

Vegetation–environment relationships and ecological species groups of an Arizona *Pinus ponderosa* landscape, USA

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Abstract

Pinus ponderosa forests occupy numerous topographic and soil complexes across vast areas of the southwestern United States, yet few data exist on species distributions and vegetation–environment relationships for these environmentally diverse landscapes. We measured topography, soils, and vegetation on 66, 0.05-ha plots within a 110,000-ha *P. ponderosa* landscape in northern Arizona, USA, to discern vegetation–environment relationships on this landscape. We analyzed associations of environmental variables with plant communities and with single-species distributions, and we classified ecological species groups (co-occurring plant species exhibiting similar environmental affinities). Gradients in community composition paralleled gradients in soil texture, available water, organic C, total N, and geographic precipitation patterns. Soil parent material, affected by the presence or absence of volcanic activity, is a primary factor constraining vegetation patterns on this landscape. Using discriminant analysis, we built a model that correctly classified the most important of four grasses (*Bouteloua gracilis*, *Muhlenbergia montana*, *Sporobolus interruptus*, or *Festuca arizonica*) on 70–80% of plots based on five environmental variables related to soil moisture and resource levels. We also classified 52 of the 271 detected plant species into 18 ecological species groups. Species groups ranged from *Phacelia* and *Bahia* groups occupying xeric, volcanic cinder soils low in organic C and total N, to *Festuca* and *Lathyrus* groups characterizing moist, loam and silt loam soils. We applied the species groups by estimating *P. ponderosa* diameter increment in a regression tree using abundances of species groups. The most rapid *P. ponderosa* diameter growth of 5 mm/year occurred on plots with high importance of the *Festuca* and *Lathyrus* groups. Our results on this semi-arid landscape support several general ecological species group principles chiefly developed in temperate regions, and suggest that vegetation–environment research has great potential for enhancing our understanding of *P. ponderosa* forests occupying vast areas of the southwestern United States.

Introduction

In combination with analyses of communities and individual species, classifying ecological species groups is one method for discerning vegetation–environment relationships. Ecological species groups consist of co-occurring plant species

sharing similar environmental affinities (Spies and Barnes 1985; Godart 1989; Grabherr et al. 2003). Species groups are based on the theory that evolutionary and community processes such as competition confine species to environmental complexes where they are best adapted (Host and Pregitzer 1992; Kashian et al. 2003). Species group

research identifies environmental gradients correlated with species distributions, classifies species assemblages occupying similar environmental complexes, and relates species distributions to management-oriented variables such as tree growth (Hix 1988; Host and Pregitzer 1991). Once species groups are developed for an area, their distribution can be used for inferring soil properties and other variables relatively difficult to measure (Pregitzer and Barnes 1982; Meilleur et al. 1992). While often all species of a group occur together on a site, presence of one species of a group has been interpreted to suggest that the site meets requirements of all species of that group (Kashian et al. 2003). Including several species in a group for indicating environmental conditions may compensate for absences of individual species resulting from reasons unrelated to environmental site factors (Barnes et al. 1998). This has been perceived as an advantage of using species groups, rather than individual species, for indicating environmental conditions (Spies and Barnes 1985).

Species groups have typically been constructed using combinations of field observations, inspection of tabular species \times site matrices, and multivariate analyses such as cluster analysis (Spies and Barnes 1985; Godart 1989; Kashian et al. 2003). The size of groups varies within and among studies, ranging from fewer than three to greater than eight species (Bergeron and Bouchard 1984; Godart 1989; Host and Pregitzer 1991). As in many multivariate studies in plant ecology, species groups are hypotheses about species distributions and their relationships to environmental factors. These hypotheses have practical value for estimating site conditions, and are tractable for refinement through experimental research developing causal relationships about species distributions (Pabst and Spies 1998).

