Journal of Biogeography, **30**, 257–276

Environmental responses of *Pinus ponderosa* and associated species in the south-western USA

H. C. Humphries* and P. S. Bourgeron *Institute of Arctic and Alpine Research, University of Colorado, 1560 30th St, UCB 450, Boulder, CO 80309-0450, USA*

Abstract

Aim We addressed four objectives: (1) Determine the regional responses of species, size classes and a vegetation type to climate and parent material predictors, including their distributions in environmental space and the relative contributions of the predictors to explained variation. (2) Determine whether size classes of a species respond similarly to climate and parent material. (3) Assess the extent to which the predicted regional distribution of a vegetation type can be approximated by the distribution of its diagnostic species and *vice versa*. The establishment of a consistent relationship between the distribution of a vegetation type and its diagnostic species would facilitate change detection, management and conservation planning by allowing the use of one distribution to generate the other when data availability is limited. (4) Examine landscape-scale environmental variability in predicted species and vegetation type distributions.

Location South-western USA (Arizona, New Mexico and southern Colorado).

Methods Ecological response surface models were developed using a data base of 1409 vegetation plots to analyse biotic–environmental relationships of (1) *Pinus ponderosa* P. & C. Lawson and *Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr. size classes, (2) *P. ponderosa, A. concolor* and *Quercus gambelii* Nutt. combined size classes, and (3) a *P. ponderosa* forest type widely distributed in the south-western USA.

Results and main conclusions *Pinus ponderosa* and *A. concolor* models generally were judged to be successful. *Quercus gambelii* models were judged unsuccessful, which may result from the influence of variables not modelled, such as soil moisture, disturbance, biotic factors and other site limiting factors. Size classes differed in the range of environmental conditions associated with high occurrence probabilities within and between species, reflecting differences in the effects of climate variability and anthropogenic changes, such as fire suppression, on the distribution of each size class. *Pinus ponderosa* alliance was predicted to be distributed over a narrower range of environmental conditions than *P. ponderosa* species models, therefore limiting the use of this vegetation type as a surrogate for the distribution of the dominant species, and *vice versa*. Maps of combinations of environmental variables that produced a high probability of *P. ponderosa* occurrence showed that some landscapes predicted to contain the species exhibited diverse environmental conditions over short distances. The use of regional environmental relationships to characterize areas with high local environmental variability may facilitate identification of areas of potential rapid biotic change.

Keywords
Abies concolor, environmental variability, *Pinus ponderosa*, predicted distribution, *Quercus gambelii*, response surface model, size class, south-western USA.

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*Correspondence: Institute of Arctic and Alpine Research, University of Colorado, 1560 30th St., UCB 450, Boulder, CO 80309-0450, USA.
E-mail: hope.humphries@colorado.edu

INTRODUCTION

Understanding the regional environmental drivers of plant species and community distributions has long been of interest in biogeography, and assumes greater importance in the face of projected climate and land use changes, which have the potential to significantly alter many biotic distributions (Kadmon & Heller, 1998; Bourgeron *et al.*, 2001 a; Shafer *et al.*, 2001). Maps of current distributions are needed as baselines for assessing future changes, but such maps for individual plant species and communities may not be available at regional scales, or if available, may be relatively imprecise delineations of extent, providing little information about continuity of occurrence within the boundaries (Huntley *et al.*, 1995). In addition, maps may not depict the distributions of particular vegetation attributes of interest. For example, remote sensing imagery can provide regional-scale maps of dominant plant species and broad-scale vegetation types, but cannot represent distributions of age or size classes (He *et al.*, 1998). An approach to overcoming some of the limitations of remotely sensed data is He *et al.*'s (1998) integration of Thematic Mapper (TM) data with field inventory data, in which information on age class distributions and occurrence of secondary and subcanopy plant species from inventory plots was associated with canopy-dominant plant species mapped in the satellite classification.

An alternative widely used approach, applied to a number of biogeographical investigations, is the construction of ecological response surfaces to relate biotic distributions to environmental driving variables (Bartlein *et al.*, 1986). Response surfaces have been developed using a variety of regression techniques, especially those that incorporate nonlinear responses, such as generalized linear modelling, generalized additive modelling, and regression trees (Franklin, 1998; Iverson & Prasad, 1998; Schwartz *et al.*, 2001). Climate has long been recognized as playing a fundamental role in determining biotic distribution patterns at regional scales (Woodward & Williams, 1987; Swetnam & Betancourt, 1998), and has therefore been a focus of many response surface studies (e.g. Bartlein *et al.*, 1986; Lenihan, 1993; Huntley *et al.*, 1995; Leathwick, 1995). Some studies have incorporated additional environmental variables as predictors, such as lithology, drainage classes and topographical variables (e.g. Austin *et al.*, 1990; Leathwick, 1995; Franklin, 1998).

The identification of significant drivers of biotic responses allows the determination of the dimensions of species niches, prediction of biotic distributions in unsampled areas and prediction of the effects of environmental changes on the biota of an area (Margules & Stein, 1989; Nicholls, 1989; Austin *et al.*, 1990; Lenihan & Neilson, 1993; Austin, 1999). Response surface models have been developed for a variety of local to regional studies of individual plant species distributions (e.g. Bartlein *et al.*, 1986; Austin *et al.*, 1990; Yee & Mitchell, 1991; Lenihan, 1993; Smith, 1994; Leathwick, 1995, 1998; Austin, 1998; Bio *et al.*, 1998; Franklin, 1998; Guisan & Theurillat, 2000) and vegetation types (Margules & Nicholls, 1987; Brown, 1994).

Plant sizes affect many aspects of vegetation structure, such as population density, spatial distribution of species, and response to disturbance (Knowles & Grant, 1983; Savage, 1997). Because of the plasticity of plant responses, Harper (1967, 1977) considered size to be a more important aspect of plant population structure than age. In addition, size classes within a plant species may exhibit differences in distribution. For example, size classes of three pine species differed in mean location along a topographical gradient in south-east Arizona (Barton, 1993). Knowledge of the size class distributions of plant species can provide important information for assessing future forest structure and composition for management purposes, including departures of existing conditions from the historical range of variability (White & Vankat, 1993; Humphries & Bourgeron, 2001). No study to date has examined the environmental relationships of size classes within a plant species using ecological response surfaces.

We developed response surfaces to analyse biotic–environmental relationships of *Pinus ponderosa* P. & C. Lawson (a dominant forest species) by size class and all size classes combined, and for a *P. ponderosa* vegetation type in the south-western USA. We also examined the environmental relationships of two species occurring in southwestern USA *Pinus ponderosa* forests, *Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr. by size class and all size classes combined, and *Quercus gambelii* Nutt. for all size classes combined.

Our research had the following objectives: (1) Determine the responses of species, size classes and a vegetation type to climate and parent material predictors, including their distributions in environmental space and the relative contributions of the predictors to explained variation. (2) Determine whether size classes of a species respond similarly to climate and parent material. (3) Assess the extent to which the predicted distribution of a vegetation type can be approximated by the distribution of its diagnostic species (Grossman *et al.*, 1998, 1999) and *vice versa*. The establishment of a consistent relationship between the distribution of a vegetation type and its diagnostic species would facilitate management and conservation planning by allowing the use of one distribution to generate the other when data availability is limited. (4) Examine landscape-scale environmental variability in predicted species and vegetation type distributions. Regional biotic–environmental relationships, used to map the expected range of local environmental conditions, could assist in locating areas of potential rapid biotic change, e.g. locations at the margins of biotic distributions in environmental space.

MATERIALS AND METHODS

Study area, vegetation data and environmental data

The study area is part of the south-western USA (hereafter referred to as the Southwest), which we define as Arizona, New Mexico and southern Colorado (Fig. 1). Forested locations included in the study range in elevation from 1500 to 3600 m, with annual average temperatures of −2 to 17 °C and annual precipitation amounts from 26 to 128 cm. In the

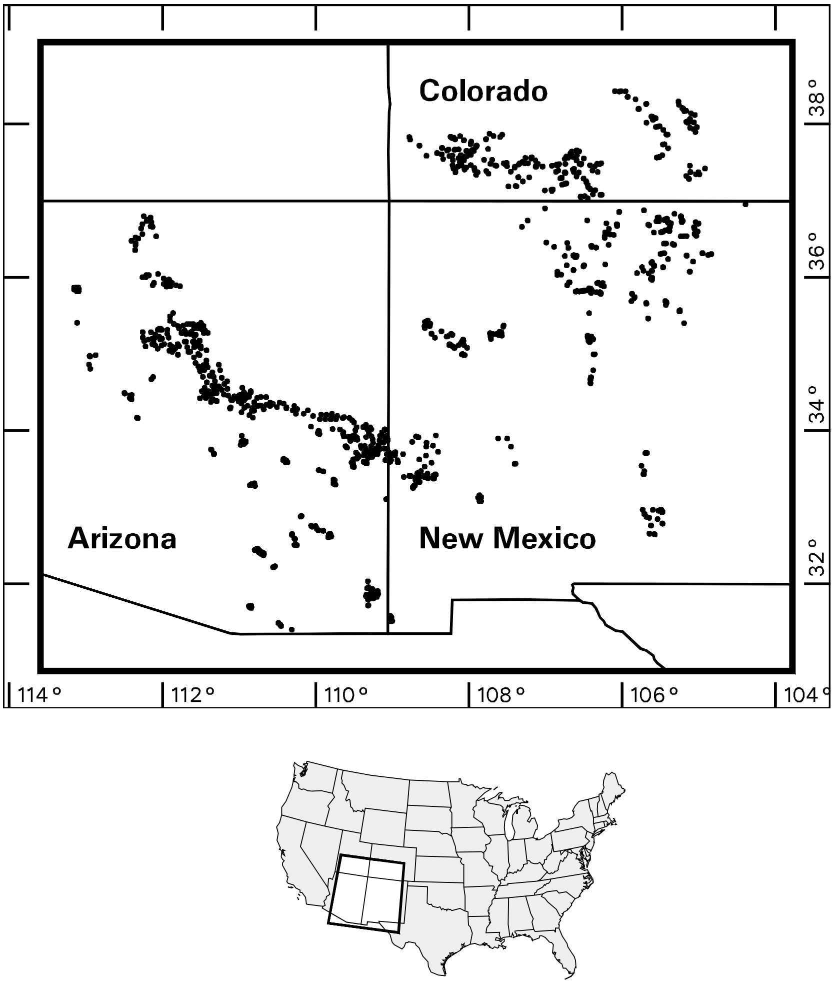


Figure 1 Locations of forested plots in the Southwest used in model development and testing.

study area, changes in elevation (corresponding to gradients in temperature and available moisture) are associated with changes in vegetation zones (Dick-Peddie, 1993). At the lowest forested elevations, *P. ponderosa*-dominated forests intergrade with grassland, shrubland or woodland vegetation (Daubenmire, 1978; Peet, 1978). With increasing elevation, mixed conifer forests replace *P. ponderosa*-dominated forests, which are in turn replaced by spruce-fir forests at the highest forested elevations (Whittaker & Niering, 1965; Peet, 1978).

