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The Relative Importance of Biotic and Abiotic Controls on Young Conifer Growth after Fire in the Klamath-Siskiyou Region

Abstract

In the Klamath-Siskiyou region of northern California and southwest Oregon, the mixed-severity fire regime and short fire return interval has created diverse vegetative landscape with frequent regenerating patches of forest vegetation. Considerable evidence from this region suggests that intense competition from neighborhood vegetation can greatly reduce the survival and growth of young conifers following severe site disturbance, including fire. However, relatively little information exists regarding the growing conditions one to three decades following disturbance, particularly in unmanaged stands. We measured the effects of neighborhood vegetation on regenerating Douglas-fir (*Pseudotsuga menziesii*) growth in northern California, 10-20 years following severe wildfires. Steep climatic gradients owing to complex topography in the region can cause significant variation in local temperatures, levels of precipitation, and solar radiation; thus our measurements were dispersed across two abiotic environmental gradients, elevation and heat load. We used a nested sampling design to elicit the tree-level effects of neighborhood vegetation, the plot-level effects of elevation and heat load, and the interactions among tree-level and plot-level variables on Douglas-fir growth. We used a combination of hierarchical regression models and non-parametric, multiplicative regression modeling for 3-dimensional graphical data presentation. Our results indicate that conifers are exposed to both positive (facilitative) and negative (competitive) neighborhood interactions depending on location in the abiotic environmental landscape. However, growth appears to be much more sensitive to abiotic environmental conditions than to the effects of neighborhood interactions. Considering the spatially explicit patterns in our data, we suggest that site-specific conditions play a significant role in the development of post-fire forest management strategies in the Klamath-Siskiyou region.

Introduction

Complex fire histories have greatly contributed to the spatially and structurally diverse plant communities found in the Klamath-Siskiyou region of northern California and southwest Oregon (Agee 1993, Taylor and Skinner 1998, Alexander et al. 2006). Many common shrub and hardwood species quickly occupy sites following disturbance from fire or logging (Tesch and Hobbs 1989, Hughes et al. 1990, Hobbs et al. 1992, Hanson and Stuart 2005). In an effort to recover economic value and speed the redevelopment of late-successional forest characteristics, post-fire forest management practices can include salvage logging and subsequent vegetation control measures (Lindenmayer 2006, Lopez Ortiz 2007). However, in recent years an increase in public awareness of large, high-severity fires across the western United States has prompted a reevaluation of post-fire management strategies on public lands (Dombeck et al. 2004).

Considerable evidence from the Klamath-Siskiyou region suggests that the survival and growth of young conifers can be greatly reduced by intense competition from woody and herbaceous species (Hobbs et al. 1992, Sessions et al. 2004). However, regeneration standards in the region (100-150 trees acre⁻¹, USFS Happy Camp Ranger District) may be met or exceeded in naturally regenerating stands (Donato et al. 2006), even in the presence of abundant woody competitors (Shatford et al. 2007). These two lines of evidence suggest that the interactions between regenerating conifers and the developing plant communities surrounding them in the post-fire landscape are not simple.

Resource competition is believed to play an important role in determining community structure of regenerating forests. This concept has become central in guiding many natural resource management plans (e.g., Hobbs et al. 1992). In the early stages of stand development, aboveground competition for light and belowground competition for moisture and nutrients are commonly cited biological constraints to forest regeneration

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generally (Balandier et al. 2006, Wagner et al. 2006) and to conifer regeneration in the Klamath-Siskiyou region specifically (Hobbs et al. 1992). However, several studies have suggested an important beneficial role of woody associates in redeveloping coniferous forests. These beneficial effects can include stabilization of soil and retention of site nutrients soon after disturbance (Conard et al. 1985), reduction of intense direct solar radiation to conifer foliage (Conard and Radosevich 1982, Gomez et al. 2004), reduction in soil and ambient air temperatures (Youngberg 1966, Scott 1970, Jones 1995), and reduction of evapotranspiration in early stand development. Indeed, recent studies suggest that both positive and negative interference between regenerating conifers and shrubs are abundant in many ecosystems of the western US (Erickson and Harrington 2006, Oakley et al. 2006). A number of studies have documented a decrease in the importance of negative interference with increasing stress (Wilson and Keddy 1986, Wilson and Tilman 1991, Kadmon 1995, Twolan-Strutt and Keddy 1996, Goldberg et al. 1999, Gaucherand et al. 2006, Brooker et al. 2008).

The Klamath-Siskiyou region is characterized by steep climatic gradients owing to its deeply dissected drainages and complex topography, and its proximity to the Pacific Ocean. A strong east-west moisture gradient overlays a coarse scale pattern of moisture availability across the region. However, local variations in temperature, precipitation, and solar radiation can affect vegetation growth particularly by altering above- and below-ground moisture availability in a climate characterized by little summer season precipitation (Hobbs et al. 1992). Aspects of the abiotic environment may interact with biotic factors in regulating seedling growth (Levitt 1980, Hobbs et al. 1992, Lambers et al. 1998). Such interactions may contribute to the complexity of net vegetation interference described above.