In North America, species groups have been most frequently developed in eastern temperate ecosystems. Species groups have been constructed in a variety of ecosystems, including Quebec southern boreal forests (Bergeron and Bouchard 1984), Michigan hardwood forests and conifer woodlands (e.g., Archambault et al. 1989; Simpson et al. 1990; Kashian et al. 2003), South Carolina Appalachian mountain forests (Abella and Shelburne 2004), and Georgia Coastal Plain *Pinus palustris* P. Mill. savannas (Goebel et al. 2001). Kashian et al. (2003), for example, classified eight

species groups incorporating 31 species occurring along soil texture and drainage gradients on a Michigan *Pinus banksiana* Lamb. landscape. Presence of a *Fragaria* group indicated soils containing fine-textured bands where *P. banksiana* height growth was rapid, whereas a *Rubus* group indicated high water tables that restricted rooting depth and slowed *P. banksiana* growth. On a southern Appalachian landscape, soil solums averaged 120 cm thick when a *Sanguinaria* group typified by *Sanguinaria canadensis* L. was abundant, compared to only 61 cm thick when this group was sparse (Abella and Shelburne 2004). Species-rich, productive sites were associated with thick soil solums, which could be readily identified without making soil measurements by observing the distribution of the *Sanguinaria* group. These studies illustrate that species groups have been useful for indicating environmental site conditions on a range of landscapes, and suites of environmental factors affecting species distributions differ among landscapes.

Species groups have largely been European and eastern North American concepts, little applied in western North America (Pabst and Spies 1998). Plant community classifications termed habitat typing (e.g., Daubenmire 1961; Hanks et al. 1983) and analyses of individual indicator species (e.g., Korstian 1917; Klinka et al. 1989) have been more common in western North America. Analyzing environmental relationships of plant communities as wholes, indicator and single-species distributions, and ecological species groups are complementary approaches to studying vegetation–environment relationships (Mueller-Dombois and Ellenberg 1974; Klinka et al. 1989; McCune and Grace 2002). Analyses of single-species distributions complement construction of ecological species groups in at least three ways: (i) single-species distributions are building blocks for classifying ecological species groups, (ii) not all species readily fit into species groups, and (iii) common species particularly faithful to environmental factors have strong indicator value by themselves.

In this study, we combine analyses of plant communities, single species, and ecological species groups to discern vegetation–environment relationships on a southwestern United States *Pinus ponderosa* P. & C. Lawson landscape. *Pinus ponderosa* forests occupy more than 3.4 million hectares in Arizona and New Mexico alone, and

inhabit a variety of landscapes differing in topography and soil parent material (Brown 1994). Few vegetation–environment data, however, have been published for this environmentally diverse and widespread forest type. We undertook this study within a 110,000-ha Arizona *P. ponderosa* landscape to: (i) determine environmental gradients most strongly correlated with plant distributions on this landscape, (ii) classify ecological species groups, and (iii) illustrate an application of the species groups by predicting diameter increments of old *P. ponderosa* based on species group abundances.

Methods

Study area

This study was performed at elevations between 1920 and 2660 m in northern Arizona, USA on the north half of the Coconino National Forest and on the Northern Arizona University Centennial Forest (Figure 1). Based on Jameson's (1969) regional climate study and three weather stations each with >35 years of records, precipitation increases and temperatures decrease from east to west across the study area. Mean total precipitation ranges from 42 to 56 cm/year, snowfall from 152 to 233 cm/year, and mean maximum daily temperatures from 15.7 to 17.5 °C (Western Regional Climate Center, Reno, NV). Slope gradients are less than 10% on most of the landscape, occasionally greater in deep ravines and on cinder cones. Volcanic activity has affected soil properties in many parts of the study area, with the most recent volcanic eruptions occurring ca. 900 years ago near Sunset Crater in the northeastern part of the study area (Moore et al. 1976). Major soil subgroups include Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (Miller et al. 1995). Forests are primarily pure *Pinus ponderosa*, but *P. ponderosa* occurs with *Populus tremuloides* Michx. or *Quercus gambelii* Nutt. in some areas.