We used existing location-specific vegetation data consisting of 1406 plots collected for the classification of forest types in the Southwest (Muldavin *et al.*, 1990). Plots had uniform size (375 m^2) and included abundance of all vascular plant species present, and spatial location, elevation, slope, aspect and parent material. Tree species abundance was recorded as stem density in three size classes (Muldavin *et al.*, 1990): young regeneration (< 5 cm diameter at breast height, d.b.h.), advanced regeneration (5–25 cm d.b.h.), and mature (>25 cm d.b.h.). Two plots collected at the Gray Ranch in south-western New Mexico and one plot from Monument Canyon Research Natural Area, New Mexico, were added to the data set for a total of 1409 plots. Parent material categories were derived from 1 : 500,000-scale geological substrate maps of Arizona, New Mexico and Colorado. A geographical information system (GIS) was used to digitize the boundaries of parent material categories and to attribute them to plots. Of a total of eleven parent material categories occurring in the study area, four (sedimentary rock, basalt, granite and other igneous rock) had sufficient plots for development and testing of individual models, for a total of 1274 plots (Fig. 1). Plots used in the analyses were divided randomly into two subsets: two-thirds of the plots (836) for model development and the remaining one-third (438) for testing the results of modelling.

We selected four important elements of Southwest landscapes for response surface modelling: *P. ponderosa*, *A. concolor* and *Q. gambelii* at the species level and *P. ponderosa* alliance (*sensu* Grossman *et al.*, 1999) as the vegetation type (Bourgeron & Engelking, 1993; Grossman *et al.*, 1998). *Pinus ponderosa* covers extensive areas in the Southwest. Although human activities have affected the area for hundreds of years, activities such as fire suppression, grazing and logging have produced heavy impacts on Southwest forests in the past century (Covington *et al.*, 1994; Kaufmann *et al.*, 1994). The resulting changes in forest structure and composition include fewer older and larger trees, increased numbers of younger and smaller trees, fuel accumulation and reduced biomass of understory species (Covington & Moore, 1994). Given these changes, it is important to understand the range of environmental conditions under which *P. ponderosa* species and alliance occur, and whether these conditions may vary among size classes of the species and between species and alliance. *Abies concolor* commonly occurs in high elevation *P. ponderosa* forests and is also found in mixture with *Pseudotsuga menziesii* (Mirbel) Franco in the Southwest (Eyre, 1980). Recent anthropogenic impacts to Southwest forests have affected the distribution of *A. concolor,* including changes in size class distributions (White & Vankat, 1993). *Quercus gambelii* is a subcanopy species often present in forests dominated by *P. ponderosa* and *A. concolor* (Muldavin *et al*., 1990). Summer precipitation amount has been shown to have a strong effect on the establishment of *Q. gambelii* seedlings (Neilson & Wullstein, 1983, 1985, 1986) and increases in abundance of *Q. gambelii* and other shrub species have been associated with fire suppression and livestock grazing in the Southwest (Madany & West, 1983).

Models for *P. ponderosa* species and *A. concolor* were constructed for each of the three size classes (mature, advanced regeneration and young regeneration) and also for all size classes combined. *Quercus gambelii* occurs as both tree (single-stemmed) and shrub (multi-stemmed) growth forms. In this study, we used data for *Q. gambelii* trees only. Models were developed for all *Q. gambelii* size classes combined because of insufficient occurrences in plots to model size classes individually.

Plots were assigned to the *P. ponderosa* alliance based on overstory species density values in a two-step classification. In the first step, all plots with *P. ponderosa* in the overstory were selected. Plots containing *P. ponderosa* × *P. arizonica* Engelm. hybrids were eliminated to avoid potential taxonomic problems (W.H. Moir, pers. comm.). In the second step, clustering was performed on these plots to distinguish the *P. ponderosa* alliance from closely related alliances such as *A. concolor, Pinus leiophylla* Schiede & Deppe and *P. engelmannii* Carr. (Bourgeron & Engelking, 1993; Grossman *et al*., 1998). Clustering was performed using Ward's technique with Euclidean distance in the software package PATN (Belbin, 1990). The classification was further refined by inspection of individual plots to resolve remaining ambiguities in class membership. Plots were coded as *P. ponderosa* alliance present or absent.

Based on the results of previous studies (e.g. Whittaker & Niering, 1965; Mackey *et al*., 1988; Allen & Peet, 1990; Austin *et al*., 1990), nine climate attributes representing temperature, precipitation and radiation regimes were selected for inclusion in models as predictors of biotic responses (Table 1). The simulation model MTCLIM (Hungerford *et al*., 1989) was modified to estimate climate attributes for plots, which were treated as point locations in simulation runs. MTCLIM extrapolates climate variables from nearby National Climatic Data Center (NCDC) weather stations and produces daily values for radiation, temperature, and precipitation at the location of interest, correcting for elevation, slope, and aspect differences between the location and the weather station. Input into the model from NCDC weather stations consisted of daily values for precipitation, maximum temperature and minimum temperature averaged over the length of the weather record, which varied from 9 to 41 years. Weather stations used in this study were selected to be as close as possible to plots in distance and elevation. Values of climate attributes for each plot were derived from MTCLIM daily estimates aggregated over the appropriate time period.

Table 1 Climate attributes used as predictors of biotic responses in models

Climate attribute	Abbreviation
Average annual temperature (°C)	AT
Maximum July temperature (°C)	HT
Minimum January temperature (°C)	CT
Annual precipitation (cm)	AP
First quarter (winter) precipitation (cm)	WP
Second quarter (spring) precipitation (cm)	SP
Third quarter (summer) precipitation (cm)	UP
Fourth quarter (fall) precipitation (cm)	FP
Annual solar radiation (W/m^2)	AR

The performance of MTCLIM in the Southwest was evaluated using ten test NCDC weather stations distributed over the study area at elevations (2280–3255 m) within the range of plot elevations and selected to have weather records of at least 20 years. Model predictions for precipitation and temperature (radiation data were not available from the weather stations) at the test weather stations were derived from other NCDC weather stations near each test station. Predicted values were compared with observed test station values (Table 2). For all climate attributes, there was good agreement between predicted and observed values ($r_s > 0.85$, $P < 0.01$ for all attributes). However, MTCLIM estimations were consistently lower than observed values for first quarter (winter) precipitation (WP) (mean absolute error of 3.74 cm) and higher than observed for third quarter (summer) precipitation (UP) (mean absolute error of 3.64 cm). The magnitude of the discrepancies varied among test weather stations, but did not appear to be related to their geographical location or elevation.

For plots, overlap in the distribution of climate attributes across parent material categories was observed (Fig. 2), along with some differences in median climate values. For example, plots on granite had higher median minimum January temperature (CT) and second quarter precipitation (SP), whereas plots on sedimentary rock had lower median annual precipitation (AP). In general, the range of climate values was greatest for other igneous rock and least for basalt, reflecting their relative abundance in plots.

Analysis

We developed response surface models of species and alliance presence/absence (coded as 1 and 0, respectively) using a generalized linear model (GLM) formulation appropriate

Table 2 Comparison of predicted MTCLIM estimates with observed values of climate attributes for averages of ten test weather stations distributed over the southwest. Climate attribute abbreviations listed in Table 1

Climate attribute	Observed average value	Predicted average value	Mean absolute error[†]	$r_s^{‡}$
Temperature (°C)				
AT	5.64	5.91	1.55	0.87
HT	23.96	23.80	0.50	0.95
CT	−10.65	−10.90	1.11	0.93
Precipitation (cm)				
AP	66.36	66.18	1.96	0.98
WP	16.87	13.53	3.74	0.94
SP	9.36	10.22	1.14	0.93
UP	23.72	27.31	3.64	0.89
FP	16.07	15.17	1.80	0.97

[†] Mean absolute error (Σ|observed−predicted|)/(n = 10) (Mayer & Butler, 1993).

[‡] Spearman's rank correlation of predicted and observed values for n = 10 test weather stations (Sokal & Rohlf, 1981).

