Available online at www.sciencedirect.com

ScienceDirect

Forest Ecology and Management 255 (2008) 2129–2137

Forest Ecology and Management

www.elsevier.com/locate/foreco

Density-dependent tree mortality in pinyon-juniper woodlands

David L. Greenwood, Peter J. Weisberg *

Department of Natural Resources and Environmental Science, University of Nevada – Reno, Reno, NV 89557, USA

Received 2 September 2007; received in revised form 13 December 2007; accepted 15 December 2007

Abstract

Pathogens and bark beetles are integral disturbance agents in many forest and woodland ecosystems. Over the past decade, pinyon *Ips* (*Ips confusus*) has interacted with regional drought to cause widespread mortality in singleleaf pinyon (*Pinus monophylla*) and Colorado pinyon (*Pinus edulis*) woodlands of western North America. We used mixed-effects and logistic regression modeling approaches to explore biotic and abiotic influences on the spatial heterogeneity of tree mortality. Stand structure, cumulative canopy and stem mortality, and occurrence of specific mortality agents were measured for 217, 0.1-ha plots, established in 2005 across 11 mountain ranges in central Nevada.

Cumulative tree mortality from multiple causes was generally associated with high stand densities and xeric site conditions. Multi-scale analysis considering subplots of varying dimension indicated that the relationship between woodland mortality and stand structure is scale dependent, with stronger correlations at coarser spatial scales. This suggests that competition between trees might not be the sole or even the primary mechanism for density-dependent tree mortality in these xeric woodlands. If site productivity is controlled for, greater density implies increased frequency of trees occupying sub-optimal microsites, which leads to increased mortality during drought years apart from direct effects of competition among neighboring trees. Experimental investigations are needed to differentiate the specific mechanisms for how resource competition interacts with abiotic limiting factors that constrain resource availability at the scale of microsites.

Keywords: Density dependence; Forest structure; Bark beetles; Dwarf mistletoe; Spatial scale; Forest health; Great Basin

1. Introduction

Forest health in western forests has become a significant concern as large-scale tree mortality has increased in the last several decades (Wickman, 1992; Savage, 1997; Ansley and Battles, 1998). Forests and woodlands are at greater risk of bark beetle attack due to fire suppression, logging practices, overgrazing, and other activities which have resulted in increasingly homogeneous landscapes with respect to species composition, age, and density of vegetative cover (Samman and Logan, 2000). Tree mortality is influenced in a pathogen-specific manner by a number of interrelated factors including: site quality, stand density, size class, age class, soil depth, crown density, the spatial arrangement of infected trees, species composition, and spatial connectivity of vulnerable conditions (Trummer et al., 1998; Samman and Logan, 2000; Shore et al., 2000; Robinson et al., 2002; Negron and Popp, 2004). These factors all influence the amount of nutrients, water, and light available to individual trees in the forest (Eager, 1999).

Great Basin woodlands are highly variable mosaics of stands varying in structure and history as a result of interacting natural and anthropogenic disturbances. While fire has been the primary disturbance studied in pinyon-juniper (P-J) woodlands (Barney and Frischknecht, 1974; Tausch and West, 1987; Baker and Shinneman, 2004; Floyd et al., 2004), an increasing amount of evidence suggests that drought, pathogens, and bark beetles may play a greater role than fire (Eisenhart, 2004). Across much of the southwestern U.S. and Rocky Mountains, tree mortality and pinyon *Ips* outbreaks are generating a profound change in the structure of pinyon-juniper woodlands (Mueller et al., 2005), potentially altering ecosystem function (Breshears et al., 2005). Although such episodic mortality events may represent natural landscape dynamics, in many situations widespread mortality can be undesirable and in conflict with management objectives. However, those characteristics that make singleleaf pinyon and Utah juniper woodlands susceptible to various mortality agents remain to be quantified. Little is known about the importance of biotic mortality agents for influencing woodland structure and

---

* Corresponding author at: Department of Natural Resources and Environmental Science, University of Nevada – Reno, Mail Stop 186, Reno, NV 89557, USA. Tel.: +1 775 784 7573; fax: +1 775 784 4583.

E-mail address: pweisberg@cabnr.unr.edu (P.J. Weisberg).

0378-1127/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2007.12.048

understory response over landscape scales. The potential consequences associated with widespread mortality include increased flammability, increased destructive crown fires, and cheatgrass (*Bromus tectorum*) occupying these areas after severe fires. A better understanding of the spatial patterning of mortality can help managers anticipate future patterns of mortality, and better understand resulting ecosystem effects.

Our main objective was to quantify how the abiotic environment and stand structure influence susceptibility of pinyon-juniper woodland to specific pathogens, as well as overall tree and crown mortality. Our study addressed cumulative mortality and not mortality rate, in that tree mortality was quantified across a large region using a one-time survey. Previous literature suggests that tree mortality in pinyon-juniper woodlands is density dependent (Negron and Wilson, 2003). Because tree density is inherently patchy we expect the effect of stand structure on mortality to be scale dependent. In relation to these objectives we evaluated the following specific hypotheses for individual trees and for patches of increasing area:

(1) Susceptibility to mortality is greater for larger trees.

Larger trees are commonly older trees that may become senescent, as evidenced by reduced growth rates, causing them to become more susceptible to bark beetles and eventual mortality (Waring, 1987; Wyckoff and Clark, 2002; Bigler and Bugmann, 2003). Slower growing trees have a decreased ability to allocate resources for defensive mechanisms such as pitch production. Larger trees may also be more susceptible to attack because they have thicker inner bark for the larvae to feed upon and offer a large surface area to support broods of beetles (Berryman, 1976).

(2) Woodland mortality is positively associated with tree density.

The ability of healthy trees to counter pathogens or insects is lessened by predisposing stress factors (Castello et al., 1995). Trees in high-density patches may experience high levels of competition and so may not provide sufficient resources for trees to fight off pathogens, insects, and drought (Eager, 1999; Samman and Logan, 2000; Negron and Popp, 2004). High stocking levels also allow easier transmission of mistletoe and *Ips* due to shorter inter-tree distances (Reich et al., 1991).

