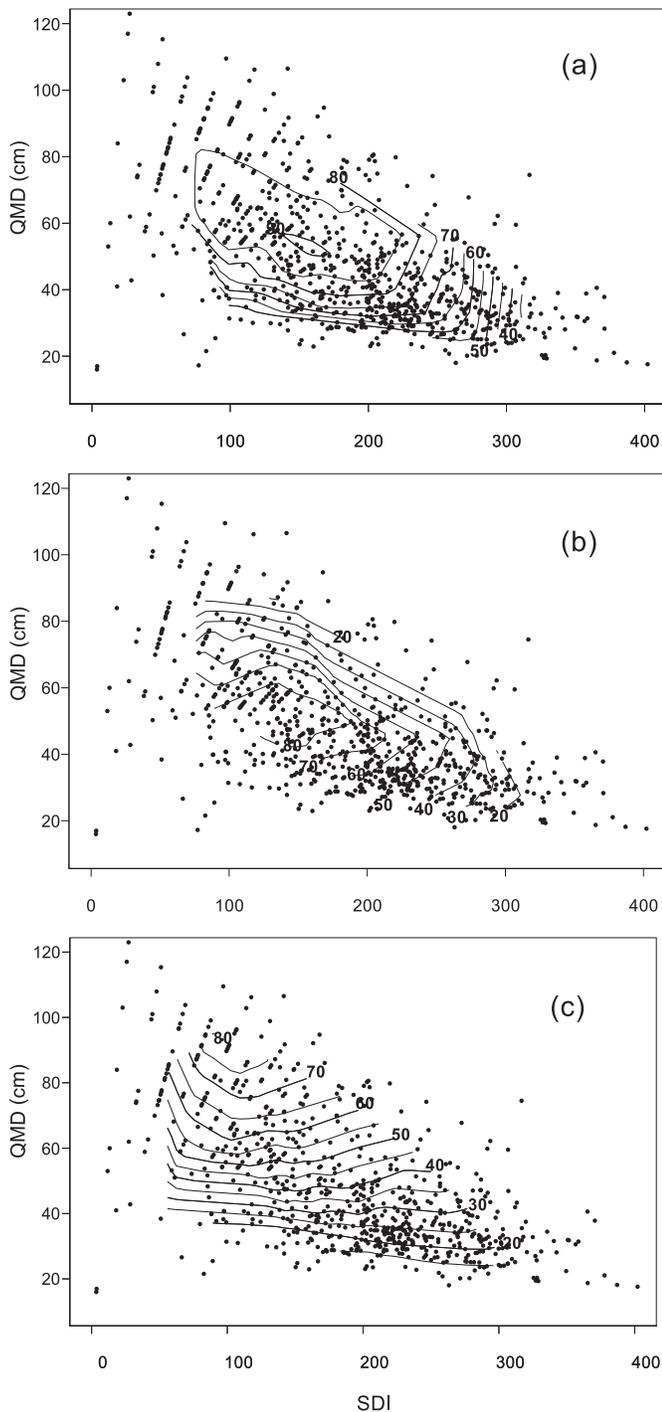
the two-dimensional models of maximum abundance for shrubs (total shrub and vine maple cover) indicates a clear limit in response to stand density. The distribution of shrub cover with respect to SDI was “triangular” (Maller et al. 1983) producing a linear decline of maximum shrub cover (Fig. 2a). Vine maple showed a similar pattern for $SDI > 150$ (Fig. 2b). SDI could be a surrogate for the relative availability of light or of nutrients, water, or growing space (Ford and Diggle 1981; Riegel et al. 1995; Morris 1998).

In the herb layer, the superiority of nonlinear (LOESS)

three-dimensional models suggests more complex interactions and possible mediation by the shrub layer. For late-seral herbs, the primary constraint may be the passage of sufficient time for populations to reestablish and expand following disturbance; maximum cover increased monotonically with decreasing SDI and increasing QMD.

In contrast, maximum cover of total herbs and dominant herbs were clearly unimodal (Figs. 3a and 3b), suggesting an interplay of limiting factors (including SDI), time, and perhaps, competition within the understory. For example,

Fig. 3. Maximum abundance models (three-dimensional LOESS) of three categories of herb cover as a function of SDI and QMD. Numbers on the contour lines represent the predicted maximum of percent cover associated with that line. For (a) total herb cover and (b) dominant herb cover, contours suggest a unimodal distribution of cover maxima in the space of the two predictors. Maximum cover is highest at intermediate values of the predictors and lower at their extremes. For (c) late-seral herb cover, contours suggest a monotonic increase of cover maxima as SDI decreases and QMD increases.



competitive advantages may shift over time between herb-layer dominants like salal (*Gaultheria shallon* Pursh) and conifer regeneration (Huffman et al. 1994; Klinka et al. 1996). Dominant herb maxima may increase through mid-succession as SDI decreases (Fig. 3b), then decrease in response to competition from shrubs or to nutrient limitations caused by slower decomposition rates in older stands (Pastor and Post 1986; Finer et al. 1997). The same scenario may apply to total herb cover.