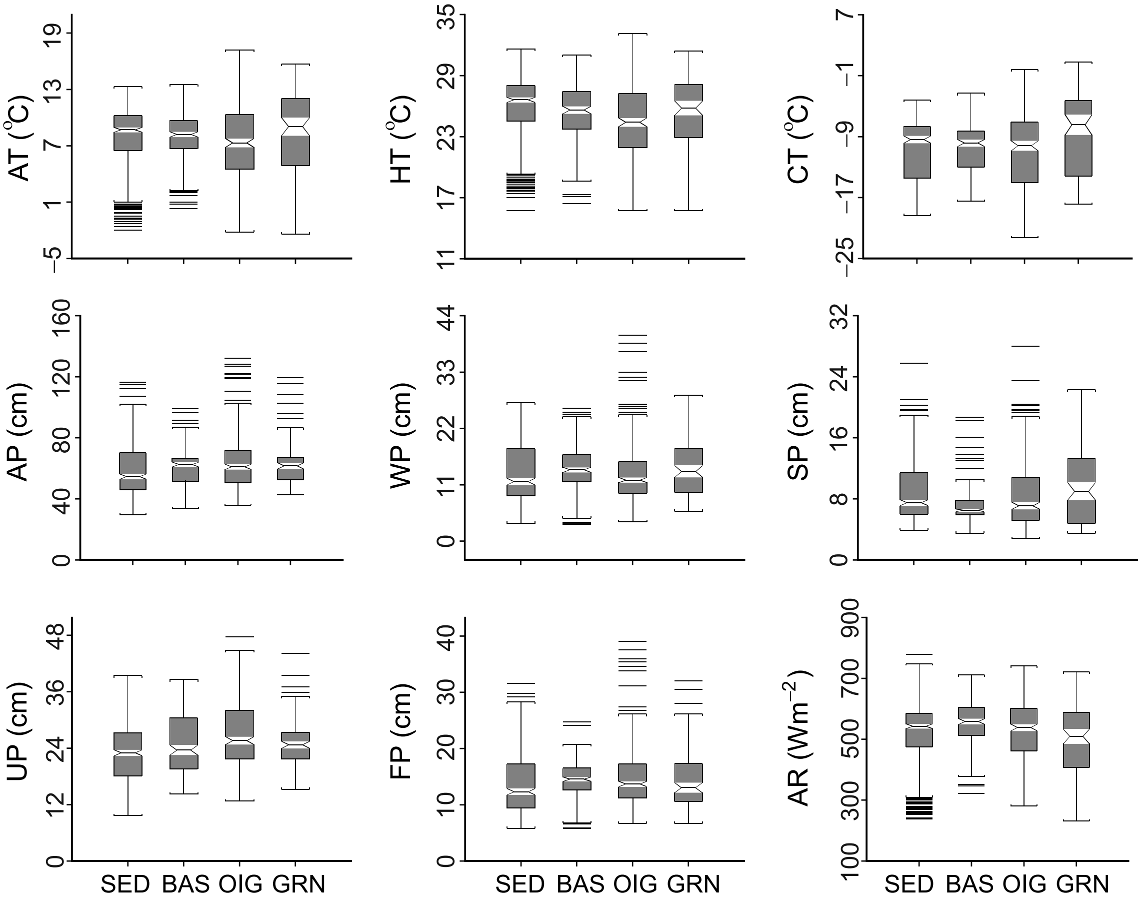


Figure 2 Notched box plots showing distribution of plot climate attributes (abbreviations listed in Table 1) by four parent material categories. Notches indicate 95% confidence limits around the median. SED, sedimentary rock; BAS, basalt; OIG, other igneous rock; GRN, Granite.

to binomial distributions (McCullagh & Nelder, 1989). The model structure consisted of a linear combination of environmental attributes linked to the predicted response by a (nonlinear) logit function, which constrains predicted values to be between 0 and 1 (McCullagh & Nelder, 1989; Nicholls, 1989; Austin *et al.*, 1990). Environmental attributes were entered into a model using a forward stepwise procedure in which at each step, an attribute was selected whose addition to the model produced the largest significant change in deviance. The change in deviance is approximately distributed as a chi-squared statistic (McCullagh & Nelder, 1989). A significance level of 1% was used for all models (Austin *et al.*, 1990). Attributes could enter the model as either linear or linear plus quadratic terms. Interactions between attributes in the model were also tested for significance during the variable selection phase of model construction. When no significant variables remained for selection, attributes in the model were tested to determine whether higher order terms (e.g. quadratic or cubic) were necessary. Terms were added or removed according to the results of this analysis. To avoid the problem of unequal classes of the response variables (Agresti, 1990), approximately equal numbers of presences and absences were randomly selected from the 836 plots designated for model development for each biotic response variable.

After a model was developed, three regression diagnostic measures were applied to evaluate and improve the fit of the model to the data. A small number of plots that had high (1) standardized residuals, (2) Cook's distance (a measure of the actual influence of an observation), or (3) leverage (a measure of potential influence) were removed from the data set and models refitted. If a substantial improvement in the percentage of plots correctly predicted was judged to have occurred, the refitted model was used. Models were then tested by applying equations to plots not used in their development.

We investigated spatial autocorrelation in model residuals. Both biotic responses and environmental predictor variables (such as climate and substrate attributes) are spatial data. When statistical models are fitted to such data, spatial autocorrelation in the errors or residuals violates the general assumption that the errors should be independent (Odland, 1988). Only a few plant studies incorporating response functions have explicitly considered spatial autocorrelation effects. Smith (1994) included the number of species presences in neighbouring pixels as an explanatory variable to reduce autocorrelation in the residuals following model fitting. Brown (1994) sampled pixels at a lag of twenty pixels to reduce response variable autocorrelation and analysed autocorrelation in residuals as part of an effort to account for discrepancies between observed and predicted vegetation patterns. Similarly, we evaluated spatial autocorrelation in model residuals by calculating Moran's I (Odland, 1988) for twenty distance classes, with a minimum of thirty pairs of points included in each autocorrelation calculation.

Model predictions are probabilities of occurrence. To compare predicted probability of occurrence with observed presence or absence on a plot, we converted probabilities of occurrence to presence or absence by designating 'presence' when a probability was ≥ 0.5, and 'absence' when < 0.5. For each model, an error matrix was constructed to compare numbers of test plots observed to be present or absent with numbers of plots predicted to be present or absent. Model accuracy was examined using the Kappa statistic (Cohen, 1960) computed for each error matrix. Monserud & Leemans's (1992) degree of agreement scale for Kappa provided a means to assess relative accuracy among models.

To compare species and alliance distributions, we developed maps of continuous predicted distributions for *P. ponderosa* models for a one by one degree area in east-central Arizona and west-central New Mexico that is known as West Clifton. MTCLIM was used to generate raster-based data layers for all climate attributes used in modelling at a 100-m resolution. Equations resulting from modelling were applied to climate values to produce maps of probability of occurrence, which were grouped into four classes [(1) $\geq 0 < 0.25$, (2) $\geq 0.25 < 0.5$, (3) $\geq 0.5 < 0.75$, (4) $\geq 0.75 \leq 1$] for display. We also mapped combinations of classes of two significant predictors [maximum July temperature (HT) and annual solar radiation (AR)] for locations in West Clifton that had a predicted probability of occurrence ≥ 0.75 for *P. ponderosa* to identify potential conservation areas for this species that contained varying environmental conditions.

Influence of parent material

Species and alliance responses were each tested for sensitivity to parent material. Significant differences in response among parent material categories were found for *P. ponderosa* and *Q. gambelii* but not for *A. concolor*. Therefore, analyses for *P. ponderosa* and *Q. gambelii* were performed in two ways. (1) A model was constructed for combined parent material categories. Parent material was available for inclusion in the model as a four-level factor. (2) The data were stratified by parent material and separate models for each response variable were developed for each of the four parent material categories to investigate whether this stratification improved model accuracy.

RESULTS AND DISCUSSION

Pinus ponderosa species models

Environmental relationships

Significant climate attributes differed among response surface models developed for *P. ponderosa*, but common features were also observed (Tables 3 and 4). AR was the attribute included most often in the models (Table 3). Many models also contained HT, average annual temperature (AT), and/or CT. AP was included in six models; a single model contained fourth quarter (fall) precipitation (FP). At least one temperature attribute was a significant predictor in each model and was the first variable selected, although the temperature attributes that were important predictors differed among size classes and parent material categories (Table 4). HT was included as a linear term in twelve of thirteen models containing this variable, indicating that *P. ponderosa* probability of occurrence increased with increasing HT. This is an expected result for a species that dominates warm temperature, low-elevation forests in the Southwest (Dick-Peddie, 1993). However, AT occurred as a

Table 3 Frequency of inclusion of environmental variables in response surface models. Climate attribute abbreviations listed in Table 1. PM(4) = parent material, fitted as a factor with four classes

Predictor variable	*Pinus ponderosa* P. & C. Lawson species (twenty models)	*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr. species (four models)	*Quercus gambelii* Nutt. species (five models)	*Pinus ponderosa* alliance (five models)
AT	10	–	2	2
HT	13	4	2	2
CT	7	–	1	2
AP	6	2	–	3
WP	–	2	–	–
SP	–	2	1	–
UP	–	–	–	–
FP	1	–	–	1
AR	15	4	–	4
PM(4)	–	–	1	1

quadratic function in nine of ten models in which it was present, indicating that the maximum predicted probability of occurrence was attained at less than the maximum AT value. This result occurred because in plots located in extreme southeast Arizona and southwest New Mexico, where the highest AT values in the data set are found, *P. ponderosa* is replaced by other low elevation *Pinus* species such as *P. leiophylla* and *P. engelmannii* (Barton, 1993). CT was included as either a linear or quadratic function in seven models. HT was included in all sedimentary rock and most basalt models, CT was present in most granite models and AT occurred in all models on other igneous rock. HT and AT or all three temperature attributes were significant predictors in combined parent material category models.

AR was usually included as an increasing linear function, but was present as a quadratic function in the model for the young regeneration size class on combined parent material categories, indicating a maximum limit to occurrence of this size class at less than the maximum AR values (Table 4). Three of the five models lacking AR as a significant predictor were on basalt. Unlike most other parent material categories, plots on basalt that contained *P. ponderosa* did not differ significantly in AR values from plots on basalt lacking the species. Temperature–radiation interaction terms occurred in all models for combined parent material categories, and for three of four other igneous rock models, indicating that the response of *P. ponderosa* to AR in these models varied with the temperature level, i.e. at low temperatures, the probability of occurrence generally increased with increasing AR, but at high temperatures, the probability of occurrence varied comparatively little with increasing AR.