(3) Sites with poor growing conditions experience greater woodland mortality.

Trees on harsh environmental sites grow less vigorously due to increased moisture stress (Kaufmann and Ryan, 1986). Trees on such sites are less able to survive periodic drought and bark beetles because depleted carbohydrate reserves are insufficient for regrowth and defensive mechanisms.

(4) The negative association between cumulative tree mortality and density is stronger at finer spatial scales.

Coulson et al. (1999) and Negron et al. (2001) indicated that conifer mortality caused by bark beetles exhibits spatial patterning at within-stand scales. Closer proximity to competitors results in increased tree mortality (Weiner, 1984). Following wildfire, singleleaf pinyon responds to death of neighboring trees through dramatically increased radial growth rates (Py et al., 2006), suggesting that resource limitation results from competition among neighbors.

2. Methods

2.1. Study area

The 3250-km^2 study area (Fig. 1) encompasses 11 mountain ranges in central Nevada (Lat. 39°28′ N, Lon. 117°28′ W).

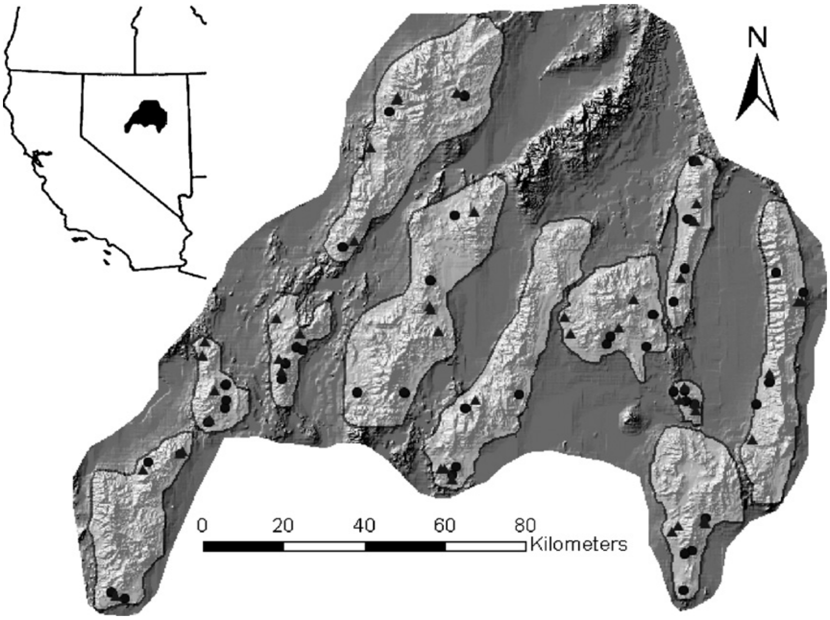

Fig. 1. Location of the study area in central Nevada. Shown are sampled plots encompassing 11 mountain ranges (light polygons). The 217 sampled plots included 43 intensive plots, 129 extensive plots, and 45 validation plots. Circles represent the intensive and extensive plots (training data); triangles represent validation plots.

Elevation ranges between 1600 m and 2500 m, and mean annual precipitation increases with elevation from approximately 20–35 cm (Desert Research Institute Western Regional Climate Center, 2006). Soils throughout the study area formed in material derived from limestone and dolomite and mixed parent material (Miller and White, 1998). The dominant tree species within the study area are singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*). Singleleaf pinyon dominates the highest elevations, while a mixture of singleleaf pinyon and Utah juniper occurs at the lower elevations. The understory vegetation cover is dominated by mountain big sagebrush (*Artemisia tridentata* ssp *vaseyana*), Sandberg bluegrass (*Poa secunda*), and low sagebrush (*Artemisia arbuscula*) at the highest elevations. The interspaces between pinyon and juniper trees are normally sparse with large areas of bare ground.

A history of human disturbance has influenced vegetation throughout the study area. In the 1860s silver mining settlements expanded into central Nevada and required pinyon and juniper charcoal and fuelwood harvested from local hillsides (Young and Budy, 1979). Severe overgrazing and deterioration of rangeland occurred as a result of the sheep and cattle industry which peaked between the 1880s and 1890s (Holechek et al., 2001). Livestock grazing of sheep and cattle, and active mines and mining claims are currently found throughout a majority of the study area.

2.2. Site and plot determination

A stratified random sampling design was used to distribute 217 plots according to strata of slope aspect, elevation, and mountain range. Within each of the resulting 44 strata, we located one site for statistical model development and another for model validation. A cluster of four 0.1-ha plots was sampled at each site. A central ''intensive plot'' was established based upon the predetermined random point, and three ''extensive plots'' surrounding the center plot were located a distance of 60 m away at compass bearings of 120°, 240°, and 360°. Information gathered from extensive plots included woodland structure and mortality data, but tree ages and soil characteristics were not measured as for the intensive plots.

2.3. Field methods

Elevation, slope aspect, and slope steepness in degrees were measured from the center of each plot. Soil measurements were randomly located in the interspaces between tree canopies. Soil texture was described in the field using a ribbon test (Thien, 1979), while soil pH was measured to the nearest 0.01 using an Extech Oyster Series soil tester. Following Harner and Harper (1976), maximum soil depth was measured using a metal rod and noting the depth of penetration to the nearest 5 cm.