Natural conifer regeneration is often considered too variable and unpredictable to meet even-age stand management objectives. However, even some early studies in the Klamath-Siskiyou region demonstrated the effectiveness of allowing conifers to regenerate naturally when speed of regeneration and species composition are not of primary concern (Hobbs et al. 1992). Recent studies suggest that natural conifer regeneration following severe disturbance by wildfire occurs

with much greater success than previously thought. Donato et al. (2006) report an average of more than 2000 conifers·ha⁻¹ in severely burned areas of the 2002 Biscuit Fire in southern Oregon just 2 years after the disturbance. In a study of natural regeneration 10-20 years after severe fires in the Klamath-Siskiyou region, Shatford et al. (2007) report conifer densities ranging from 83 to 8188 trees·ha⁻¹ in lower elevation Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests (average: 1694 trees·ha⁻¹) and 688 to 16,671 trees·ha⁻¹ in higher elevation white fir (*Abies concolor*) forests (average: 7621 trees·ha⁻¹). These studies suggest that natural conifer regeneration in the Klamath-Siskiyou region may be more abundant and persistent than previously thought. However, incorporating the variability in tree densities into management plans necessitates additional research regarding the factors influencing conifer development across landscapes in the region. Our study aims to explore the dynamic nature of the interactions between regenerating conifers and their surrounding plant communities (interference) in the context of the complex abiotic environment of the Klamath-Siskiyou region.

Our goals are to 1) evaluate the effects of neighborhood interactions on the growth of regenerating Douglas-fir trees, 2) evaluate the effects of topographic landscape position on the growth of regenerating Douglas-fir trees, and 3) evaluate the interactions between these biotic and abiotic environmental influences on the growth of regenerating Douglas-fir trees, 10-20 years following severe wildfire in the Klamath-Siskiyou region.

Methods

Regional Description

The vegetative landscape mosaic found in the Klamath-Siskiyou region of northern California and southwest Oregon is evidence of the region's diverse geologic origins, complex topography, and a host of mixed-severity fire regimes (Franklin and Dyrness 1973, Agee 1993). Its latitude and proximity to the Pacific Ocean produces a Mediterranean-like climate with a predictably warm, dry summer season and cool, moist winters. A strong west-east moisture gradient exists over much of the Klamath-Siskiyou region; however, steep topography can strongly influence local precipitation patterns through orographic lifting (Skinner et al. 2006). Normal daily maximum

temperatures in July vary across the region from 34.7 °C in the southwestern extent (Willow Creek, CA) to 32.9 °C in the northeast (Fort Jones, CA), whereas normal daily maximum temperatures in January vary from 11.1 °C to 6.6 °C. Annual rainfall ranges between 143.5 cm·year⁻¹ (Willow Creek) and 57.6 cm·year⁻¹ (Fort Jones), with most of the precipitation falling between October and April (Skinner et al. 2006).

Mixed Douglas-fir/hardwood forests and mixed conifer forests dominate much of the Klamath-Siskiyou landscape throughout the middle and low elevations (Frost and Sweeney 2000). In the Douglas-fir vegetation series, co-dominance is shared by tanoak (*Lithocarpus densiflorus*) toward the wetter end of the moisture gradient (Atzet et al. 1992). At the drier end of the moisture gradient on south facing slopes and on coarse, well-drained soils, conifer abundance declines and forests become dominated by hardwood trees and/or shrubs.

Field Methods

All sampling took place during July and August, 2006. All plots were located in the Happy Camp and Yolla Bolly Ranger Districts within the Klamath and Shasta-Trinity National Forests in California, between 4-51-994 – 4-93-165 E and 44-48-111 – 46-37-383 N (UTM Zone 10, Figure 1). Aerial photographs taken 1-3 years after historical burns were used in combination with US Forest Service Geographic Information System (GIS) layers to compile data on the expanse and severity of wildfires that occurred in the region 11-19 years prior to our sampling. Sampling locations were selected in areas previously dominated by conifers based on three criteria: 1) burned 10-20 years ago, 2) high burn severity (>90% tree mortality) and, 3) no serpentine-derived (ultramafic) soils. Plot locations were selected across an elevation gradient from 544 m to 1625 m (median: 1081 m), across all aspects, and across slopes ranging between 18% and 82% (median: 60%). Plots were

located in both managed and unmanaged areas. Unmanaged areas received no post-fire treatments; managed areas were salvage logged, planted within a 3-year period after fire, and released (manual vegetation control) soon thereafter. At least eight years had elapsed between the time of release and our sampling. Thus, the ‘environmental memory’ growth response, a delayed response in seedling growth attributable to a change in neighborhood dynamics, was assumed to be insignificant by the time of sampling (Howard and Newton 1984). Including trees grown in managed stands therefore widened our sampling range of neighborhood conditions by including more trees growing under open conditions.

A total of 63 plots were randomly placed within regenerating sites meeting the above criteria. Thirty of these plots, which contained at least 9 Douglas-fir seedlings, were included in this analysis. Plots were aligned to run parallel to the slope contour and measured 12 m x 40 m (0.048 ha). At each plot, latitude, longitude, aspect,

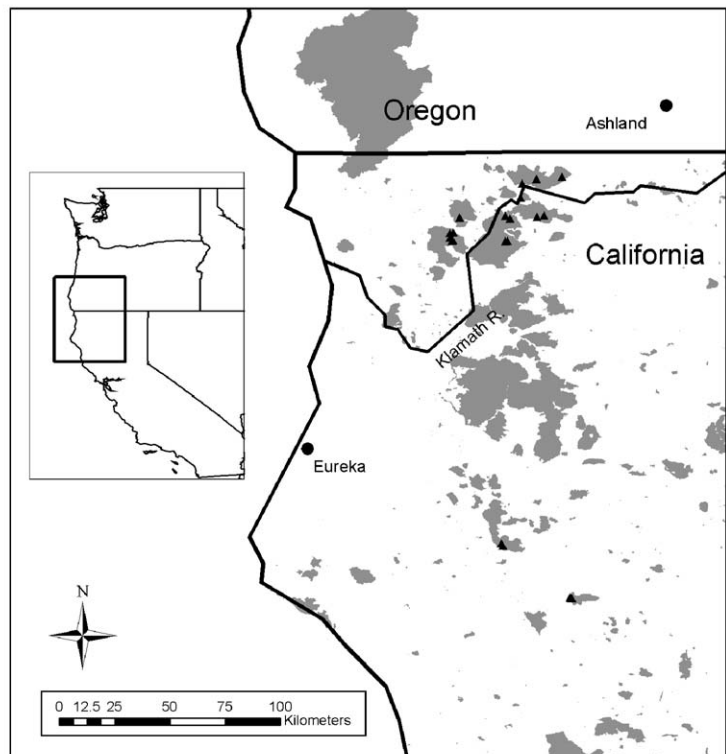


Figure 1. Study plots were located within the Klamath and Shasta-Trinity National Forests of northern California. Plot locations are represented by black triangles. Grey patches represent burn areas from fires recorded between 1985 and 2007.