Precipitation attributes were included in seven of the twenty *P. ponderosa* species models. All models developed for other igneous rock contained AP, which was included as a decreasing linear term, indicating that the probability of occurrence increased with decreasing AP. FP was present as a decreasing linear term in the model for advanced regeneration on combined parent material categories.

Most models were judged to be accurate in predicting presence or absence on test plots (Table 5). Association of the Kappa statistic with the rating system of Monserud & Leemans (1992) produced ratings of very good (five models), good (seven models) and fair (seven models). Only one model, for advanced regeneration on basalt, was rated poor. The advanced regeneration model on granite was not successful in predicting absence (48% correct), although the percentage of correctly predicted presences was high (93% correct). Most models (fifteen of twenty) had a slightly to moderately higher percentage correct for presence than absence. The greatest degree of overall success in test plot prediction was achieved in combined and mature size class models, which generally also had higher percentage deviance explained (range of 36–74%; Table 4) than advanced and young regeneration size class models (range of 16–46%; Table 4).

Distribution in environmental space

Response surfaces were graphed with respect to environmental variables for models developed on all parent material categories combined, sedimentary rock and other igneous rock (Figs 3–5). Other parent material categories contained only one predictor or lacked sufficient common predictors among size classes to compare response surfaces. For all parent material categories combined, response surfaces were produced using the significant predictors HT and AR (Fig. 3). In general, high predicted probabilities of occurrence (≥ 0.75) were found at relatively high temperature and radiation values. These results are in agreement with experimental studies of *P. ponderosa* seedlings, which had significantly higher survival and biomass under high than low light conditions (Barton, 1993), and require warmer temperatures than a higher-elevation pine species (Cochran & Berntsen, 1973). The ranges of HT and AR resulting in high probabilities within the limits of the data (convex hulls in Fig. 3) were broadest for the combined, mature and advanced regeneration size class models, in which the highest probabilities of occurrence (≥ 0.75) were predicted by intermediate to high HT and AR values (Fig. 3 a–c). A narrower range of HT and AR produced high probabilities of occurrence in the young regeneration size class model, reflecting the inclusion of AR as a quadratic function (Fig. 3d; Table 4).

Response surfaces for models on sedimentary rock exhibited the highest predicted probabilities of occurrence at

Table 4 Response surface modelling results. Model terms are predictor variables in order of entry into model; superscripts indicate order of polynomials. Climate attribute abbreviations listed in Table 1

Parent material	Model terms	Deviance explained (%)	*n*
Pinus ponderosa – all size classes combined			
All PM	HT + AT + AT^{2} + AR + (AT^{2}*AR) + AP	53.1	491
Sedimentary rock	HT + AR	73.9	185
Basalt	HT	36.2	68
Granite	AT + AT^{2} + AR	69.3	49
Other igneous rock	AT + AT^{2} + AP + AR + (AT*AR)	55.7	200
Pinus ponderosa – mature size class			
All PM	HT + AR + AT + AT^{2} + (AT^{2} *AR) + CT	43.8	570
Sedimentary rock	HT + AR	55.8	215
Basalt	HT + AR	46.1	80
Granite	CT + CT^{2} + AR + HT	62.9	52
Other igneous rock	AT + AT^{2} + AP + AR + (AT^{2}*AR)	51.7	223
Pinus ponderosa – advanced regeneration size class			
All PM	HT + AR + (HT*AR) + AT + AT^{2} + CT + FP + (CT*FP)	32.4	720
Sedimentary rock	HT + AR + AP	40.3	277
Basalt	HT	15.5	141
Granite	CT + CT^{2}	27.8	63
Other igneous rock	AT + AT^{2} +AP + AR + (AT^{2}*AR)	45.9	234
Pinus ponderosa – young regeneration size class			
All PM	AT + AT^{2} + AR + AR^{2} + (AT^{2}*AR) + HT + CT	33.3	719
Sedimentary rock	HT + AR	41.1	270
Basalt	AT	32.9	96
Granite	CT + AR	32.8	82
Other igneous rock	AT + AT^{2} + AP + CT + CT^{2} + HT + HT^{2}	37.8	219
Abies concolor – all size classes combined			
All PM	HT + HT^{2} + SP + SP^{2} + SP^{3} + (HT*SP) + AR + (HT^{2}*AR)	49.9	365
Abies concolor – mature size class			
All PM	HT + HT^{2} + AP + (HT^{2}*AP) + AR	43.8	201
Abies concolor – advanced regeneration size class			
All PM	HT + HT^{2} + AR + (HT*AR) + AP + (HT*AP) +WP	46.7	292
Abies concolor – young regeneration size class			
All PM	HT + HT^{2} + SP + SP^{2} + SP^{3} + (HT*SP) + AR + WP + WP^{2} + (HT*WP)	51.8	333
Quercus gambelii – all size classes combined			
All PM	HT + HT^{2} + PM(4)	21.0	511
Sedimentary rock	HT + AT + CT + (HT + CT)	23.7	251
Basalt	AT + AT^{2}	23.1	136
Granite	SP + SP^{2}	18.5	48
Other igneous rock	AT + AT^{2}	31.5	70
Pinus ponderosa alliance			
All PM	HT + AR + AR^{2} + AT + AT^{2} + AT^{3} + (AT^{2} +AR) + AP + PM(4)	53.4	711
Sedimentary rock	AR + AR^{2} + AP + CT + (CT^{2}*AP) + FP	65.9	276
Basalt	HT + AR	66.2	96
Granite	CT + CT^{2}	45.0	34
Other igneous rock	AP + AT + AT^{2} + AT^{3} + AR + AR^{2} + (AT^{2}*AR)	56.8	159

All PM = all parent material classes combined. PM(4) = parent material fitted as a factor with four classes. *n* is the number of plots used to develop a model.

intermediate to high values of HT and AR within the limits of the data (convex hulls in Fig. 4). All predicted responses to HT and AR were linear; these variables were the only predictors included in three of the four models. Combined and mature size class models had the broadest range of HT and AR combinations resulting in probabilities ≥ 0.75 (Fig. 4 a, b). This range was somewhat narrower for advanced and young regeneration models (Fig. 4c, d).

Response surfaces for models on other igneous rock were developed for AT and AP, two important predictors on this

Table 5 Response surface modeling results for equations applied to test data plots. A probability of 0.5 was used as a cutoff for determining presence or absence. Percent correct refers to number correctly predicted expressed as a percentage of the number observed

	Number observed			Number correctly predicted			Percent correct			
Parent material	Present	Absent	Total	Present	Absent	Total	Present	Absent	Kappa	
Pinus ponderosa – all size classes combined										
All PM	122	123	245	101	107	208	82.8	87.0	0.70	Very good
Sedimentary rock	43	38	81	42	31	73	97.7	81.6	0.80	Very good
Basalt	12	10	22	11	8	19	91.7	80.0	0.72	Very good
Granite	16	16	32	12	11	23	75.0	68.8	0.44	Fair
Other igneous rock	54	59	113	48	47	95	88.9	79.7	0.68	Good
Pinus ponderosa – mature size class										
All PM	140	149	289	122	119	241	87.1	79.9	0.67	Good
Sedimentary rock	52	49	101	49	37	86	94.2	75.5	0.70	Very good
Basalt	11	11	22	10	9	19	90.9	81.8	0.73	Very good
Granite	17	18	35	12	16	28	70.1	88.9	0.60	Good
Other igneous rock	66	71	137	53	53	106	80.3	74.6	0.55	Good
Pinus ponderosa – advanced regeneration size class										
All PM	172	173	345	140	121	261	81.4	69.9	0.51	Fair
Sedimentary rock	56	54	110	42	38	80	75.0	70.4	0.45	Fair
Basalt	27	23	50	21	12	33	77.8	52.2	0.30	Poor
Granite	27	25	52	25	12	37	92.6	48.0	0.41	Fair
Other igneous rock	66	71	137	53	53	106	80.3	74.6	0.55	Good
Pinus ponderosa – young regeneration size class										
All PM	180	172	352	146	134	280	81.1	77.9	0.59	Good
Sedimentary rock	56	57	113	51	37	88	91.1	64.9	0.56	Good
Basalt	25	21	46	19	16	35	76.0	76.2	0.52	Fair
Granite	20	22	42	13	17	30	65.0	77.3	0.42	Fair
Other igneous rock	65	72	137	46	57	103	70.8	79.2	0.50	Fair
Abies concolor – all size classes combined										
All PM	80	83	163	60	65	125	75.0	78.3	0.53	Fair
Abies concolor – mature size class										
All PM	41	42	83	34	28	62	82.9	66.7	0.49	Fair
Abies concolor – advanced regeneration size class										
All PM	53	45	98	46	28	74	86.8	62.2	0.50	Fair
Abies concolor – young regeneration size class										
All PM	76	81	157	60	60	120	78.9	74.1	0.53	Fair
Quercus gambelii – all size classes combined										
All PM	149	148	297	105	88	193	70.5	59.5	0.27	Poor
Sedimentary rock	71	77	148	53	42	95	74.6	54.5	0.29	Poor
Basalt	30	32	62	20	16	36	66.7	50.0	0.17	Poor
Granite	14	14	28	11	12	23	78.6	85.7	0.64	Good
Other igneous rock	34	34	68	28	17	45	82.4	50.0	0.32	Poor
Pinus ponderosa alliance										
All PM	187	193	380	160	161	321	85.6	83.4	0.69	Good
Sedimentary rock	56	54	110	50	48	98	89.3	88.9	0.78	Very good
Basalt	16	15	31	12	13	25	75.0	86.7	0.61	Good
Granite	16	16	32	15	9	24	93.8	56.3	0.50	Fair
Other igneous rock	33	26	59	26	21	47	78.8	80.8	0.59	Good