To estimate percent tree cover, tree canopy intercepts were recorded along eight 17.85-m transects to the nearest 0.1 m. All trees, snags, and down logs were mapped to within one meter to provide a complete stand map. A Biltmore stick was used to measure diameter for tree species as close to the base as possible to the nearest 1 cm (precision estimated to be within 2–3 cm). For trees with multiple boles diameter was estimated as:

$$\text{Diam} = \sqrt{\sum_{i=1}^{n} \text{RCD}_i^{\,2}} \tag{1}$$

where Diam is the equivalent diameter and RCD_i is the root collar diameter of each of the individual i stems (Grier et al., 1992). We calculated mean diameter at root collar, total basal area, trees per hectare, and stand density index (SDI) for pinyon and juniper combined and separately. Stand density index values were obtained for each plot according to Reineke (1933):

$$\text{SDI} = N\left(\frac{d_\text{q}}{25.4}\right)^{1.605} \tag{2}$$

where N is the number of trees/ha by plot; d_q is the plot quadratic mean diameter (cm)

Since our SDI values were based on root collar diameters and not the breast height diameters for which Reineke's equation was developed, the SDI values we calculated should only be used in a relative sense, for comparisons within our study area. Diameters taken at breast height are generally inappropriate for short-statured, singleleaf pinyon pine.

Mortality cause was identified to the specific pest and pathogen, where possible, according to Skelly and Christopherson (2003). Mortality rate was not quantified, as data were collected for only a single year. However, the observed tree mortality has been spread over numerous years as indicated by the advanced wood decay and numerous secondary pests and diseases found on most dead trees. Our study thus quantifies cumulative tree and crown mortality. Percent dead crown was determined by ocular estimate from several perspectives around each tree to the nearest five percent. Live crown dwarf mistletoe rating (DMR) followed Hawksworth's (1977) six-class system, which assigns a 0, 1, or 2 to each third of the live crown based on visible infections: 0, no visible infections; 1, less than half of the branches contain infections; or 2, more than half of the branches contain infections. A tree-level DMR was calculated for live trees, after examining tree crowns from several directions, by adding the ratings for each crown third. A plot-level DMR was calculated as the average DMR of all live trees per plot. Beetle damage was characterized following Negron and Popp (2004): branches infested, bole infested, previous beetle evidence, and current beetle evidence. Needle color, presence or absence of needles, and presence or absence of frass was used to indicate previous or current year's beetle infestation.

2.4. Environmental variables derived from GIS and remote sensing

Several topographical variables were derived in a GIS using a 30-m resolution digital elevation model (DEM). Slope aspect (degrees), slope steepness (percent), slope position, and solar radiation were calculated over the entire study area. Aspect values were linearized ranging from 0 on southwestern slopes, to 2 on northeastern slopes using a cosine transformation. Slope position grid values range from 0 at valley floors to 100 at ridgetops (Hatfield, 1999). A clear sky solar radiation index (Kumar et al., 1997) was derived from the DEM for the time period from June 21 to July 21 (Zimmermann, 2006).

The Soil Survey Geographic (SSURGO) database (Soil Survey Staff, 2007) contained soil survey attributes at 30-m resolution (mapping scales 1:12,000–1:63,000). GIS layers for soil depth, soil pH, and soil texture were created over the entire study area using the Soil Data Viewer extension in ArcMap (USDA Natural Resources Conservation Service, 2006).

An object-oriented classification method, implemented in eCognition software using black and white aerial photography, was used to differentiate pinyon and juniper (tree) from all other vegetation types (non-tree). Multiresolution segmentation used combinations of spectral and spatial parameters to derive patches (image objects) of similar characteristics. Image objects were classified according to algorithms that utilized textural analysis, the mean brightness difference among neighboring objects, mean brightness value of a given object, and the relative border shared with neighboring objects of the same type. Based on an accuracy assessment using independent field data for a nearby study area (Weisberg et al., 2007), overall classification accuracy was 86% (kappa = 0.65). Canopy cover was then derived as the ratio of area of tree cover to total area of the spatial neighborhood considered. For further explanation regarding image processing of remotely sensed canopy cover, refer to Weisberg et al. (2007).

2.5. Data analysis

Linear mixed-effects (LME) models using the maximum likelihood algorithm were applied to account for possible pseudoreplication among multiple plots within the same site (Fig. 2). The ‘‘site’’ (i.e. cluster of plots) was treated as a random effect. Mixed-effects models provide flexibility in modeling the within-group correlation often present in grouped data (Pinheiro and Bates, 2000). Several ecological studies that compared mixed-effects models with ordinary regression models found that the latter underestimated the true variance and therefore had artifactually low standard errors due to ignoring the grouped nature of their samples (Bartolome et al., 2004; Helser et al., 2004; Jackson and Allen-Diaz, 2006).