slope, and elevation were recorded. Plots were further divided into three 12 m x 12 m subplots for ocular estimations of average vegetation cover and these three estimates were averaged to give plot cover. Plots were exhaustively searched to locate all tree seedlings using a 4x4m interior grid to increase search effectiveness. Growth and neighborhood vegetation data were collected for up to the first 25 Douglas-fir encountered. More detailed information on plot design is available in Shatford et al. (2007).

Only plots containing growth and neighborhood vegetation data for a total of at least 9 Douglas-fir seedlings were included in the analysis (the standard deviation in relative growth rate values began to stabilize at $n \geq 9$). Thus, the number of sample trees in each plot ranged from 9 to 25. Sample trees were required to be greater than two years old and at least 10 cm total height (range: 10 cm – 530 cm). For each tree, total height (H_{Total}), crown height (vertical length of the live crown, H_c), and internode length of the previous two seasons' (2004-5) height growth (G_{row}) were taken to the nearest 1 cm. A total of 451 trees were included in our study.

Competing vegetation around each sample tree was measured using two ocular estimations of percent cover according to methods described by Howard and Newton (1984, Figure 2). These measurements stratify neighboring vegetation into two groups, that which overtops the top node in an inverted 60° cone rising above the tree (overtopping), and that which encroaches in an area surrounding the conifer (encroaching).

Vegetation Conditions on Plots.

All plots were occupied by a significant component of shrub and hardwood species (Table 1). Common shrub species included greenleaf manzanita (*Arctostaphylos patula*, present on 42% of plots),

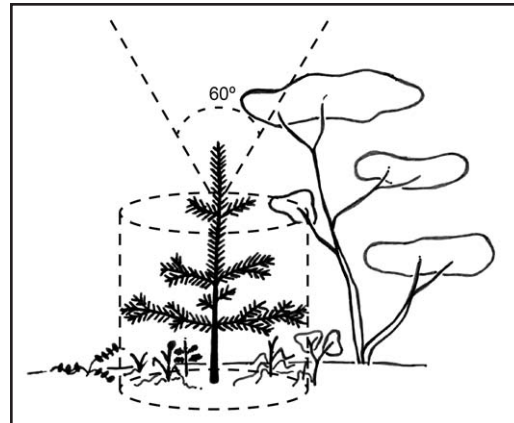


Figure 2. Ocular estimates of overtopping vegetation cover were made inside an inverted 60° cone centered at the bottom of the current leader. Encroaching vegetation cover was estimated in a cylinder whose radius equaled the longest lateral branch of the target tree and whose height was equal to the height of the conifer at the bottom of the current leader. Schematic adapted by Fernando Gonzalez from Howard and Newton (1984).

thimbleberry (*Rubus parviflora*) and creeping snowberry (*Symphoricarpos mollis*), both present on 84% of plots, *Rosa* spp. and *Ribes* spp. (present on 89% of plots) and deerbrush (*Ceanothus integerrimus*, present on 95% of plots). Common hardwood tree species included tanoak, golden chinkapin (*Castanopsis chrysophylla*), and Pacific madrone (*Arbutus menziesii*), which were present on 37%, 42%, and 95% of plots, respectively.

Combined shrub/hardwood cover ranged between 34% and 104% across all plots (mean: 66%, median: 64%, Table 1). Forbs and Grasses were present on 95% of plots with 3% and 2% average cover, respectively. Nitrogen-fixing *Ceanothus* species comprised a plot mean of 20% cover (range: 1%-86%, median: 13%) and were present on all plots.

TABLE 1. Summary plot-level data from all 30 plots. n is the number of seedlings per plot, RGR is relative growth rate on a natural log scale, ENCR is an index of encroaching (lateral) vegetation, and OVER is an index of overtopping vegetation.

Year of Burn	n	Mean	Mean	Mean RGR (1n)	Mean ENCR (%)	Mean OVER (%)	Total Plot Cover (%)	Shrub Cover (%)	Hardwood Cover (%)	Conifer Cover (%)	Herbaceous Cover (%)	
		Tree Height (cm)	Tree Growth (cm)									
Mean	n/a	15	146	29	-1.94	28	27	85	48	18	12	7
Range	1987-1995	9-24	8-530	1-55	-4.3-+0.3	0-95	0-95	49-117	8-90	0-74	1-37	0-32

Conifers accounted for an average of 12% plot cover (median: 8%), ranging between 1 – 37% (Table 1). Douglas-fir was the dominant conifer component in average plot cover, followed by ponderosa pine (*Pinus ponderosa*), white fir, knobcone pine (*Pinus attenuata*), incense cedar (*Calocedrus decurrens*) and sugar pine (*Pinus lambertiana*). Conifer density averaged 2771 trees·ha⁻¹ (range: 479 to 9292 trees·ha⁻¹). Conifer ages were relatively well dispersed on each plot, with natural establishment accruing on most sites for more than 10 years following disturbance (Shatford et al. 2007).