Bounds for Kappa degree of agreement scale (Monserud & Leemans, 1992): < 0.2, very poor; 0.2–0.4, poor; 0.4–0.55, fair; 0.55–0.7, good; 0.7–0.85, very good; > 0.85, excellent.

parent material category (Fig. 5). The highest predicted probabilities of occurrence (≥ 0.75) within the limits of the data were found at intermediate values of AT and low values of AP. Greater tolerance of low moisture conditions in *P. ponderosa* seedlings compared with higher-elevation spruce and fir species has been attributed to possession of a rapidly growing taproot and long lateral roots (Schubert, 1974). The shapes of the response surfaces reflected the

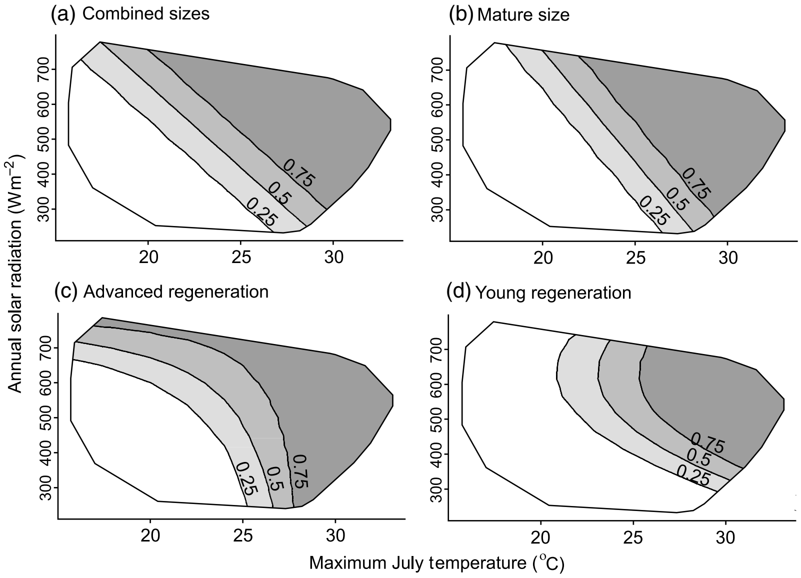


Figure 3 Predicted probabilities of occurrence for *Pinus ponderosa* size classes on all parent material categories combined as functions of the predictor variables maximum July temperature (HT) and annual radiation (AR) (other model predictors set to average values if present). Polygon containing probability contours indicates convex hull enclosing predictor variable limits for 1274-plot data set.

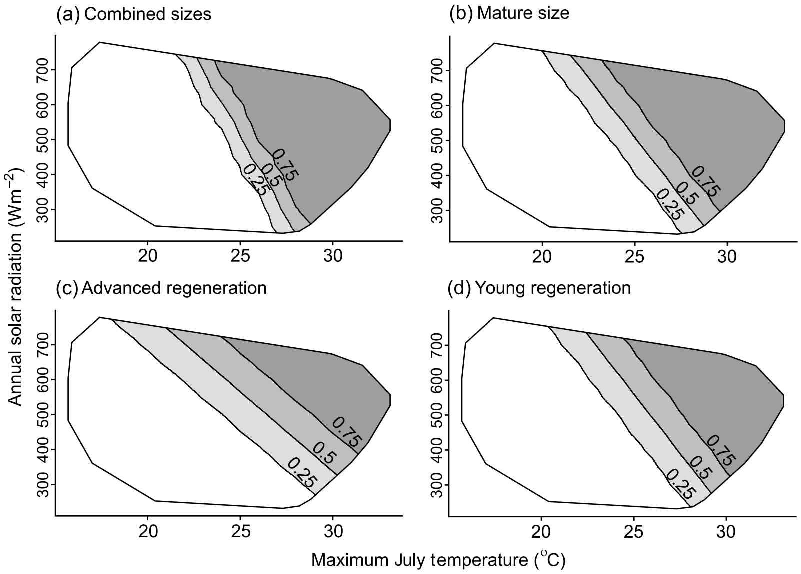


Figure 4 Predicted probabilities of occurrence for *Pinus ponderosa* size classes on sedimentary rock as functions of the predictor variables maximum July temperature (HT) and annual radiation (AR) (other model predictors set to average values if present). Polygon containing probability contours indicates convex hull enclosing predictor variable limits for 1274-plot data set.

combination of AT as a quadratic function and AP as a linear function in all models. The broadest range of temperature–precipitation combinations resulting in probabilities of occurrence ≥ 0.75 were observed for the combined, mature and advanced regeneration size class models (Fig. 5 a–c), with a narrower range for the young regeneration model (Fig. 5d).

Model results for size classes indicated that, in general, high predicted probabilities of occurrence were produced under a narrower range of environmental conditions for young regeneration than for advanced regeneration and mature size classes, which may be a consequence of historical factors affecting distributions of *P. ponderosa* size classes. As *P. ponderosa* trees of a given age may vary widely in size (Cooper, 1960; Knowles & Grant, 1983; Moir & Dieterich, 1988; Savage *et al.*, 1996), association of unaged trees of a particular size with historical events must be made with caution. However, a significant correlation of measured ages and sizes (d.b.h.) of 721 *P. ponderosa* trees in or near our plots ($r^2 = 0.72$) (H.C. Humphries, unpublished data) provided a basis for making tentative interpretations. *Pinus ponderosa* trees originating prior to impacts of Euro-American settlement (beginning in the 1870 s in many Southwest locations) established episodically during intermittently favourable conditions in forests that maintained an open, park-like structure as a result of frequent, low-intensity fires, as determined from dendroecological reconstructions of tree age structure and density (White, 1985; Covington & Moore, 1994; Savage *et al.*, 1996; Covington *et al.*, 1997; Mast *et al.*, 1999). Such pre-settlement trees were likely to have attained sufficient size to be classified as mature in our data set.

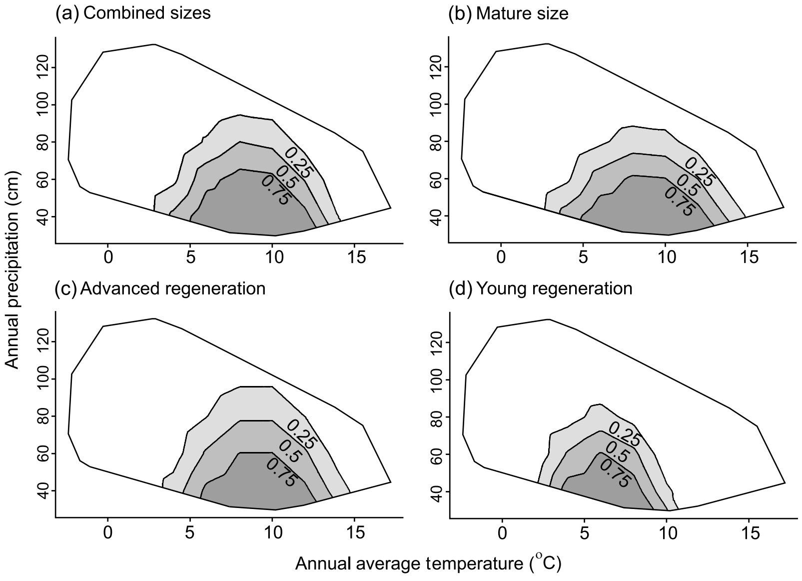


Figure 5 Predicted probabilities of occurrence for *Pinus ponderosa* size classes on other igneous rock as functions of the predictor variables annual temperature (AT) and annual precipitation (AP) (other model predictors set to average values if present). Polygon containing probability contours indicates convex hull enclosing predictor variable limits for 1274-plot data set.

Sources of mortality for *P. ponderosa* seedlings include drought, grass competition and surface fires (White, 1985). In the late 1800 s, extensive grazing reduced fine fuels and competition from grasses in *P. ponderosa*-dominated forests; in the early 1900 s, a reduction in grazing pressure coincided with the beginning of active fire suppression in the Southwest (Swetnam, 1990; Savage *et al.*, 1996). These anthropogenic changes affecting the fire regime, in conjunction with favourable (warm, wet) climate conditions from 1905 to 1930 (Savage & Swetnam, 1990; Swetnam & Betancourt, 1998), led to an increase in *P. ponderosa* establishment, culminating in the year 1919, in which an unprecedented *P. ponderosa* recruitment pulse occurred (Savage *et al.*, 1996; Fulé *et al.*, 1997; Mast *et al.*, 1999). Although some trees designated 'mature' in our data set may have established under these post-settlement conditions, the advanced regeneration size class is most likely comprised primarily of trees originating in this recruitment pulse.

Trees comprising the young regeneration size class likely established after the 1930 s up to the 1970 s in forests with greatly increased tree density as a result of the recruitment pulse and reduced fire frequency (Covington & Moore, 1994; Savage *et al.*, 1996; Fulé *et al.*, 1997, 2002; Mast *et al.*, 1999). Climate conditions during part of this period included hotter summer temperatures than average in conjunction with the most extreme drought of the past 400 years (1942–57) (Cooper, 1960; Swetnam & Betancourt, 1998), and resources were dominated by the existing dense post-settlement canopy (Mast *et al.*, 1999). These unfavourable temperature and precipitation conditions may account in part for the narrower realized niches predicted for the young regeneration size class.

Combined size predicted responses were most similar to mature size class responses because this size class was present in more plots containing *P. ponderosa* than other size classes. As a consequence, when size classes differ in environmental response, models developed using a data set that does not differentiate among size classes may over- or under-represent the predicted distributions of particular sizes. For this reason, knowledge of differences in size class-realized niche dimensions may be required for biogeographical interpretations of past, current and future distributions.