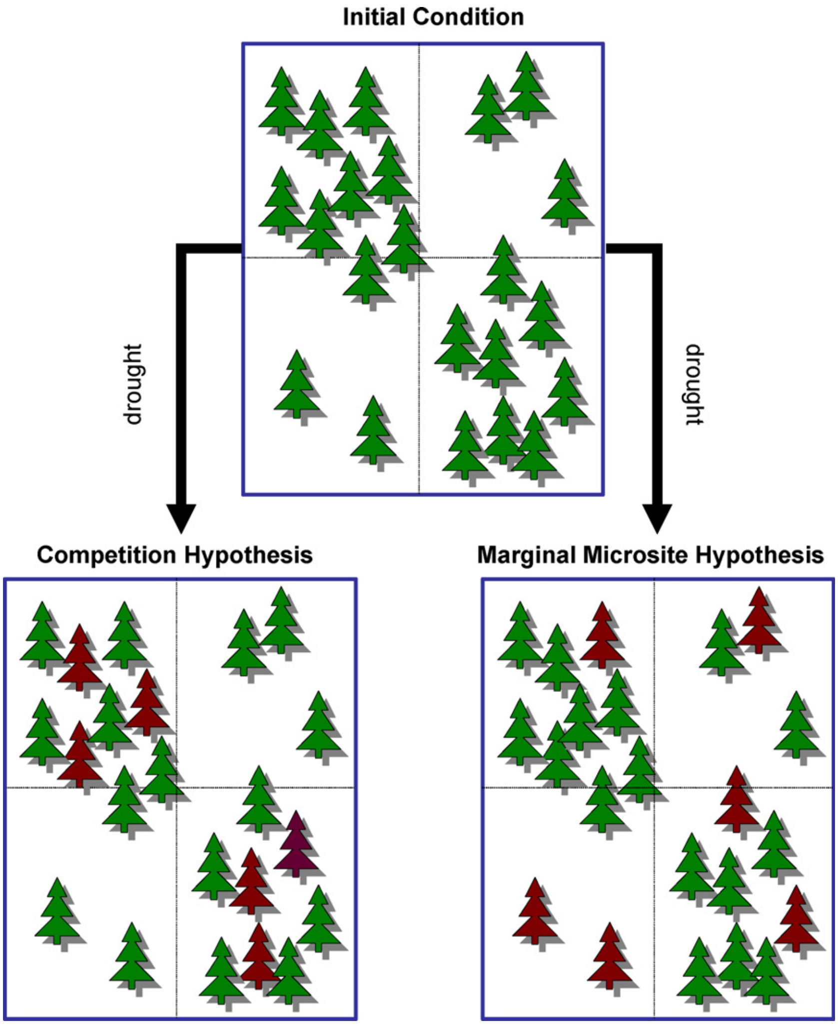

Fig. 2. Alternative hypotheses for density-dependent mortality of pinyon trees in a dense but patchy pinyon-juniper woodland. According to the ‘‘Competition Hypothesis’’ most tree mortality (brown trees in figure) occurs in the locally dense patches. According to the Marginal Microsite Hypothesis, tree mortality is scattered throughout the site and may be more likely to occur for trees growing in locally sparse areas.

To examine Hypothesis # 1, the effect of tree diameter on percent dead crown, independently of environmental factors, was assessed using likelihood ratio tests to compare nested models including the variable of interest, environmental covariates, and a null, intercept-only model. At the plot level, DMR was fit with LME models including both environmental and woodland structure predictor variables. Logistic regression analysis was used to model the probability of a plot having at least one *Ips*-killed tree as a binary response variable.

To examine Hypotheses # 2–4, cumulative woodland mortality was described as percent crown mortality and examined at five spatial scales within each 0.1-ha plot, including the 0.1-ha "plot" scale. The subplot scale was created by splitting the plot into quarters using the four transects along the cardinal directions. Three finer spatial scales were created using 2.5 m, 5.0 m, and 7.5 m circular buffers around each tree, created from the stem map using ArcGIS software. Woodland structure and cumulative mortality measures were then summarized for each of the five spatial scales. The significance of woodland structural factors for predicting percent dead crown, after accounting for environmental influences, was assessed using an information theoretics approach to model comparisons (Burnham and Anderson, 2002), where AIC differences and Akaike weights were used to evaluate the support for competing models. AIC differences (ΔAIC) are rescaled AICs expressed as the difference between the AIC score of a given model and that of the model with the lowest AIC. The AIC statistic minimizes a function that balances model fit against model complexity, such that more negative values indicate models with greater support. Models with $\Delta\mathrm{AIC} \leq 4$ were evaluated as potentially useful models in this study. Akaike weights (w_i) are the normalized relative AIC statistics for each candidate model (R):

$$w_i = \frac{\exp(-1/2\Delta\mathrm{AIC})}{\sum_{r=1}^{R}\exp(-1/2\Delta\mathrm{AIC})} \tag{3}$$

We additionally assessed the strength of the relationship between stand density index and cumulative woodland mortality across multiple spatial scales using coefficients of determination and effect sizes from simple linear regressions, as well as partial regression analysis using mixed-effects models with Site as the fixed effect. We report simple R^2 coefficients to describe the relationship between the two variables, as well as partial R^2 coefficients that describe the effects of SDI on percent canopy mortality after accounting for covariate environmental variables. For each spatial scale considered, the covariate model included the effects of percent clay, slope aspect, slope position, and soil pH. These variables were significant predictors of percent canopy mortality when stand structure variables were not included in the model.

Stand density index was log-transformed and, for all analyses, percent dead crown was arcsine square root transformed. Adjusted R^2 values, calculated to compare the strength of the relationship across multiple spatial scales where models had different numbers of parameters, were calculated as:

$$R^2_{\mathrm{adj}} = \left(1\left[\frac{(n-1)}{(n-p)}\right]\times[1-R^2]\right), \tag{4}$$

where n is the number of observations and p is the number of parameters in the model (Burnham and Anderson, 2002). McFadden's R^2 was used to explain the variation in mixed-models using the following formula (Maddala, 1996):

$$1-\left[\frac{\mathrm{LL}(\alpha B)}{\mathrm{LL}(\alpha)}\right] \tag{5}$$

where LL(αB) is the log likelihood of the intercept and covariate model and LL(α) is the log likelihood of the intercept-only model.

3. Results

3.1. Influence of environment and stand structure on woodland mortality

On a per-plot basis, the mean percent dead crown and mean percentage of dead trees were 17.74 ± 0.76 and 7.27 ± 0.64, respectively. Linear mixed-effects models were used to examine the influence of diameter and environmental covariates on percent dead crown of individual trees. The most parsimonious model included only tree diameter (Table 1). There was a strong effect where larger diameter trees had greater percent dead crown. The model including only environmental covariates was a marginally significant improvement over the null model ($p = 0.05$), weakly suggesting that trees on steeper slopes, drier aspects, and thinner soils had greater crown mortality.

For predicting the occurrence of *Ips* within each 0.1-ha plot, the most parsimonious model included only a positive association with tree density (Table 2). Results weakly suggested that *Ips* occurrence has been more likely at higher elevations and on more acid soils. Dwarf mistletoe rating was better predicted by increasing tree cover and not stem density (Table 3). Dwarf mistletoe was generally less severe on more acidic soils with lower clay content. Across multiple spatial scales, percent dead crown was greater on sites with greater stand density index and basal area, more mesic aspect, lower slope position, and sandier soils (Table 4). For all spatial scales, the most parsimonious models for predicting crown mortality included one woodland structure variable and at least one environmental variable. In all cases, stand density index was the strongest predictor from among the structure variables. Mortality was generally greater on acidic soils with low clay content and on lower slope positions.