Data Analysis

Relative growth rate (RGR) was used to compare the effects of abiotic environment and competition on conifer development. Prior to data analysis, we examined scatterplots to ensure that RGR varied independently of tree height ($r^2 = 0.05$). Absolute height growth was correlated with tree height ($r^2 = 0.66$); thus, RGR was used in the analysis in order to compare height growth among trees of different sizes.

Because leader length was not measured in the field, we assumed that leaders had achieved 90% of their total length for the 2006 growing season at the time of measurement (July-August). Thus, current leader lengths were estimated by multiplying the average height growth of the previous two years (2004 and 2005) by 0.90 (Table 2, Equation 1). An estimate of the current season's (2006) growth was made to calculate total tree height following the 2003 and 2005 growing seasons (Equations 2 and 3, respectively). Relative height growth rate calculations were adapted from Evans' (1972, Equation 4) equations for estimating relative growth rate.

Two surrogates of microclimatic environment, elevation and heat load, were used to represent components of the moisture gradient across the study area. Latitude along with slope and aspect were used in McCune and Keon's (2002) Equation 3 for calculating heat load (Table 2, Equation 6).

We used two complimentary statistical approaches to evaluate and graphically represent our

TABLE 2. Equations for calculating tree height, relative height growth (Evans 1972), heat load (McCune and Keon 2002), and the proportion of variation in RGR explained by model *i*.

Equation 1	Leader = 0.90 * (Grow/2)
Equation 2	$H_1 = H_{Total} - (Leader) - Grow$
Equation 3	$H_2 = H_{Total} - (Leader)$
Equation 4	$RGR = \ln[(H_2 - H_1)/2] / (H_1)$
Equation 5	$A = \pi - \text{aspect} - (5 \pi / 4) $
Equation 6	$HL = 0.339 + 0.808 * \cos(L) * \cos(S) - 0.196 * \sin(L) * \sin(S) - 0.482 * \cos(A) * \sin(S)$
Equation 7	$r^2_{int} = (\text{intercept}_{null} - \text{intercept}_i) / (\text{intercept}_{null})$
Equation 8	$r^2_{res} = (\text{residual}_{null} - \text{residual}_i) / (\text{residual}_{null})$

Leader = current season (2006) leader length estimate (cm)

H_1 = total sapling height at the beginning of the 2004 growing season (cm)

H_2 = total sapling height at the beginning of the 2006 growing season (cm)

H_{Total} = total sapling height at the time of sampling (July/August 2006, cm, measured)

Grow = sum of height growth during 2004 and 2005 growing seasons (cm, measured)

RGR = relative growth rate

L = latitude (radians)

A = folded aspect (radians)

aspect = must be in radians (measured)

S = slope (radians, measured)

HL = heat load (unitless)

intercept_{null} = proportion of variation in RGR attributed to plot-to-plot variation in the null model

intercept_i = proportion of variation in RGR attributed to plot-to-plot variation in model *i*

residual_{null} = proportion of variation in RGR attributed to tree-to-tree variation in the null model

residual_i = proportion of variation in RGR attributed to tree-to-tree variation in model *i*

data. First, we used model selection procedures based on Akaike's Information Critereon (AIC) in SAS (v9.2) PROC MIXED (SAS Institute, Cary, NC) to evaluate a set of candidate models (Singer 1998). An adjustment of AIC to control for small sample sizes, AICc, was used because AIC is sensitive to small sample sizes when the number of explanatory variables in the candidate models is relatively large (Burnham and Anderson 2002). Once a set of best models was established and most important predictor variables identified, we used HyperNiche v1.36 (McCune and Mefford 2004) for nonparametric multiplicative regression (NPMR) and for graphical presentation of our data.

Statistical analyses were conducted using hierarchical models regressing RGR against tree-level and plot-level predictors. These two-level models account for similarities among within-plot (tree-level) data due to our nested sampling design, while exploring trends in the plot-level data used to explain the variation among plots. Explanatory variables measured at the tree-level included individual tree estimates of overtopping and encroaching vegetation. Plot-level explanatory variables included estimates of heat load and elevation. Hierarchical equation modeling allows the analysis of data in situations where explanatory variables are not all measured on the same scale as the response variable of interest. Thus, layers or levels of explanatory variables are grouped and used to develop models accounting for this multi-level variability. Twenty one hierarchical models were developed based on our *a priori* hypotheses regarding the tree-level and plot-level environmental influences on conifer growth (Table 3).

Model assumptions of normality and constant variance were examined prior to reviewing the results of model selection. We visually examined residuals and scatter plots of the response variable against each explanatory variable to check for data normality and constant variance. Elevation was transformed from meters to thousands of meters to adjust for the scale of the other variables. No additional transformations were needed. We identified outliers and influential data points using residual plots and a scatter plot matrix of the response variable versus all explanatory variables. We also used SAS PROC CORR to check for correlations among explanatory variables and found that no pair of explanatory variables was correlated above 0.3 (Pearson correlation coefficient).

We determined that the assumptions about distribution and variance were met and continued with model selection procedures.

The analysis produces a list of candidate regression models and their relative strengths in explaining variation in the response variable. Because AICc is a tool for model selection and not hypothesis testing, the statistical power of individual models is not specified (Burnham and Anderson 2002). Rather, a ranking of the relative importance of the candidate models is produced. An AICc value is computed for each candidate model and the model with the lowest value is said to be the best model. The difference between the AICc of a given candidate model and the best model (Δ_i) determines the level of support for that model. The larger the value of this difference, the less support for a given model; thus, the model with the most support relative to the rest of the candidate models has a $\Delta_i = 0$. For the purposes of our analysis, only Δ_i values between 0 and 2 indicated strong support for a candidate model. In general, Δ_i values greater than 2 indicate considerably less support for a model's approximating power, and values greater than the Δ_i value attributed to the null model demonstrate very little support (Burnham & Anderson 2002).