***Abies concolor* species models**

Environmental relationships

All *A. concolor* models contained HT, AR and at least one precipitation variable as predictors (Table 3). The first variable included was HT, which occurred as a quadratic function (Table 4), indicating that intermediate HT values were associated with the highest probabilities of occurrence. AR was included in all models as a decreasing linear term, resulting in increased probability of occurrence with decreasing AR values. SP occurred as a cubic function in the combined size and young regeneration size class models, producing a skewed response to this predictor. WP was a significant predictor in the advanced and young regeneration models; AP was included in the mature size and advanced regeneration models. All models contained an HT–precipitation interaction term. In addition, the combined size and advanced regeneration models included an interaction between HT and AR. The percentage deviance explained for *A. concolor* models ranged from 44 to 52% (Table 4).

Accuracy in predicting presence or absence for test plots was rated fair for all *A. concolor* models (Table 5). Models for combined and young regeneration size classes predicted presence and absence about equally well, but models for mature size and advanced regeneration were less accurate in predicting absence than presence (67 and 62% versus 83 and 87% correct, respectively).

Distribution in environmental space

The shape of the response surfaces for the two predictors present in all *A. concolor* models, HT and AR, reflected the

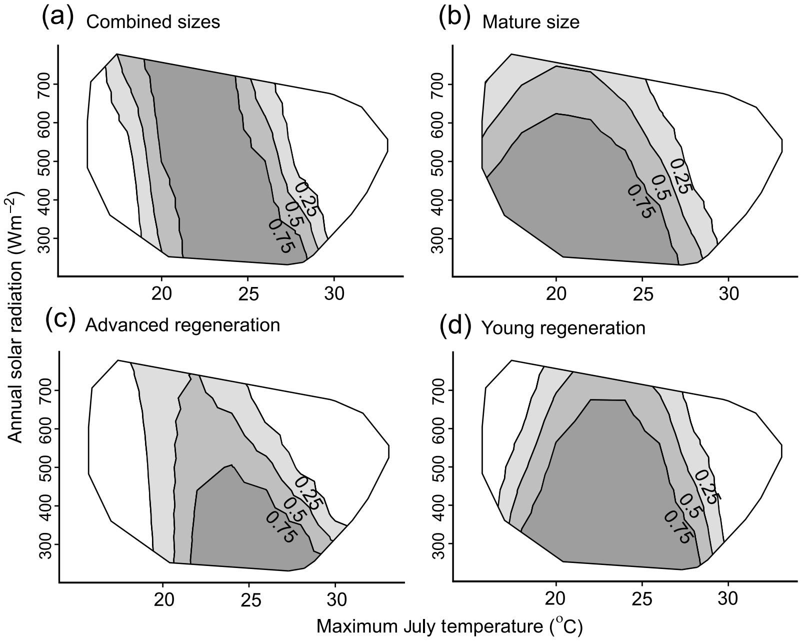


Figure 6 Predicted probabilities of occurrence for *Abies concolor* size classes on all parent material categories combined as functions of the predictor variables maximum July temperature (HT) and annual radiation (AR) (other model predictors set to average values if present). Polygon containing probability contours indicates convex hull enclosing predictor variable limits for 1274-plot data set.

inclusion of HT as a quadratic function and AR as a decreasing linear function, resulting in the highest probabilities of occurrence (≥ 0.75) at intermediate HT (Fig. 6). A wide range of AR values produced high probabilities of occurrence for all models except advanced regeneration, in which high probabilities were associated with low to intermediate AR. *Abies concolor* models differed in the range of temperatures that produced predicted probabilities of occurrence ≥ 0.75. A broad range was observed for the young regeneration model; a much narrower range occurred for the advanced regeneration model, but both size classes had high probabilities of occurrence at higher HT values than the mature size class. This may result from increased post-settlement *A. concolor* regeneration in areas where fire suppression has enabled trees to establish that formerly would have been killed by fire (Fulé *et al.*, 1997; Moir *et al.*, 1997). Increased abundance of fire-sensitive species such as *A. concolor* has been observed throughout the western USA under conditions of fire suppression (Savage, 1997). In addition, this relatively shade-tolerant species can establish in dense post-settlement forests (White & Vankat, 1993; Fulé *et al.*, 1997; Moir *et al.*, 1997). In the mixed conifer forests of northern Arizona, *A. concolor* currently dominates age classes < 150 years old, but is much less abundant in older age classes (White & Vankat, 1993).

The combined size predicted response was most similar to the young regeneration response, the size class present in the largest number of plots containing *A. concolor*.

Quercus gambelii species models

Models developed for *Q. gambelii* showed great variation among parent material categories in attributes selected as predictors of responses (Table 3). A temperature attribute was the most important predictor in four of five models; three models contained only temperature attributes (Table 4). In addition to HT, the model for combined parent material categories included parent material as a factor. The model for granite contained only SP. Only the model for sedimentary rock included an interaction term, between HT and CT. Percentages of deviance explained were relatively low for all models (19–32%; Table 4).

Accurate prediction of *Q. gambelii* on test plots occurred only for the model on granite, which was rated good ($\kappa = 0.61$, Table 5). All other models were rated poor, which was reflected in the low accuracy in predicting absence (50–60% correct; Table 5). Response surfaces for *Q. gambelii* models were not generated because of low model accuracy.

Lack of success in modelling *Q. gambelii* distribution as a function of climate and parent material may result in part from the influence of environmental factors not modelled on the distribution of the species. For example, soil moisture in fine-scale microhabitats may influence *Q. gambelii* seedling survival (Neilson & Wullstein, 1983, 1985, 1986). Seedling abundance differed greatly in two nearby sites in New Mexico that experienced the same climate conditions but differed in hydrological input to the soil (Neilson & Wullstein, 1986). In addition, fire and biotic factors such as grazing and competition from *P. ponderosa* may play important roles in determining post-establishment *Q. gambelii* distributions in the Southwest (Neilson & Wullstein, 1986; Riegel & Miller, 1992).

Pinus ponderosa alliance models

Environmental relationships

As in *P. ponderosa* species models, at least one temperature attribute was present in each alliance model and was the first variable selected in all models except other igneous rock (Tables 3 and 4); HT was the first variable selected for the alliance model on sedimentary rock, but was later eliminated from the model as a result of a high correlation with AR. AT occurred as a cubic function in the models for all parent material categories combined and other igneous rock, the only significant skewed responses found in the *P. ponderosa* models. In addition, inclusion of temperature–radiation interaction terms in these two models resulted in bimodal maximum probabilities of occurrence at both intermediate and low AT values. AR was present in four of five models and was usually represented as a quadratic function, indicating maximum probability of occurrence at intermediate AR values. Three models contained AP as a significant decreasing linear predictor and FP was present as a decreasing linear term in the sedimentary rock model, which also contained a temperature–precipitation interaction term. The effect of PM, a significant predictor in the model for all parent material categories combined, was to increase the probability of occurrence for the alliance on basalt and decrease its probability on other igneous rock, with an intermediate effect on sedimentary rock and granite.

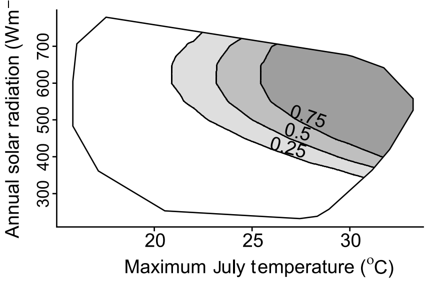
Most alliance models had a fairly high percentage of deviance explained (45–66%; Table 4) and were successful in predicting test plot presence or absence, with ratings for Kappa of very good (one model), good (three models), or fair (one model; Table 5). Absence was poorly predicted in the model on granite (56% correct), although the percentage of correctly predicted presences was high (94% correct).

Distribution in environmental space

Pinus ponderosa alliance response surface graphs were produced for all parent material categories combined and other igneous rock (Fig. 7) for comparison with *P. ponderosa* species response surfaces (Figs 3 and 4); elimination of HT from the alliance model on sedimentary rock precluded comparison with species sedimentary rock models. For all parent material categories combined, the predicted distribution of the alliance in environmental space was narrower than for any species model (Figs 7 a and 3, respectively), because of the inclusion of AR as a quadratic term.

Unlike the species models on other igneous rock in which a quadratic function described the response to AT (Fig. 5), the alliance model contained a cubic term for AT (Fig. 7b), resulting in areas of high predicted probability of occurrence for the alliance at both high and low AT values. Both alliance and species were present on high elevation plots in Colorado that had low AT and AP values, but the addition of a cubic term describing this response was significant only for the alliance model. The skewed shape of the alliance response to temperature resulted in high probabilities of occurrence at low AT values over an unrealistically wide range of AP values. Substitution of a logarithmic function (AT + log AT) for the cubic polynomial function (Austin *et al.*, 1996) did not correct this problem and resulted in an 8% reduction in deviance explained. Therefore, the cubic polynomial function was retained in the model. If the anomalous low AT maximum is not considered, the areas with high probability of occurrence (≥ 0.75) for the alliance model are generally similar to species model areas (Figs 7b & 5, respectively).

(a) All parent material categories combined



(b) Other igneous rock

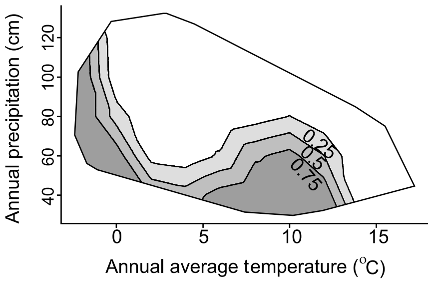


Figure 7 Predicted probabilities of occurrence for *Pinus ponderosa* alliance (a) on all parent material categories combined as functions of the predictor variables maximum July temperature (HT) and annual radiation (AR), and (b) on other igneous rock as functions of annual temperature (AT) and annual precipitation (AP) (other model predictors set to average values if present). Polygon containing probability contours indicates convex hull enclosing predictor variable limits for 1274-plot data set.