3.2. Scale dependence of mortality factors

Linear mixed model regression analyses were used to model the effects of environmental and structure factors on canopy mortality at five spatial scales (Table 4). Models at coarser spatial scales exhibited consistently greater explanatory power

Table 1

Results of model comparisons for mixed-effects models evaluating the impact of diameter and environmental covariates on tree canopy mortality

Model: tree canopy mortality[a]	k[b]	AIC	ΔAIC[c]	w_i[d]	logLik[e]	Model test	LR	p-value
1. Diam (+)	4	69670	0.00	0.73	−37831	1 vs. 4	68.29	<0.0001
2. Diam (+), slope (−), aspect (−), clay (−), soild (−)	8	69672	2.15	0.27	−24828	2 vs. 3	70.89	<0.0001
3. *Slope (−), aspect (−), clay (−), soild (−)*	7	69738	68.00	0.00	−34862	3 vs. 4	9.4	0.05
4** Intercept-only model**	3	69739	69.00	0.00	−34867			

Site was included as a random effect. Fixed effects were tested against covariate and null models using a likelihood ratio (LR) test ($\alpha = 0.05$). The environmental covariate model is bracketed by one asterisk and the null (intercept-only) model is bracketed by double asterisks.

[a] Abbreviations for variables are as follows: Diam, tree diameter at root crown (cm); Clay, percent clay content of the soil obtained from the SSURGO database; Soild, soil depth (cm).

[b] k = number of estimated parameters for the model.

[c] $\Delta\text{AIC} = \text{AIC}_{\text{min}} - \text{AIC}_{\text{model}}$.

[d] w_i = the rounded Akaike weights.

[e] logLik = the log-likelihood value.

than those at finer scales. Adjusted R^2 values for the most parsimonious models ranged from 0.25 for the 0.1-ha scale to 0.08 for the 0.002-ha scale (Table 4).

Simple R^2 values for the effect of SDI on percent canopy mortality, and partial R^2 values that considered the effect of SDI on percent canopy mortality after accounting for important environmental covariates, showed a stronger relationship at coarser spatial scales (Table 5). The proportion of variation explained by SDI was reduced for levels of aggregation below 0.025 ha. However, the effect size (i.e. slope coefficient) was greater at fine spatial scales.

4. Discussion

4.1. Effects of tree size, stand structure and abiotic factors

As hypothesized, trees of larger diameter were more likely to have experienced greater crown mortality. Reduced growth rates are typical for large trees (Waring and Schlesinger, 1985), a decline that can be attributed to increased carbon allocation to maintain respiration and fine roots, decreased photosynthetic efficiency due to reduced leaf surface area, and increased hydraulic resistance. Slower growing trees generally experience the greatest risk of drought and beetle induced mortality, suggesting that radial growth rate may provide a useful indicator for the ability of a tree to defend itself against attack (Wyckoff and Clark, 2002; Bigler and Bugmann, 2003). Higher percent dead crown in larger diameter trees may also result from larger trees being older and hence exposed to a greater variety of mortality factors over their lifetimes.

Studies of various coniferous forests have linked high tree stocking with greater rates of tree mortality and pathogen occurrence (Schmid and Mata, 1992; Negron and Wilson, 2003; Negron and Popp, 2004). In this study woodland structure attributes were positively correlated with tree canopy mortality, pinyon *Ips* occurrence and dwarf mistletoe rating. Percent dead crown was higher on areas with a higher stand density index. These results are consistent with the tree resistance hypothesis, which proposes that tree resistance to attack is reduced in high-density stands due to increased competition for resources that limit resource partitioning to resistance mechanisms (Berryman, 1976).

Density was found to be the structural variable important for occurrence of both pinyon *Ips* and dwarf mistletoe, while canopy cover was more important for dwarf mistletoe rating. Increased crown closure can be expected to facilitate tree-to-tree movement of dwarf mistletoe. Other studies have shown that the spread of the sticky, wind-borne seeds is more likely in

Table 2

Results of model comparisons for logistic regression models evaluating the impact of environmental and woodland structure attributes on the probability with which an I*ps*-killed tree occurs in a 0.1-ha plot

Model: presence of *Ips*-killed tree[a]	k[b]	AIC	ΔAIC[c]	w_i[d]
Dens (+)	4	537.81	0.00	0.37
Dens (+), SoilpH (−)	5	538.36	0.55	0.28
Dens (+), Elev (+)	5	539.81	2.00	0.14
Dens (+), Elev (+), SoilpH (−)	6	540.35	2.54	0.11
Dens (+), Elev (+), SoilpH (−), SlopePos (−)	7	541.40	3.59	0.06

[a] Abbreviations for variables are as follows: Dens, tree density (trees ha^{-1}); Elev, elevation above sea level (m) as obtained from a 30-m resolution digital elevation model; SlopePos, relative slope position from valley bottom to ridge top.

[b] k = number of estimated parameters for the model.

[c] $\Delta\text{AIC} = \text{AIC}_{\text{min}} - \text{AIC}_{\text{model}}$.

[d] w_i = the rounded Akaike weights.

Table 3

Results of model comparisons for mixed-effects multiple linear regression models evaluating the impact of environmental and woodland structure attributes on the level of dwarf mistletoe infection, described using Hawksworth's (1977) six-class system

Model: dwarf mistletoe rating[a]	k[b]	AIC	ΔAIC[c]	w_i[d]
Rcov (+), SoilpH (−)	5	217.98	0.00	0.43
Rcov (+), SoilpH (−), Clay (−)	6	218.18	0.25	0.38
Rcov (+), SoilpH (−), Clay (−), SlopePos (−)	4	219.54	1.56	0.09

[a] Abbreviations for variables are as follows: Rcov, tree canopy cover as derived from image analysis of digital orthophotography; Clay, percent clay content of the soil obtained from the SSURGO database; SlopePos, relative slope position from valley bottom to ridge top.

[b] k = number of estimated parameters for the model.