A second value that helps determine relative model importance is the Akaike weight (ω_i). The weight of each candidate model in explaining variation in the response variable is normalized such that the total Akaike weight of all candidate models is $\omega_i = 1$. Thus, ω_i for individual models is proportional to the strength of the model in comparison with all other candidate models. Models resulting in greater Akaike weights therefore have a greater proportion of evidence in support of their explanatory strength (Burnham and Anderson 2002). Further support for a given model is provided in AICc by the negative 2-log likelihood value, $-2\log L$. This value demonstrates the relative strength of evidence against a candidate model, akin to performing a lack of fit test (lower is better).

Due to the hierarchical nature of our data, each candidate model contained two sources of variance, one from the plot-to-plot variation in RGR and one from the tree-to-tree variation. We calculated the amount of variation in RGR attributable to each source of variance explained by each model (Table 2). We report these statistics as proportions

TABLE 3. Hierarchical models were based on our *a priori* hypotheses regarding biotic and abiotic environmental factors influencing Douglas-fir height growth. Models 2-5 model RGR as a function of elevation or heat load, regardless of encroaching or overtopping vegetation. Models 6-12 model RGR in terms of some combination of elevation, heat load, and overtopping vegetation, regardless of encroaching vegetation. Models 13-19 model RGR in terms of some combination of elevation, heat load, and encroaching vegetation, regardless of overtopping vegetation, while models 20-21 model RGR as a function of overtopping and encroaching vegetation, regardless of elevation or heat load.

Model Number	Model	Model Description
1	NULL	Null model, no effect of elevation, heat load, encroaching or overtopping vegetation
2	ELEV	linear effect of elevation
3	HL	linear effect of heat load
4	ELEV HL	linear effect of elevation and heat load
5	ELEV HL ELEV*HL	effect of heat load varies with elevation
6	OVER	linear effect of overtopping vegetation
7	HL OVER	linear effect of heat load and overtopping vegetation
8	ELEV OVER	linear effect of elevation and overtopping vegetation
9	ELEV HL OVER	linear effect of elevation, heat load, and overtopping vegetation
10	ELEV HL ELEV*HL OVER	linear effect of overtopping vegetation, but effect of heat load varies with elevation
11	HL OVER HL*OVER	effect of overtopping vegetation varies with heat load
12	ELEV OVER ELEV*OVER	effect of overtopping vegetation varies with elevation
13	ENCR	linear effect of encroaching vegetation
14	HL ENCR	linear effect of heat load and encroaching vegetation
15	ELEV ENCR	linear effect of elevation and encroaching vegetation
16	ELEV HL ENCR	linear effect of elevation, heat load, and encroaching vegetation
17	ELEV HL ELEV*HL ENCR	linear effect of encroaching vegetation, but effect of heat load varies with elevation
18	HL ENCR HL*ENCR	effect of encroaching vegetation varies with heat load
19	ELEV ENCR ELEV*ENCR	effect of encroaching vegetation varies with elevation
20	OVER ENCR	linear effect of overtopping and encroaching vegetation
21	OVER ENCR OVER*ENCR	effect of encroaching vegetation varies with level of overtopping vegetation
22	ELEV HL ELEV*HL OVER ENCR	linear effect of overtopping and encroaching vegetation, but effect of heat load varies with elevation

of the total variation in RGR associated with each source of variance in the null model. For each model, we report r^2_{int} to represent the proportion of total plot-to-plot variation explained by the model (Equation 7), and r^2_{res} to represent the proportion of total tree-to-tree variation explained by the model (Equation 8).

Given the complexity of the interactions found in the list of top-ranked models, we used HyperNiche v1.36 for NPMR and graphical presentation (McCune and Mefford 2004, McCune 2006a).

Nonparametric multiplicative regression automatically represents interactions among predictors. We used a local mean and Gaussian kernel to produce models and 3-dimensional surfaces. We specified a minimum average neighborhood size of 22.5 (5% of our sample size) to keep models from overfitting our data (McCune and Mefford 2004). Neighborhood size refers to the amount of information borrowed from neighboring data points in the surrounding regression surface used to calculate an estimate for a given point, and can

be thought of as similar to a local sample size. If the neighborhood is small (e.g., 1-10), highly influential data points can skew the model; larger neighborhood sizes therefore result in a less responsive regression surface, but limit the influence of unusual data points (McCune and Mefford 2004). Unpopulated neighborhoods appear as gaps in a surface.

In addition to visualization, HyperNiche provides several quantitative methods for evaluating model strength in complex models as well as the strength of individual explanatory variables. Nonparametric regression models with quantitative response variables are evaluated using a cross-validated R^2 (xR^2) technique (Antoine and McCune 2004). The xR^2 value is a comparison of the residual sum of squares (RSS) to the total sum of squares (TSS) and is calculated by systematically excluding each observation from the dataset to calculate an estimate for that point (see McCune [2006b] for equations to calculate xR^2). We gauged model responsiveness to individual predictor variables in HyperNiche using sensitivity analyses (McCune 2006b).

Sensitivity analyses in HyperNiche gauge the relative importance of individual predictors by measuring the magnitude of model response to

incremental changes in observed values of each predictor variable (McCune 2006b). We used McCune's (2006b) Sensitivity 1 to estimate variable sensitivity, reported as a proportion of the change in the response over the change in a predictor. Variable changes are reported as fractions of their observed ranges. Therefore, a sensitivity value of 1.0, for example, indicates that a given change in the predictor variable causes a scaled change of equal magnitude in the response.