Landscape-scale environmental variability in the predicted distribution of *Pinus ponderosa* in West Clifton

West Clifton contains considerable topographical relief, but elevation generally increases from south to north, culminating in two mountain peaks in the central and eastern portions of the northern edge of the area (Fig. 8). *Pinus ponderosa* species and alliance distribution maps were constructed only for models developed with all parent material categories combined because a higher proportion of these models was rated good or very good than models for individual parent material categories (Table 5).

Pinus ponderosa has a widespread distribution in upland regions of West Clifton (Cooper, 1960). As expected, areas with a predicted probability of *P. ponderosa* species occurrence ≥ 0.75 were found primarily in the northern half of West Clifton between *c.* 2000 and 3000 m elevation (Fig. 9a–d). A lower probability of occurrence (< 0.75) was predicted for the highest elevations (centre and east of northern edge), below 2000 m in the southern half of West Clifton and in river drainages. Among size classes, predicted

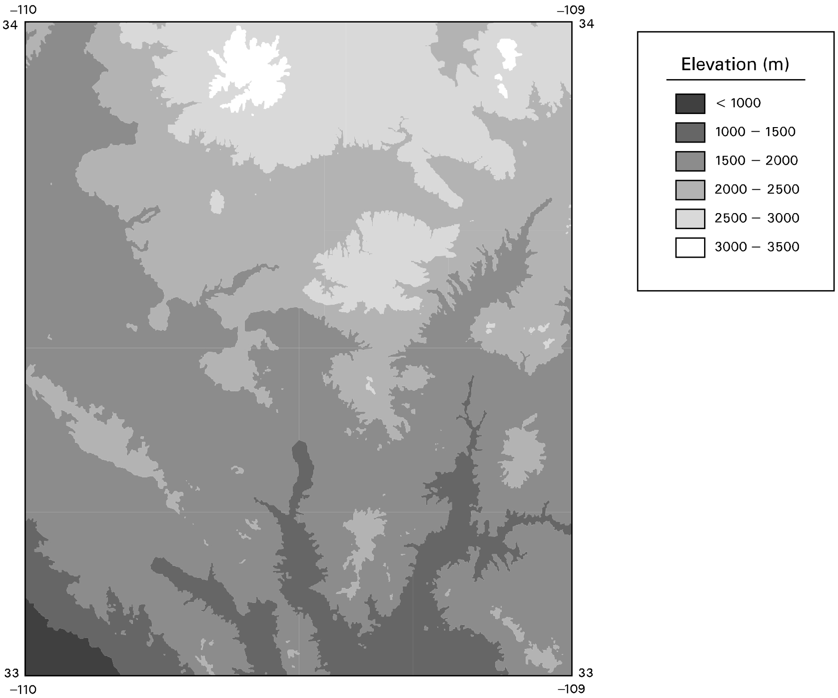


Figure 8 Distribution of elevation classes in one by one degree West Clifton area in southeast New Mexico and southwest Arizona (north at top).

probabilities ≥ 0.75 were most broadly distributed for the mature size class, occupying 3800 km^2 in West Clifton (Fig. 9b). Locations with probabilities of occurrence ≥ 0.75 for the young and advanced regeneration size classes were more restricted in distribution, occupying 2600 km^2 (Fig. 9c, d). In addition, the young regeneration size class had less area (2700 km^2) than the advanced regeneration size class (3200 km^2) for probabilities ≥ 0.50 to < 0.75 (Fig. 9c, d).

The *P. ponderosa* alliance was predicted to have a much more restricted distribution (510 km^2 with probabilities of occurrence ≥ 0.75) than species models, in part because of the inclusion of parent material as a factor in the model (Fig. 9e). In the alliance model, probabilities of occurrence were lower for other igneous rock, the most abundant parent material category in West Clifton, than for other parent material categories, thus reducing the alliance's predicted geographical extent. As a consequence, the more restricted alliance distribution in West Clifton did not include many locations in which *P. ponderosa* was predicted to be present but not diagnostic of the vegetation type.

Locations with the highest probability of occurrence (≥ 0.75) for combined size *P. ponderosa* (Fig. 9a) were mapped by combinations of classes of two important predictors, HT and AR (Fig. 10) to depict the range of environmental conditions most likely to contain *P. ponderosa* in West Clifton. Most high-probability locations had intermediate to high HT and AR values, but some areas with high topographical relief exhibited a greater diversity of HT and AR combinations over short distances (e.g. inset in Fig. 10). Sites containing *P. ponderosa* that differ in environmental conditions may respond differently to the effects of disturbances, management activities and global climate change (Arno, 1988; Touchan *et al.*, 1996; Veblen *et al.*, 2000). Inclusion of the range of variability in environmental driving variables for species or vegetation types of interest has been suggested as a means to ensure the representativeness (Austin & Margules, 1986) of networks of conservation areas (Bourgeron *et al.*, 2001b).

Spatial autocorrelation in model residuals

Most models exhibited positive spatial autocorrelation in model residuals at small lag distances, indicating similarity in residual values among nearby plot locations (not shown) (Sokal & Oden, 1978). In addition, models developed on sedimentary rock, basalt and other igneous rock showed variation in positive and negative autocorrelation at greater lag distances, which may result in part from the patchy distribution of these parent material categories in the landscape (Sokal & Oden, 1978).

To attempt to account for the spatial autocorrelation detected in the residuals, additional models were developed in which plot latitude and longitude were tested as predictor variables in addition to all previously selected environmental variables. One or more location terms were found to be significant predictors for seven of the thirty-four models (Table 6). Longitude was included in six models, whereas latitude was present in three models. A single latitude–longitude interaction was significant in the model for *Q. gambelii* on basalt. Increases in percentage deviance explained by the addition of location variables ranged from 1.5 to 14.4%. Degree of agreement as measured by Kappa increased in the

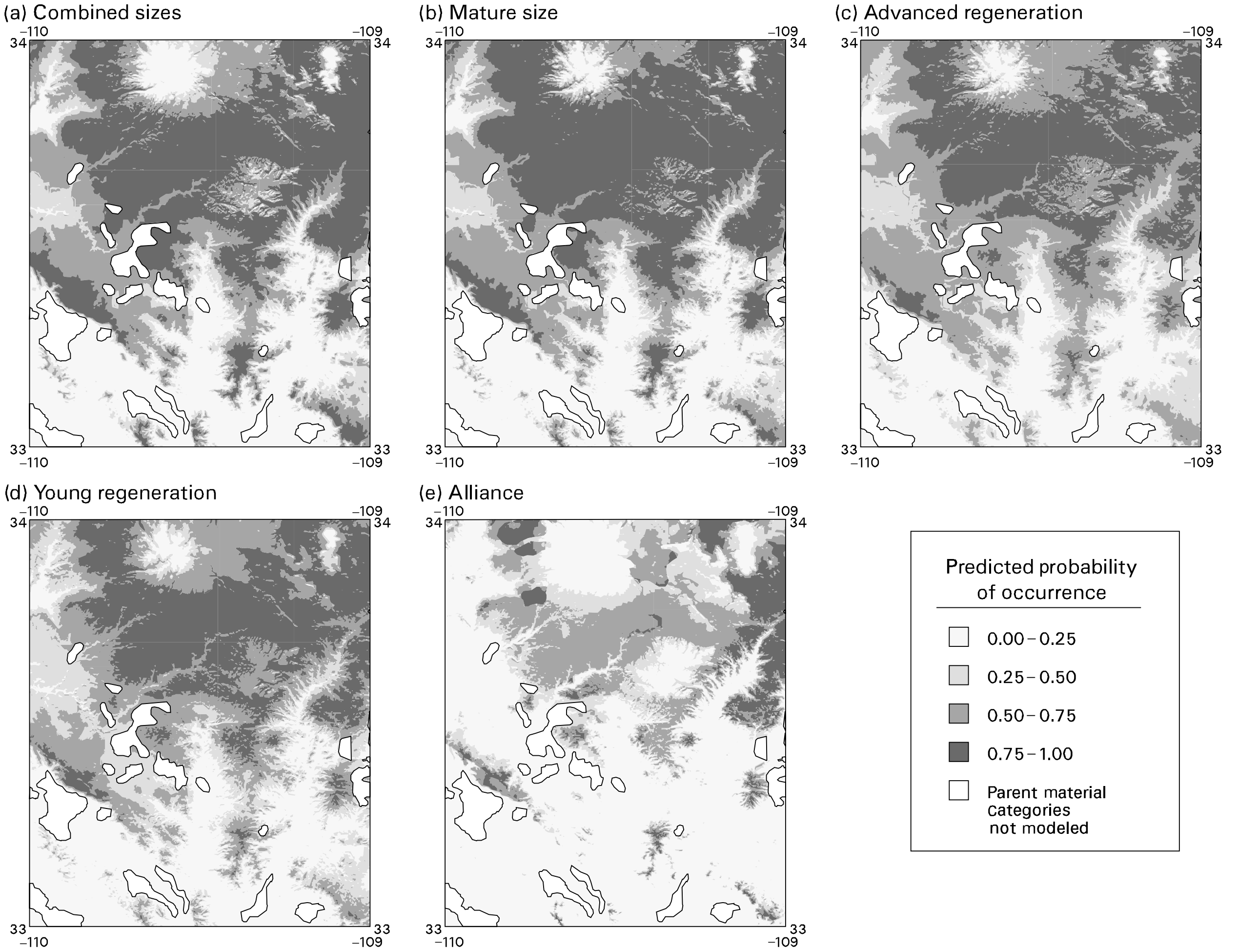


Figure 9 Mapped predicted probability of occurrence classes for *P. ponderosa* models developed with all parent material categories combined in West Clifton.

three *Q. gambelii* models and resulted in a change of rating from poor to fair in the model for other igneous rock. No change in Kappa occurred in one *P. ponderosa* model; Kappa decreased in three *P. ponderosa* models. Inclusion of location variables did not appear to reduce spatial autocorrelation in model residuals (not shown). The fixed form of the polynomial functions in latitude and longitude may limit their ability to capture complex spatial autocorrelation patterns in variables not modelled, such as soils, disturbance, biotic factors or land use (Legendre, 1993; Leathwick, 1998).