[c] $\Delta\text{AIC} = \text{AIC}_{\text{min}} - \text{AIC}_{\text{model}}$.

[d] w_i = the rounded Akaike weights.

Table 4
Results of model comparisons for mixed-effects statistical models of percent crown mortality at multiple scales, including both stand structure and environmental variables

	k[a]	AIC	ΔAIC[b]	w_i[c]	Adjusted R^2
Plot (0.1 ha)[d]					
SDI (+), Clay (−)	5	1267.45	0.00	0.23	0.25
SDI (+), SoilpH (−), Slopepos (−), Clay (−)	7	1267.62	0.17	0.22	0.29
BA (+), Clay (−)	5	1268.19	0.74	0.16	0.25
BA (+), Clay (−), Slopepos (−)	6	1268.21	0.76	0.16	0.24
SDI (+), Slopepos (−), Aspect (−), Clay (−)	7	1269.54	2.09	0.08	0.24
SDI (+), SoilpH (−), Slopepos (−), Aspect (−), Clay (−)	8	1269.56	2.11	0.08	0.30
BA (+)	4	1270.08	2.63	0.06	0.15
Subplot (0.025 ha)[d]					
SDI (+), SoilpH (−), Slopepos (−)	6	5338.66	0.00	0.25	0.24
SDI (+), SoilpH (−), Slopepos (−), Aspect (−)	7	5339.30	0.64	0.18	0.26
SDI (+), Clay (−)	5	5339.49	0.83	0.16	0.23
SDI (+), SoilpH (−), Slopepos (−), Clay (−)	7	5339.75	1.09	0.14	0.26
SDI (+), SoilpH (−), Slopepos (−), Aspect (−), Clay (−)	8	5340.29	1.63	0.11	0.27
SDI (+)	4	5340.68	2.02	0.09	0.22
BA (+), Clay (−), Slopepos (−), Aspect (−)	7	5341.54	2.88	0.06	0.25
7.5 m Buffer (0.018 ha)[d]					
SDI (+), SoilpH (−)	5	84191.79	0.00	0.88	0.18
SDI (+), SoilpH (−), Slopepos (−)	6	84195.84	4.05	0.12	0.19
5.0 m buffer (0.008 ha)[d]					
SDI (+), SoilpH (−)	5	77150.17	0.00	0.79	0.13
SDI (+), SoilpH (−), Slopepos (−)	8	77153.68	3.51	0.14	0.14
SDI (+), Clay (−)	5	77155.02	4.85	0.07	0.11
2.5 m buffer (0.002 ha)[d]					
SDI (+), Clay (−)	5	68649.95	0.00	0.76	0.08
SDI (+), SoilpH (−)	5	68652.22	2.27	0.24	0.08

Adjusted R^2 was calculated for the purposes of comparing the strength of the relationships at multiple spatial scales, where the number of parameters varied between models.

[a] k = number of estimated parameters for the model.

[b] $\Delta\text{AIC} = \text{AIC}_{\text{min}} - \text{AIC}_{\text{model}}$.

[c] w_i = the rounded Akaike weights.

[d] Abbreviations for variables are as follows: SDI, stand density index; BA, stand basal area; other variable abbreviations are as presented for Tables 1–3.

dense stands with large tree crowns (Reich et al., 1991), especially in areas of low species diversity and few intervening non-host species (Maloney and Rizzo, 2002), such as the pinyon-juniper woodlands.

We hypothesized that woodland sites with poor growing conditions (i.e. too dry or too cold) experience greater mortality. Our hypothesis is generally supported although environmental variables only weakly influenced canopy mortality (Table 4). Results suggest that crown and tree mortality arising from drought, DMR and bark beetles are more likely on sites that occupy lower slope positions and drier slope aspects, and have coarse-textured, more acidic soils. Such sites are more likely to experience water stress during drought. Sandier soils have reduced water holding capacity, potentially shortening the effective growing season in this semi-arid system and limiting the ability of woodland trees to withstand episodic drought or pathogen and insect outbreaks. Other studies have found that trees on drier aspects grow less vigorously due to increased moisture stress (Kaufmann and Ryan, 1986), which could also make these trees less resistant to mortality outbreaks (Orwig et al., 2002). However, counter to our results, Lei (1999) found that dwarf mistletoe infestation in pinyon-juniper woodlands was more prevalent in more mesic stands.

Table 5
Model fit across five levels of spatial aggregation for both the response variable, percent crown mortality, and predictor, stand density index

Spatial scale	N	R^2	Partial R^2	Slope coefficient (standard error)
Plot (0.1 ha)	172	0.47	0.11	0.047 (0.010)
Subplot (0.025 ha)	688	0.47	0.09	0.046 (0.005)
7.5 m Buffer (0.018 ha)	7443	0.33	0.04	0.054 (0.002)
5.0 m buffer (0.008 ha)	7443	0.31	0.06	0.065 (0.004)
2.5 m buffer (0.002 ha)	7443	0.26	0.06	0.072 (0.003)

The R^2 coefficient describes a simple linear regression between the two variables. The partial R^2 and slope coefficients are with respect to a covariate model, considering the effects of stand density index after accounting for percent clay, slope aspect, slope position, and soil pH. Mixed-effects models were used, with site as the fixed effect.

4.2. Scale-dependent effects on woodland mortality

A positive effect of density on tree mortality was expected. However, it was surprising that the negative association between woodland vigor and tree density was strongest at coarser spatial scales. We expected that tree competition would be most intense with closer proximity, and that competition among trees sharing limited resources would result in reduced capacity to respond to drought and pathogens (i.e. ‘‘Competition Hypothesis’’). The expected outcome for this hypothesis would be greater predictive power for models representing the effects of density on mortality at finer spatial scales (Fig. 2, left-hand column).