Results

Selection of Hierarchical Models

Model selection in AICc indicated that eight of the 21 candidate models had substantial empirical support of their explanatory power in predicting the rate of Douglas-fir height growth as evidenced by Δ_i values less than two (Table 4). The top-ranked candidate model (model 8, $r^2_{int} = 0.34$) contained an additive relationship between elevation and overtopping vegetation ($\Delta_i = 0$). Although overtopping vegetation cover was included in the top model, individual P -values for the parameters in this model suggest that elevation ($P = 0.0124$) was a better predictor of RGR than overtopping vegetation ($P = 0.1123$). The second-ranked model

TABLE 4. Selection of hierarchical models for explaining Douglas-fir RGR was based on AICc. Only models with $\Delta_i >$ the null model are shown. The negative 2-log likelihood, Neg2LogL, the c-Akaike's Information Critereon, AICc, the difference in AICc between a model and the best model, Δ_i , the Akaike weight, ω_i , and the proportion of plot-to-plot variation (r^2_{int}) explained by each model are listed. Models are listed in order of decreasing importance, the top ranked model appearing first.

Model Number	Model	Δ_i	AICc	ω_i	Neg2LogL	r^2_{int}
8	ELEV OVER	0	761	0.15	740.5	0.34
2	ELEV	0.29	761.3	0.13	742.9	0.34
10	ELEV HL ELEV*HL OVER	0.89	761.9	0.09	737.2	0.57
5	ELEV HL ELEV*HL	1.31	762.3	0.08	739.7	0.57
15	ELEV ENCR	1.44	762.5	0.07	742	0.35
9	ELEV HL OVER	1.62	762.6	0.07	740	0.43
18	HL ENCR HL*ENCR	1.96	763	0.06	742.5	0.07
4	ELEV HL	1.97	763	0.05	742.5	0.42
12	ELEV OVER ELEV*OVER	2.1	763.1	0.05	740.5	0.34
22	ELEV HL ELEV*HL OVER ENCR	2.13	763.1	0.05	736.3	0.61
17	ELEV HL ELEV*HL ENCR	2.34	763.4	0.05	738.7	0.59
19	ELEV ENCR ELEV*ENCR	2.68	763.7	0.04	741.1	0.38
16	ELEV HL ENCR	3.23	764.3	0.03	741.7	0.41
1	NULL	3.81	764.8	0.02	748.5	0

based on AICc explained an equal amount of the among-plot variation in Douglas-fir growth with the elevation parameter alone (model 2, $r^2_{\text{int}} = 0.34$), further support of the importance of the elevation term in the top model.

The top ranked models indicated the biotic and abiotic environmental parameters we measured interact additively, as separate individual variables, and multiplicatively, as complex, interacting influences. The multiplicative interactions found in the top-ranked models reflect the complex and variable nature of the neighborhood environment in the context of broader topographic landscape gradients such as elevation and heat loading. Model 5 ($r^2_{\text{int}} = 0.57$) and model 10 ($r^2_{\text{int}} = 0.57$) demonstrate the importance of considering the multiplicative influence of elevation and heat load in determining tree growth. Other highly ranked models (8, 9, and 15) indicate that additive interactions among neighborhood vegetation parameters (encroachment and overtopping) and topographic landscape variables (elevation and heat load) are relatively common as well.

In general, models including neighborhood vegetation parameters but not topographic landscape position variables were ranked poorly by AICc (Table 4). The amount of tree-to-tree variation in RGR, the variation in growth attributable only to tree-level parameters and not to plot-level factors, was not reduced by any of the top models ($r^2_{\text{res}} \leq 0.004$). These data demonstrate the relatively weak influence of neighborhood vegetation on Douglas-fir RGR when compared with elevation or heat load.

NPMR

Non-parametric multiplicative regression modeling in HyperNiche identified the variables Elevation,

Heat Load, and Encroaching Vegetation in the best model of regenerating Douglas-fir growth. However, parsimony declined with additional predictor variables, and models began to over-fit our data as evidenced by declining xR^2 values (Table 5).

Sensitivity values for individual explanatory variables also supported indications from AICc which suggest that Douglas-fir growth is more responsive to landscape position variables than to habitat alterations from neighborhood interactions (Table 5). The sensitivity analysis indicated that, given a 10% change in Heat Load, we would expect a response of 7.6% change in Douglas-fir RGR. Similarly, given a 10% change in Elevation, we would expect a response of 6.4% change in Douglas-fir RGR. In contrast, for the same model, a change of 10% in Encroaching vegetation would only be expected to cause a response of 0.7% change in Douglas-fir RGR.

Three-dimensional projections in HyperNiche helped visualize the complex interactions occurring among biotic and abiotic influences on conifer growth in the post-fire environment (Figure 3). Relative growth rates are reported on a natural log (\ln) scale (Table 2, Equation 4), such that higher numbers represent greater levels of growth. The results reveal interesting insights into the dynamics of the regeneration environment. In general, conifer growth was most sensitive to the multiplicative influences of heat load and elevation (Table 4), and to neighborhood interactions occurring near the extremes of these environmental gradients (Figure 3b), indicated by the magnitude of response in RGR apparent on the z-axis. At low elevations, high heat loading resulted in a net negative effect on tree growth (Figure 3a). However, this relationship reversed at higher elevations, where higher heat loading was associated with increased tree growth

TABLE 5. Results of model selection in HyperNiche provided a list of the best models for predicting Douglas-fir height growth using n predictor variables. Model xR^2 is calculated using a leave-one-out cross-validated R^2 procedure and measures model fit. Sensitivity values (S) reflect a proportional change in the response relative to a given change in a predictor variable. Variables are abbreviated as follows: Heat Load, HL, Elevation, ELEV, Encroachment, ENCR, Overtopping, OVER.