Site selection and ecosystem classification

We used a terrestrial ecosystem survey (TES) soil map (Miller et al. 1995) of the study area to

randomly select six mapping units for sampling in each of 11 TES types (55, 500, 513, 523, 536, 551, 558, 570, 582, 585, and 611) covering a range of soil types. TES classifies soils to families and provides information similar to county soil surveys common in the eastern United States (Miller et al. 1995). We did not sample springs, deep ravines, or other rare ecosystems (Crawford Zimmerman et al. 1999), as our focus was on widespread landscape ecosystems occupying >95% of the study area. We sampled one 20 × 25 m (0.05 ha) plot in each mapping unit ($n=66$ plots) in areas exhibiting open canopies, relatively intact understories, and no visual indications of major recent disturbance. Areas dominated by old trees (establishing before 1875) most frequently met these criteria (Kerns et al. 2003). The utility of ecological species groups and site relationships across disturbance gradients (e.g., sites burned by crown fire) were not assessed in this study. Disturbance effects on ecological species groups depend on species persistence and re-colonization processes (Kashian et al. 2003). These processes are poorly known in *Pinus ponderosa* forests, and are important to study in future research.

Ecological species groups often are developed in conjunction with ecosystem classification because species distributions can then be interpreted among environmental gradients treated as continuums or compared among ecosystem types (Archambault et al. 1989; Goebel et al. 2001; Abella et al. 2003). We classified the 66 plots into 10 ecosystem types (Figure 1) internally similar in environmental and vegetational characteristics detailed in Abella (2005). We named ecosystems based on environmental features (topography or soil parent material) and diagnostic plant species. Ecosystems ranged from sandy-textured black cinders/*Phacelia* ecosystems containing dry volcanic cinder soils and low plant cover, to silt loam mesic basalt/*Festuca* ecosystems with high cover of *Festuca arizonica* Vasey, *Carex geophila* Mackenzie, and *Lupinus argenteus* Pursh. Other ecosystems included treeless park/*Symphotrichum* ecosystems occupying depressions often with clay loam soils, and aspen/*Lathyrus* ecosystems containing mixed *Populus tremuloides*-*Pinus ponderosa*- forests with loamy soils high in total N and plant cover. Aspen ecosystems were named for their dominant vegetation rather than soil or topographic properties, because *P. tremuloides* likely influences soils differently than