Our unexpected results lead us to propose an alternative hypothesis, the ‘‘Marginal Microsite Hypothesis’’ (Fig. 2, right-hand column). Trees establish on unfavorable microsites only during periods of favorable climate conditions. During times of drought, such as occurred in the study area from 1999 to 2002, trees on these unfavorable microsites experience higher rates of mortality than the trees growing on favorable microsites. Therefore, apparent density-dependent mortality may not be due to direct competition and the effects of density are then more predictive when considered at coarser spatial scales. Selby (2005) suggested a similar explanation for pinyon pine on the Uncompahgre Plateau. More generally, this particular mechanism for density-dependent mortality provides an example of site-dependent population regulation (*sensu* Rodenhouse et al., 1997) for species whose members select for high-quality sites and subsequently pre-empt other individuals from occupying those sites.

5. Conclusions

Cumulative woodland mortality appears to be density dependent with stocking level interacting with site environment. High densities of pinyon and juniper growing in xeric, nutrient-limited environments exhibit greater levels of mortality. However, results hint that such mortality represents primarily the loss of trees growing on less suitable microsites, and may be part of the natural variability of tree population dynamics in this drought-prone system.

The mechanisms underlying density-dependent tree mortality may not be strictly due to direct effects of intraspecific competition. The availability of favorable microsites may be the primary limiting factor in pinyon-juniper woodlands. The relative influence of biotic vs. abiotic controls over population dynamics has long been a classic question in ecological research focused on animals (Krebs, 1995; Bjornstad and Grenfell, 2001) but is not often addressed for tree mortality processes in forests and woodlands. Future experimental investigations would be valuable for differentiating which microsite factors influence tree survival, and the specific mechanisms by which competition for resources interacts with abiotic limiting factors that constrain resource availability.

Our findings are of particular importance as public land agencies in the western United States accelerate active restoration management of P-J woodlands. In this region and elsewhere, many woodland management plans specify average desired stand conditions over large spatial scales. This has the advantage of simplicity but is not supported by the results of this study, where high variability in stand structure and tree mortality was influenced by many interacting biotic and abiotic factors at tree, plot and landscape scales. Mortality is influenced by both direct competition among conspecific trees and fine-scale variation in abiotic factors. Restoration efforts aware of these relationships will likely be more successful in achieving their objectives.

Acknowledgements

The United States Bureau of Land Management (Battle Mountain Field Station) provided funding through the Great Basin Cooperative Ecosystem Studies Unit (Cooperative Agreement # FAA010017). We thank J. Ratliff for inspiration, ideas and logistical support, and J. Propp and L. Potvin for assistance with field data collection.

References

Ansley, J.S., Battles, J.J., 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. J. Torrey Bot. Soc. 125, 297–308.

Baker, W.L., Shinneman, D.J., 2004. Fire and restoration of pinyon-juniper woodlands in the western United States: a review. Forest Ecol. Manage. 189, 1–21.

Barney, M.A., Frischknecht, N.C., 1974. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. J. Range Manage. 27, 91–96.

Bartolome, J.W., Fehmi, J.S., Jackson, R.D., Allen-Diaz, B., 2004. Response of a native perennial grass stand to disturbance in California's coast range grassland. Restor. Ecol. 12, 279–289.

Berryman, A.A., 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ. Entomol. 5, 1225–1233.

Bigler, C., Bugmann, H., 2003. Growth-dependent tree mortality models based on tree rings. Can. J. Forest Res. 33, 210–221.

Bjornstad, O.N., Grenfell, B.T., 2001. Noisy clockwork: time series analysis of population fluctuations in animals. Science 293, 638–643.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Nat. Acad. Sci. USA 102, 15144–15148.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference. A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York.

Castello, J.D., Leopold, D.J., Smallidge, P.J., 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45, 17–24.

Coulson, R.N., McFadden, B.A., Pulley, P.E., Lovelady, C.N., Fitzgerald, J.W., Jack, S.B., 1999. Heterogeneity of forest landscapes and the distribution and abundance of the southern pine beetle. Forest Ecol. Manage. 114, 471–485.

Desert Research Institute Western Regional Climate Center. Available online at http://www.wrcc.dri.edu/; last accessed June 11, 2006.

Eager, T.J., Factors affecting the health of pinyon pine trees (*Pinus edulis*) in the pinyon-juniper woodlands of western Colorado, 1999. In: Monsen, S.B., Richards, S., Tausch, R.J., Miller, R.F., Goodrich, C., (Eds.), Proc. Ecology and Management of Pinyon-Juniper Communities within the Interior West. USDA Forest Service, RMRS-P-9.

Eisenhart, K.S., 2004. Historic range of variability of pinon-juniper woodlands on the Umcompahgre Plateau, western Colorado. Ph.D. Dissertation, University of Colorado, Boulder, CO.

Floyd, M.L., Hanna, D.D., Romme, W.H., 2004. Historical and recent fire regimes in Pinon-Juniper woodlands on Mesa Verde, Colorado, USA. Forest Ecol. Manage. 198, 269–289.

Grier, C.C., Elliott, K.J., McCullough, D.G., 1992. Biomass distribution and productivity of *Pinus edulis*-Juniperus monosperma woodlands of north-central Arizona. Forest Ecol. Manage. 50, 331–350.

Harner, R.F., Harper, K.T., 1976. The role of area, heterogeneity, and favorability in plant species diversity of pinyon-juniper ecosystems. Ecology 57, 1254–1263.

Hatfield, D., 1999. Slopeposition.AML. USDA Forest Service. Available online at: http://www.fs.fed.us/digitalvisions; last accessed Jan. 16, 2007.

Hawksworth, F.G., 1977. The 6-class dwarf mistletoe rating system. General Technical Report RM-48, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Helser, T.E., Punt, A.E., Methot, R.D., 2004. A generalized linear mixed model analysis of a multi-vessel fishery resource survey. Fish. Res. 70, 251–264.

Holechek, J.L., Pieper, R.D., Herbel, C.H., 2001. Range Management Principles and Practices. Prentice-Hall Inc., Upper Saddle River, New Jersey, 575 p.

Jackson, R.D., Allen-Diaz, B., 2006. Spring-fed wetland and riparian plant communities respond differently to altered grazing intensity. J. Appl. Ecol. 43, 485–498.