Full Model	Variables	Model xR^2	HL S	ELEV S	ENCR S	OVER S
HL	1	0.1784	1.69	-	-	-
HL, ELEV	2	0.2039	0.84	0.68	-	-
HL, ELEV, ENCR	3	0.2062	0.76	0.64	0.07	-
HL, ELEV, ENCR, OVER	4	0.1923	0.81	0.24	0.07	0.04

Figure 3

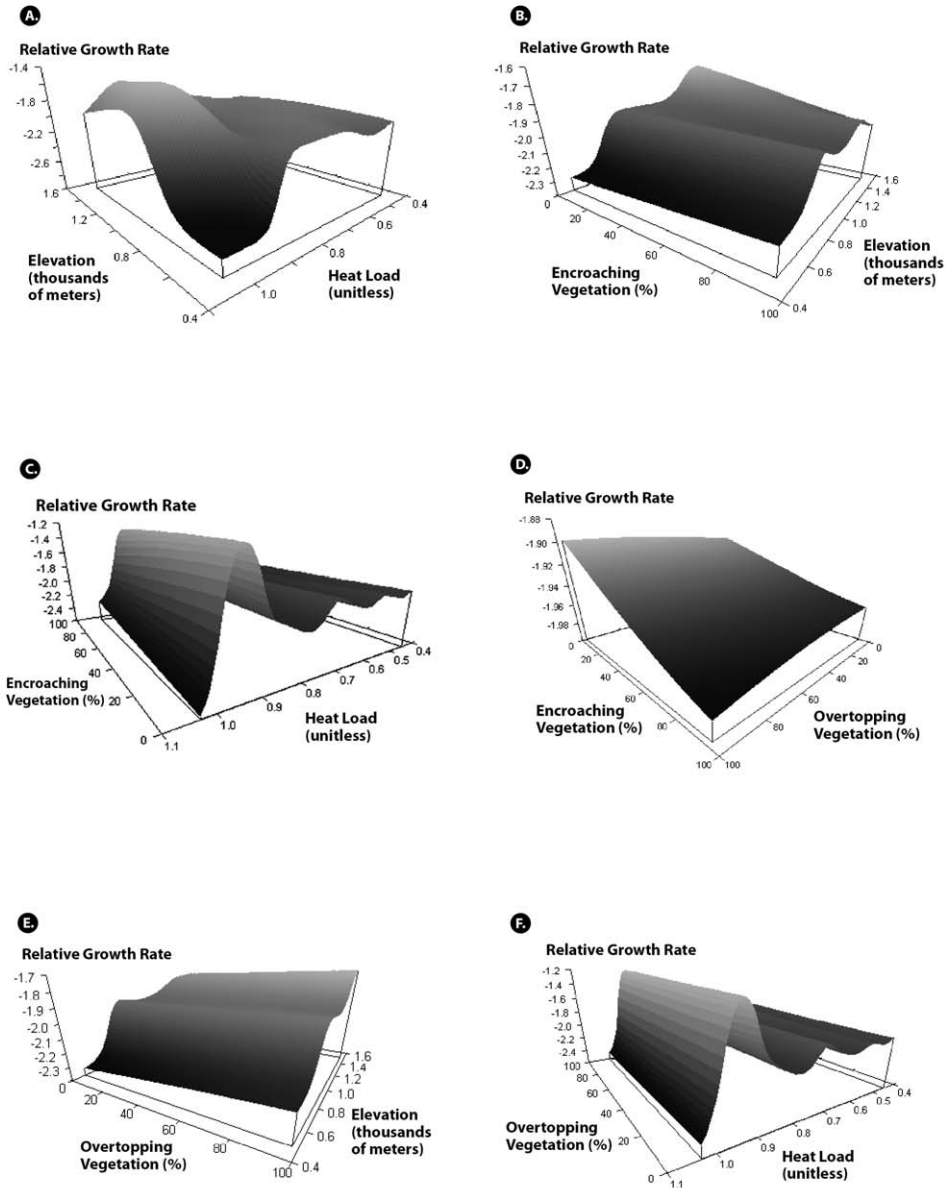


Figure 3. Nonparametric multiplicative regression modeling (NPMR) in HyperNiche produced 3-D projections of our data. These 3-D projections demonstrate the effects of two predictor variables on a single quantitative response variable at any point within the data range. Relative growth rates were transformed using a natural log (\ln) scale, such that smaller negative numbers represent greater levels of actual growth. Note that the scales shown on z-axes differ, thus the apparent magnitude of the response in RGR is not consistent among figures.

(Figure 3a). In contrast, the influence of encroachment on conifer growth transitioned from positive at low elevations to negative at the higher end of our elevation gradient (Figure 3b). With increasing heat load, the effect of encroachment transitioned from neutral to positive (Figure 3c).

The effects of overtopping vegetation on conifer growth were not sensitive to landscape position (Figure 3e). Rather, the positive effects of overtopping vegetation we observed were relatively constant throughout our topographic landscape gradients. A 3-D projection of the combined effects of overtopping and encroaching vegetation on conifer growth supported indications from AIC that Douglas-fir RGR is relatively insensitive to the effects of encroaching and overtopping vegetation, compared to the effects of heat load and elevation (Figure 3d, RGR range: 13.8% to 15.3%). This projection reveals that some level of interaction may be beneficial, but suggests that too much neighborhood interaction can be detrimental to conifer growth (Figure 3d). These results suggest that neighborhood interactions in regenerating forests are not only a function of site conditions owing to broader environmental gradients, but also, to some extent, a result of microsite conditions influenced by the plant communities themselves.