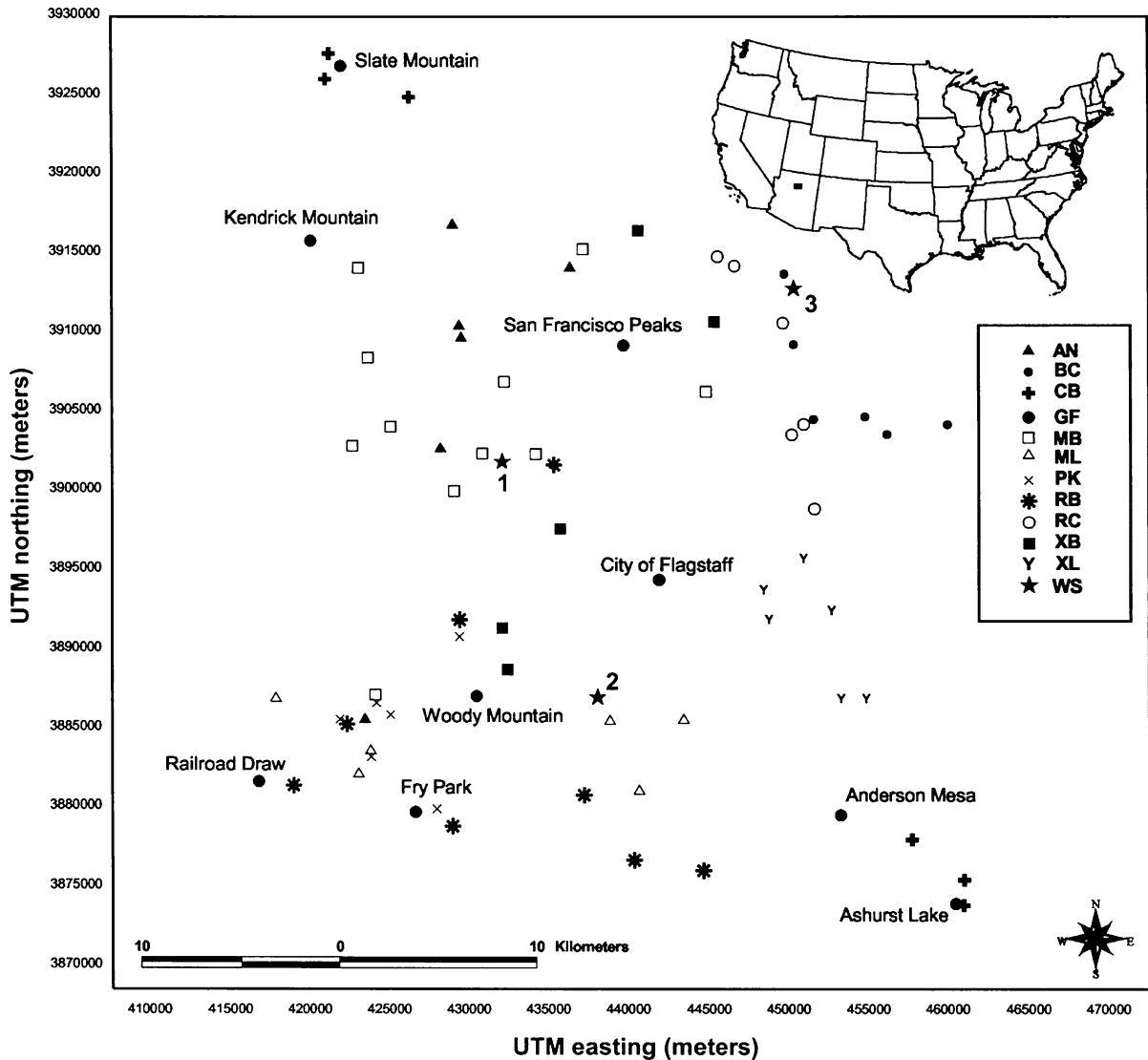


Figure 1. Location of 66 sample plots classified into ecosystem types within a 110,000-ha Arizona *Pinus ponderosa* landscape, USA (UTM zone 12). Geographic features are abbreviated as GF and weather stations as WS. Although at similar elevations (2128–2244 m), precipitation averages 56 cm/year at Fort Valley (station 1), 54 cm/year at the Flagstaff Airport (station 2), and 42 cm/year at Sunset Crater (station 3). Ecosystem type abbreviations are as follows: AN = aspen/*Lathyrus*, BC = black cinders/*Phacelia*, CB = clay basalt/*Gutierrezia*, MB = mesic basalt/*Festuca*, ML = mesic limestone/mixed flora, PK = park/*Symphytotrichum*, RB = rocky basalt/*Sporobolus*, RC = red cinders/*Bahia*, XB = xeric basalt/*Muhlenbergia*, and XL = xeric limestone/*Bouteloua*.

does *P. ponderosa*. Also, it is unclear how long *P. tremuloides* clones have occupied our sample plots to influence soils. There is some circularity in comparing species distributions among ecosystem types partially classified based on vegetation composition. We make these comparisons in this study for their descriptive value, recognizing that vegetation and abiotic components of ecosystems are interrelated.