CONCLUSIONS

Response surface models developed as functions of climate and parent material in the Southwest were judged successful for *P. ponderosa* and *A. concolor* species and *P. ponderosa* alliance, but generally were not successful for *Q. gambelii,* probably reflecting the greater influence of other fine-scale environmental factors on this species. The distribution of *P. ponderosa* was associated with relatively high temperature, high radiation environments, and in models containing a precipitation variable as a significant predictor, relatively low precipitation values. Similar results were obtained in a study measuring environmental conditions at the upper elevational limit of *P. ponderosa* in southern Utah (Stein, 1988). Sites containing *P. ponderosa* had significantly higher radiation and soil temperatures and lower moisture availability than randomly selected sites in the same elevation range. *Pinus ponderosa* size classes differed in the range of environmental conditions that generated high predicted probabilities of occurrence. The generally narrower range of conditions predicted for the young regeneration size class may have resulted from the effects of earlier high recruitment episodes, anthropogenic changes, and unfavourable climate conditions during the expected period of establishment of this size class. Response models for the *P. ponderosa* alliance were similar to *P. ponderosa* species models, but had more complex functional forms in some cases, resulting in high predicted

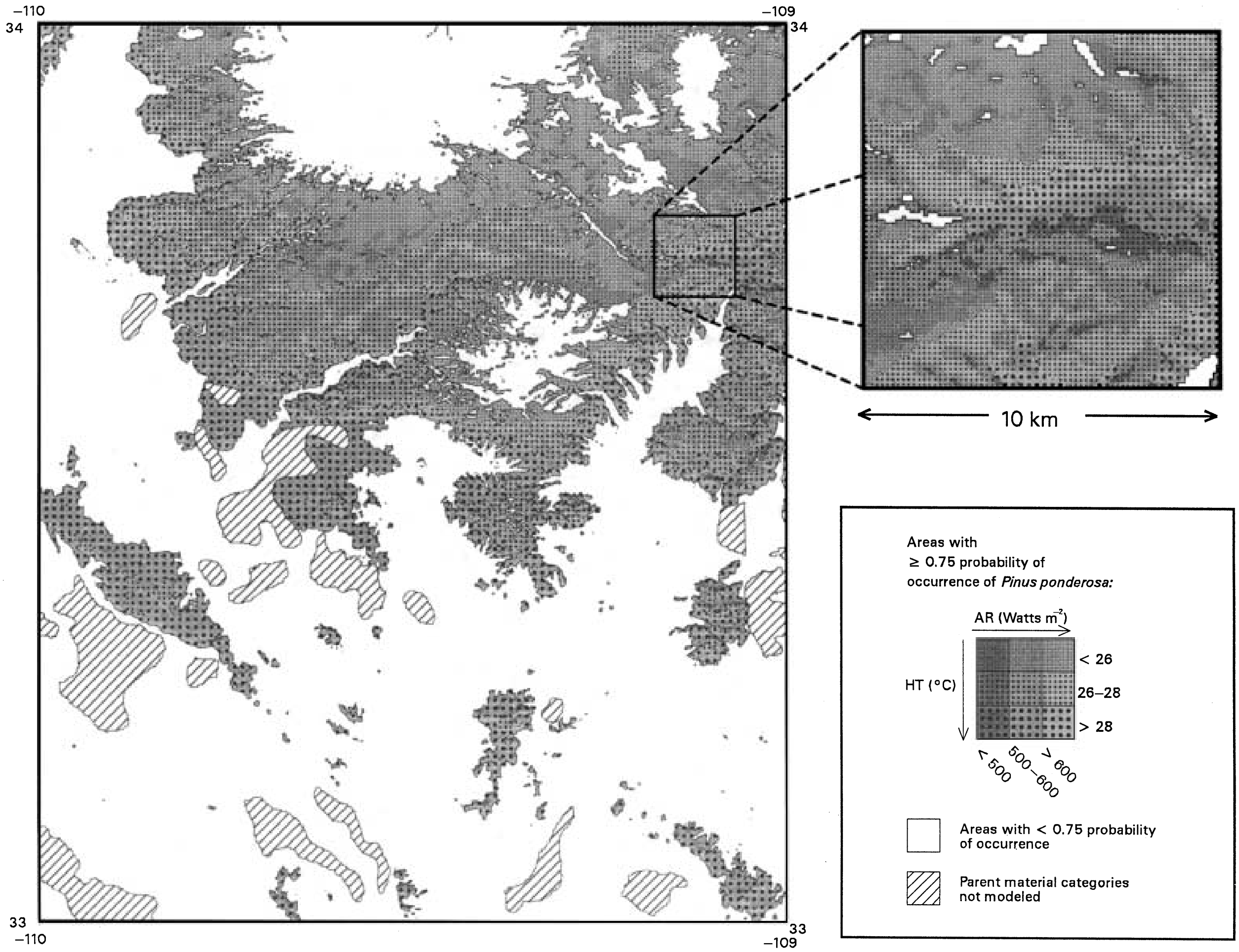


Figure 10 Mapped predicted *P. ponderosa* probabilities of occurrence ≥ 0.75 categorized by combinations of HT and AR values in West Clifton.

Table 6 Response surface modeling results for inclusion of latitude and longitude as predictor variables (LAT = latitude, LONG = longitude). Other model terms listed in Table 3. Only models with significant location terms are shown. Superscripts indicate order of polynomials

Parent material	Location terms added	Deviance explained (%)	Change in deviance explained (%)	Kappa		Change in Kappa
Pinus ponderosa – all size classes combined						
All PM	+ LONG	56.6	3.5	0.64	Good	−0.06
Pinus ponderosa – mature size class						
All PM	+ LAT + LONG	46.6	2.8	0.67	Good	0.00
Pinus ponderosa – young regeneration size class						
All PM	+ LONG	34.8	1.5	0.57	Fair	−0.02
Quercus gambelii – all size classes combined						
All PM	+ LONG	24.1	3.1	0.34	Poor	0.07
Basalt	+ LAT + LONG + (LAT × LONG)	27.6	4.5	0.26	Poor	0.09
Other igneous rock	+ LAT + LAT^2	45.9	14.4	0.49	Fair	0.17
Pinus ponderosa alliance						
All PM	+ LONG	55.7	2.3	0.66	Good	−0.03

probabilities of occurrence over a narrower range of environmental conditions than was observed in species models.

Environmental conditions associated with *A. concolor* occurrence were more mesic than those of *P. ponderosa,* with the highest probabilities of occurrence of *A. concolor* at intermediate temperature values. The ranges of temperature and radiation conditions producing high probabilities of occurrence differed among *A. concolor* size classes, with the broadest range of conditions predicted for the young regeneration size class, which may result from increased establishment of trees under conditions of fire suppression in the Southwest.

The contrasting distributions of *A. concolor* and *P. ponderosa* in environmental space for models on all parent material categories combined (Figs 6 & 3, respectively) were in general agreement with differences in their observed distributions in geographical space, i.e. occurrence of *P. ponderosa* in high temperature, high radiation environments occurring at low forested elevations compared with lower temperatures and, to some extent, lower radiation at higher elevations for *A. concolor*. Combined size models for both species most closely resembled models of the size class present in the largest number of plots. As a consequence, models developed with data sets that do not distinguish among size classes may not reflect the influence of historical factors on the distribution of the species, and therefore, may have more limited use than size class-specific models for understanding species dynamics and for some management and planning applications.

Pinus ponderosa was predicted to be distributed over a range of environmental conditions in West Clifton, with more restricted distributions predicted for the young regeneration size class, and especially, the alliance than for other *P. ponderosa* models. Differences between the predicted distributions of a vegetation type and its diagnostic species are a function of the criteria used to characterize the type. Therefore, relationships between these distributions will vary from type to type, and within the geographical range of distribution of a type of interest.

Our results indicated the complex nature of the environmental relationships of the three species and the alliance. The environmental relationships we elucidated were generally consistent with previous descriptions (e.g. Dick-Peddie, 1993). However, clear differences were apparent in environmental relationships among size classes within a species. Our study extended previous work by quantifying probabilities of occurrence over a wide range of climate and parent material attributes in the study area, and in addition, the models identified particular attributes and interactions as important predictors that may previously have been overlooked. The results point to areas of future study on the impact of environmental changes on the species and alliance. For example, modelled differences among parent material categories in significant climate predictors of *P. ponderosa* response indicate a need for wider consideration of the use of environmental stratification in developing dynamic models, such as those developed to predict global changes (Cramer *et al.*, 1999; Goudriaan *et al.*, 1999).

A map of temperature and radiation combinations producing high *P. ponderosa* probabilities of occurrence enabled identification of areas containing the entire range of variability in such predictors for change detection, conservation and management applications. Knowledge of this range of environmental variability based on biogeographical analysis is critical in ecological assessments, in designing efficient sampling schemes for identification of changes, and in selecting networks of representative conservation areas (Bourgeron *et al.*, 2001b). The ability to identify small areas that capture this range (such as the inset in Fig. 10) can make an important contribution to the process of efficiently selecting areas for change detection and conservation.

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BIOSKETCHES

Hope C. Humphries and **Patrick S. Bourgeron** are research associate and fellow, respectively, at the Institute of Alpine and Arctic Research, University of Colorado. H.C. Humphries received a Ph.D. from Colorado State University, USA, for work on modeling alpine species distributions. Her research interests include statistical and simulation modeling of biotic-environmental relationships, conservation planning, and multivariate analysis. P.S. Bourgeron received a Ph.D. from the University Denis Diderot, Paris, France. His research interests include integrating (1) geographical information system technology, (2) modeling approaches, and (3) natural, physical, and socio-economic sciences into regional land use planning, multi-scale ecological assessments, and environmental management.