Discussion

Our results indicate that conifers regenerating on the post-fire landscape in the Klamath-Siskiyou region are exposed to both positive (facilitative) and negative (competitive) neighborhood interactions depending on location in the abiotic environmental landscape. Although the effects of neighborhood vegetation were relatively small in comparison to the effects of elevation and heat load (Tables 4 and 5), we observed changes in the direction of some neighborhood interactions along abiotic environmental gradients (Figure 3). In addition, neighborhood interactions occurring in the lower canopy due to encroachment generally appeared to be more influential than those occurring due to vegetation overtopping sample trees (Tables 4 and 5).

The encroachment effect varied along abiotic environmental gradients, with facilitative interactions increasing and competitive interactions decreasing with increasing abiotic environmental stress (low elevation sites, particularly those

also experiencing high heat loads, Figure 3). We expected that higher levels of neighborhood vegetation cover would generally lead to reduced conifer growth through increased competition. We anticipated that the context of a relatively hot, dry environment would exacerbate the negative effects of competition associated with moisture (Hobbs et al. 1992). Thus, the topographic landscape parameters we measured—elevation and heat load—represent components of a moisture gradient in the Klamath-Siskiyou region. The effects of encroachment elicited in our study reflect a trend expected of interactions associated with limited moisture availability but in the opposite direction. Our data suggest that encroachment facilitated conifer growth as moisture availability decreased and moisture demand increased, and that neighborhood associates may ameliorate some microsite conditions in an otherwise harsh growing environment (Figure 3b). Similar shifts towards net positive neighborhood interactions under increasingly stressful environmental conditions have been documented in other ecosystems (Wilson and Keddy 1986, Kadmon 1995, Twolan-Strutt and Keddy 1996, Goldberg et al. 1999, Gaucherand et al. 2006, Brooker et al. 2008). As moisture increased, the effects of facilitation diminished and we observed a net negative effect of encroaching neighborhood vegetation on our cooler, higher elevation sites (Figure 3b). This result may be attributable to an increase in competitive below-ground interactions as well as a decrease in facilitative above-ground interactions as resource availability improved (see Pugnaire et al. [2001]).

We observed a generally positive effect of overtopping vegetation throughout the range of elevations sampled (Figure 3e), suggesting that competition for light is not a limiting factor for Douglas-fir in regenerating forests of the Klamath-Siskiyou region. Rather, our results indicate that some level of protection may be afforded young Douglas-fir overtopped by neighboring vegetation. Several studies conducted in similar climates have suggested a net beneficial role of overtopping neighborhood associates attributable to reductions in excessively high levels of direct solar radiation (Conard and Radosevich 1982, Gomez 2004), and associated lessening of plant moisture stress (Monteith 1973, Lanini and Radosevich 1986). Whereas the encroachment effect appeared to change with abiotic environmental conditions, the

effect of overtopping vegetation we observed was constant across elevations and heat loads (Table 4, Figures 3e and 3f).

As seen in the AIC analysis and HyperNiche visualizations, overtopping and encroaching vegetation explained less of the variation in conifer growth than did abiotic variables. Attributed little support by AICc, the interaction between the biotic variables encroaching and overtopping vegetation explains little variation in Douglas-fir RGR. However, the simultaneous influence of high levels of overtopping and encroachment generally decreased conifer growth, with encroachment having a much stronger effect (Table 5, Figure 3d). Indeed, below-ground competition for water and nutrients exerted on regenerating conifers by neighborhood vegetation often outweighs the benefits gained from shading (Zavitkovski et al. 1969, Lanini and Radosevich 1986, Tesch and Hobbs 1989). Our data also demonstrate that some level of biotic interaction can be beneficial some places (Figure 3d). Erickson and Harrington (2006) reported increased growth rates associated with conifers growing near the edge of *Ceanothus* canopies, but negative growth rates associated with too much interaction.

While neighborhood interactions undoubtedly play an important role in developing plant communities, their relative importance in the broader abiotic landscape should be carefully considered (Brooker et al. 2008). Both the direction and intensity of neighborhood interactions varied across the environmental gradients we measured. However, the sensitivity of conifers to these neighborhood interactions was relatively low when compared with heat load or elevation (Table 5).

When considered together, these topographic landscape-position variables provide a model of the regeneration environment to which Douglas-fir growth is highly sensitive (Table 5, Figure 3a). Our results support earlier hypotheses (Whittaker 1960) and subsequent studies (Hermann 1968, Hobbs et al. 1992) regarding productivity and slope position in the Klamath-Siskiyou region. Low elevation sites experiencing high heat loads are particularly vulnerable to low productivity,

creating an apparent threshold near 800 m, below which Douglas-fir growth is dramatically reduced (Figure 3a). In contrast, high elevation sites experiencing high heat loads maximize Douglas-fir growth, presumably by extending the growing season, increasing photosynthetic activity, or increasing effective available moisture.

Wilson (2007) echoes the importance of placing neighborhood interactions within the context of broader environmental conditions, and provides tools for considering neighborhood interactions across productivity and other environmental gradients. In the Klamath-Siskiyou region, steep climatic gradients owing to complex topography and deeply dissected drainages produce highly variable growing environments, especially in the years immediately following fire. Our results suggest that the consideration of site-specific environmental conditions is an important step towards understanding the complex competitive and facilitative influences affecting conifer growth on the post-fire landscape.

Land managers should note that Douglas-fir height growth in regenerating stands is relatively insensitive to the effects of neighborhood competitors compared to the effects of elevation, slope and aspect. At low elevations and on well-drained, south facing slopes, neighbors may in fact provide some beneficial effects, but these appear to be largely outweighed by the effects of site conditions owing to topographic landscape position. Vegetation control measures in the region focusing on reducing neighborhood interactions among Douglas-fir seedlings and surrounding vegetation therefore may be most effective on mid- to high elevation, and more north-facing sites.

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