Field and laboratory procedures

We sampled ground flora in 15, 1-m² subplots centered at 0.5, 5, 12.5, 20, and 24.5 m along the bottom, middle, and top axes of each of the 66, 0.05-ha plots. We visually categorized areal percent cover of each species rooted in each subplot as 0.1, 0.25, 0.5, and 1% up to 1% cover, at 1% intervals to 10% cover, and at 5% intervals above

10% cover. We also surveyed the whole 0.05-ha plot for species not already occurring in subplots. We recorded these species on a presence/absence basis, and assigned them a frequency of one and the lowest cover value for computing importance values. We calculated importance values on a plot basis for each species as the average of relative frequency and relative cover (summing to 100% for each plot). Frequency, cover, and importance values provided similar results in statistical analyses, so we chose to use importance values to integrate frequency and cover. Sampling occurred from May-August 2003. Nomenclature follows USDA-NRCS (2004).

Topographic variables we collected on each plot included slope gradient, transformed aspect (Beers et al. 1966), and terrain shape index (a measure of local topographic shape; McNab 1989). We measured rock cover every 0.3 m on a 25-m transect by recording the percentage of rock intercepts out of 83 points. We collected composite soil samples from 0 to 15 and 15 to 50 cm layers by digging a 50-cm deep pit at the northwest and southeast corners of each plot.

Soil samples were air dried, sieved through a 2-mm sieve, and analyzed for CaCO_3 equivalent (Goh et al.'s [1993] approximate gravimetric method), texture (hydrometer method), pH (1:2 soil:0.01 M CaCl_2), and organic C and total N (C/N analyzer after HCl removal of inorganic C) following Bartels and Bigham (1996) and Dane and Topp (2002). Analysis of duplicate samples every 10 samples indicated that analytical error averaged < 5%. We estimated soil available water capacity for each plot based on texture, gravel, and organic matter (organic C \times 1.724) using Saxton et al.'s (1986) equations.

We measured *Pinus ponderosa* diameter growth on all plots except for six treeless plots in park/*Symphyotrichum* ecosystems by coring two trees per plot at 40 cm above ground level. We selected trees for coring that were open-grown dominants establishing before 1875 (prior to Euro-American settlement of the study area). We used annual mean increment from age 50–150 years averaged on a plot basis as a growth measure to represent the early-middle life stage of *P. ponderosa* (Schubert 1974). These data facilitate identification of productive sites in presettlement forests, before growth was impacted by exclusion of historically frequent fire, competition from increased densities

of small-diameter stems, and other factors associated with settlement (Feeney et al. 1998). Old trees also were most readily available for sampling on our plots because relatively intact understories formed part of our plot location criteria, and these understories most commonly occurred outside patches of old trees (Kerns et al. 2003). We mounted, sanded, and cross-dated cores using local tree-ring chronologies.

Statistical analyses

To identify environmental variables most strongly correlated with plant community composition, we ordinated the vegetation importance value matrix with environmental vectors using non-metric multidimensional scaling (autopilot, thorough mode) in PC-ORD (McCune and Mefford 1999). We used discriminant analysis (SAS Institute 1999) to model distributions of four major grasses based on environmental variables. We employed stepwise selection ($p < 0.15$ to enter or stay) to identify variables for inclusion in the model, and we also manually entered combinations of variables (Tabachnick and Fidell 1996). Five of the six variables identified in stepwise selection provided high discriminatory power for as few variables as possible. We used equal prior probabilities, and employed cross-validation (jackknifing) for examining model robustness (SAS Institute 1999).

We developed ecological species groups in an R-mode analysis (McCune and Grace 2002) including hierarchical cluster analysis (Sørensen distance and –0.25 Flexible Beta group linkage method) and non-metric multidimensional scaling in PC-ORD (McCune and Mefford 1999). We relativized importance values for these analyses by species sums of squares to emphasize habitat preferences, avoiding groupings based on the commonness or rarity of species (McCune et al. 2000). Species groups identified in non-metric multidimensional scaling were similar to those identified in cluster analysis, and we also examined species \times plot matrices to refine groupings portrayed by these multivariate analyses (Kashian et al. 2003). We included 52 species in species groups, representing common species whose distributions could be assessed based on available data. While species groups identified in these analyses are a logical classification of species

displaying similar environmental affinities, this classification is one of a few reasonable groupings arriving at similar conclusions (Kashian et al. 2003; Abella and Shelburne 2004).