Kaufmann, M.R., Ryan, M.G., 1986. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. Tree Physiol. 2, 47–59.

Krebs, C.J., 1995. Two paradigms of population regulation. Wildl. Res. 22, 1–10.

Kumar, L., Skidmore, A.K., Knowles, E., 1997. Modelling topographic variation in solar radiation in a GIS environment. Int. J. Geogr. Inf. Sci. 11, 475–497.

Lei, S.A., Gradient analysis of pinyon-juniper woodland in a southern Nevada mountain range, 1999, In: Monsen, S.B., Richards, S., Tausch, R.J., Miller, R.F., Goodrich, C., (Eds.), Proc. Ecology and Management of Pinyon-Juniper Communities within the Interior West. USDA Forest Service, RMRS-P-9.

Maddala, G.S., 1996. Limited Dependent and Qualitative Variables in Econometrics. Cambridge University Press, New York.

Maloney, P.E., Rizzo, D.M., 2002. Pathogens and insects in a pristine forest ecosystem: The Sierra San Pedro Martir, Baja, Mexico. Can. J. Forest Res. 32, 448–457.

Miller, D.A., White, R.A., 1998. A conterminous United States multilayer soil characteristics dataset for regional climate and modeling. Earth Interact. 2, 1–26.

Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter TalbotJIII, R., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. 93, 1085–1093.

Negron, J.F., Anhold, J.A., Munson, S., 2001. Within-stand spatial distribution of tree mortality caused by Douglas-fir beetle (Coleoptera: Scolytidae). Environ. Entomol. 30, 215–224.

Negron, J.F., Popp, J.B., 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. Forest Ecol. Manage. 191, 17–27.

Negron, J.F., Wilson, J.L., 2003. Attributes associated with probability of infestation by the pinion ips, *Ips confusus* (Coleoptera: Scolytidae), in pinion pine, *Pinus edulis*. West. N. Am. Nat. 63, 440–451.

Orwig, D.A., Foster, D.R., Mausel, D.L., 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. J. Biogeogr. 29, 1475–1487.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects Models in S and S-PLUS. Springer, New York.

Py, C., Bauer, J., Biondi, F., Weisberg, P.J., 2006. Radial growth responses of singleleaf pinyon (*Pinus monophylla*) to wildfire. Dendrochronologia 24, 39–46.

Reich, R.W., Mielke Jr., P.W., Hawksworth, F.G., 1991. Spatial analysis of ponderosa pine trees infected with dwarf mistletoe. Can. J. Forest Res. 21, 1808–1815.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.

Robinson, D.E., Geils, B.W., Muir, J.A., Spatial statistical models for the spread of dwarf mistletoe within and between stands, 2002. In: Crookston, N.L., Havis, R.N. (Eds.), Proceedings-Second Forest Vegetation Simulator Conference. USDA Forest Service, RMRS-P-25.

Rodenhouse, N.L., Sherry, T.W., Holmes, R.T., 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78, 2025–2042.

Samman, S., Logan, J. (Eds.), 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. Report to congress from Forest Health Protection, Washington Office, Forest Service, U.S. Department of Agriculture. General Technical Report RMRS-GTR-62. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 46 p.

Savage, M., 1997. The role of anthropogenic influences in a mixed-conifer mortality episode. J. Veg. Sci. 8, 95–104.

Schmid, J.M., Mata, S.A., 1992. Stand density and mountain pine beetle-caused tree mortality in ponderosa pine stands. Research Note RM-515. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 4 p.

Selby, D.C., 2005. Assessing pinyon pine mortality on the Uncompahgre Plateau in western Colorado, USA. M.Sc. Thesis, Colorado State University, Fort Collins, CO.

Shore, T.L., Safranyik, L., Lemieux, J.P., 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Can. J. Forest Res. 30, 44–49.

Skelly, J., Christopherson, J., 2003. Pinyon Pine Management and Guidelines for Common Pests. EB 03-02, 37 p.

Soil Survey Staff, 2007. Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database for Nevada. Available URL: "http://soildatamart.nrcs.usda.gov". Accessed 10/2005.

Tausch, R.J., West, N.E., 1987. Differential establishment of pinyon and juniper following fire. Am. Mid. Nat. 119, 174–184.

Thien, S.J., 1979. Determining soil texture by the "feel method". J. Agric. Ed. 8, 54–55.

Trummer, L.M., Hennon, P.E., Hansen, E.M., Muir, P.S., 1998. Modeling the incidence and severity of hemlock dwarf mistletoe in 110-year-old wind-disturbed forests in Southeast Alaska. Can. J. Forest Res. 28, 1501–1508.

USDA Natural Resources Conservation Service, 2006. Soil Data Viewer 5.1 Users Guide.

Waring, R.H., 1987. Characteristics of trees predisposed to die. Bioscience 37, 569–574.

Waring, R.H., Schlesinger, W.H., 1985. Forest Ecosystems: Concepts and Management. Academic Press, San Diego.

Weiner, J., 1984. Neighborhood interference amongst Pinus rigida individuals. J. Ecol. 72, 183–195.

Weisberg, P.J., Lingua, E., Pillai, R.B., 2007. Spatial patterns of pinyon-juniper expansion in central Nevada. Rangeland Ecol. Manage. 60, 115–124.

Wickman, B.E., 1992. Forest health in the Blue Mountains: the influence of insects and diseases. USDA Forest Service Pacific Northwest Research Station. General Technical Report PNW-GTR-295, 15 p.

Wyckoff, P.H., Clark, J.S., 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. J. Ecol. 90, 604–615.

Young, J.A., Budy, J.D., 1979. Historical use of Nevada's pinyon-juniper woodlands. J. Forest Hist. 23, 112–121.

Zimmermann, N., 2006. Tools for analyzing, summarizing, and mapping of biophysical variables. Available online: http://www.wsl.ch/staff/niklaus.-zimmermann/progs.html; last accessed Mar. 14, 2006.