A wide range of ecological interactions can be inferred from bivariate scatterplots, even if there are no clear functional (e.g., linear or curvilinear) relationships (Thomson et al. 1996; Scharf et al. 1998). When there are clear edges for the maxima of a response variable, the predictor may represent a limiting factor or a surrogate thereof. The interpretation of SDI as a limiting factor for shrub maxima is thus supported by the tight fit of the two-dimensional models. In the three-dimensional herb models, however, distributions of cover maxima in the two-dimensional space of SDI and QMD follow expected trajectories through successional time, and there is no obvious interpretation of a direct limitation by one or more overstory variables.

Model applications

In addition to providing insights into understory dynamics in these forests, our regression models could be incorporated into either process-based ("gap") or empirically based models of forest growth and succession in the Pacific Northwest (e.g., Hann et al. 1992; Urban et al. 1993). The predictive models for shrub and late-seral herb cover are comparable in explanatory power to those for tree-layer responses in well-validated simulation models (e.g., ORGANON; Ritchie and Hann 1985; Hann and Larsen 1991). Widely used models such as ORGANON, the Landscape Management System (McCarter et al. 1998) or FVS/PROGNOSIS (Wyckoff 1990) either ignore the understory (the first two), or only include it with inland forest types (the third). Our predictive models for shrub- and herb-layer components should be applicable to low- and mid-elevation forests (western hemlock and Pacific silver fir zones) in western Washington. Because they were developed from intensive sampling at four geographic locations, the chance that model sites are not representative of the full range of mature forests in western Washington is greater than had more extensive sampling occurred. However, the wide range of site conditions (Table 1) and dearth of "location" effects suggest that the models are probably robust to this type of "sampling" error.

The models predict the abundance of a response variable conditional on its presence on a plot. Presence or absence of a species or functional group on a plot is likely to depend on different factors (e.g., mode of dispersal, distance to seed source, or site history) from those that affect abundance, but some estimate of the probability of occurrence is still necessary for use in simulations. In the absence of predictive models, estimates of the probability of occurrence in similar forests can be obtained from the simple proportions of occurrence in our raw data (Table 4), or from other published sources (e.g., plant association and management guides of the USDA Forest Service Area Ecology Program).

Tree-based models are mainly used for exploratory purposes, because predictions are limited to discrete values de-

terminated when the model is initially built (Clark and Pregibon 1992). Nevertheless the tree-based models in this study suggest potential refinements to the regression relations that might enhance the realism of predictions from gap models and enable managers to anticipate when structural changes will affect understory composition. For example, our model for late-seral cover indicated a substantial difference between plots with QMD <60 cm versus QMD >60 cm; over half the reduction in deviance occurred at this partition alone (Fig. 1a). This discontinuity suggests a threshold response for late-seral herbs not captured by a regression equation with constant coefficients. A similar, but opposite, effect was observed for late-seral herbs and SDI. Thus, the abundance of late-seral herbs may remain low, with little change, until stand density is reduced, and tree sizes increase sufficiently to permit the expansion of late-seral herbs. At this point, relatively rapid changes could be anticipated in the absence of confounding effects from disturbance.

For relatively undisturbed forests, our models should predict future conditions, but disturbances that produce abrupt changes in the predictor variables would change relationships significantly. Thus, extrapolation outside the conditions represented by our data base would be unwise. For example, silvicultural manipulations (e.g., thinning of subcanopy trees or partial retention) could instantly produce higher values of QMD, but changes in the understory would take more time and might not produce the same patterns of abundance as when overstory and understory develop together more gradually.

In summary, our analyses suggest a conceptual model for how understory communities in mature forests change through time in response to, and coincidentally with, changes in overstory structure. Secondary layers (shrubs) respond directly to, and are limited by, overstory variables. When tertiary layers (herbs) are partitioned into functional groups, they appear to respond to a combination of overstory variables and, indirectly, to the passage of time. Of the variety of methods used to elucidate these relationships, maximum abundance models produced the least ambiguous and most easily interpreted result. In contrast, mean-response models, while statistically significant, offer fewer insights into the factors that shape forest understory development, although tree-based models demonstrate the potential value of nonparametric approaches that can reveal complex interactions among variables. We suggest that forest researchers can fruitfully explore a variety of empirical methods for estimating both mean and maximum responses; no single method is superior for all objectives. However, improved methods for modeling maximum responses will likely lead to the greatest advances in ecological understanding.

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