We used a regression tree model (Breiman et al. 1984) in SAS JMP software (SAS Institute 2002) to estimate *Pinus ponderosa* diameter increment based on species group importance values (sums of importance values of constituent species in a group). Regression trees partition independent variables similar to a dichotomous botanical key, and provide point estimates for dependent variables corresponding to different levels of independent variables (McCune and Grace 2002).

Results and discussion

Community–environment gradients

Plant community composition was correlated with moisture-affecting soil physical properties such as texture, Universal Transverse Mercator (UTM) easting probably partly reflecting a precipitation gradient (Jameson 1969; Figure 1), and soil-resource gradients such as total N (Figure 2). Variables most strongly correlated (Pearson $r^2 > 0.2$) with axis 1 or 2 of the community ordination included 0–15 cm sand, 0–50 cm available water capacity, 15–50 cm silt, 0–15 cm organic C, 15–50 cm total N, UTM easting, and 15–50 cm pH. *Festuca arizonica* and *Lupinus argenteus* increased in community importance with increasing soil available water capacity, silt, organic C, and total N concentrations. *Bahia dissecta* (Gray) Britt., in contrast, increased with increasing sand and decreasing available water, organic C, and total N.

Species composition was not strongly correlated ($r^2 < 0.08$) with the topographic variables of slope gradient, aspect, and terrain shape index. Gently sloping ravines and drainages on this landscape are common, but these topographic features apparently need to be especially large or steep before they appreciably affect vegetation patterns (Crawford Zimmerman et al. 1999). Soil parent material, rather than topography, primarily structures vegetation patterns at broad scales on this landscape (Figure 2). Parent material on this landscape largely depends on the presence or absence of volcanic activity and on the age and type of volcanic material (Welch and Klemmedson 1975; Moore et al. 1976).

Modeling species distributions

Grasses had the highest average importance among plant lifeform groups in all 10 classified ecosystem types, consistent with these forests being described as forested grasslands (Cooper 1960). We modeled which one of four dominant grasses had the highest importance value at different levels of five environmental variables using discriminant analysis (Table 1). The model correctly classified the most important grass on 80% of plots in resubstitution and 70% in cross-validation. Consistent with ordination results (Figure 2), *Festuca arizonica* was most important on plots with high soil available water capacity. *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, however, dominated plots with lower water-holding capacities and also occurred in clay basalt/*Gutierrezia*, xeric limestone/*Bouteloua*, and cinder ecosystems where precipitation is sparse (Figure 1). *Sporobolus interruptus* Vasey occupied clayey sites and was largely restricted to plots of the rocky basalt/*Sporobolus* ecosystem exhibiting high surface rock cover (>10%) usually occurring in the study area's south half. *Muhlenbergia montana* (Nutt.) A.S. Hitchc. was important on a range of plots, but importance of this species declined while importance of *F. arizonica* increased in moist, loam-silt loam basalt/*Festuca* and aspen/*Lathyrus* ecosystems. This concurs with Hanks et al. (1983), who noted that *F. arizonica* occupied moister sites than *M. montana*, which occurred over a broader range of dry-moist sites. These distributional differences may be related to photosynthetic pathways, with the C₄ *M. montana* more competitive on drier sites than the C₃ *F. arizonica* (Sage and Monson 1999).

Plots misclassified by the model mostly occurred where two species had nearly equal importance values. Misclassifications occurred for dry plots where *Bouteloua gracilis* and *Muhlenbergia montana* were co-dominant, and on plots of mesic limestone/mixed flora ecosystems where *Festuca arizonica* and *M. montana* were co-dominant (Table 1). Nevertheless, this model's reasonably good accuracy suggests that quantitative species–environment models have potential for predicting plant distributions across southwestern *Pinus ponderosa* landscapes.

Similar to grasses, many forbs occupied characteristic environmental complexes, illustrated for

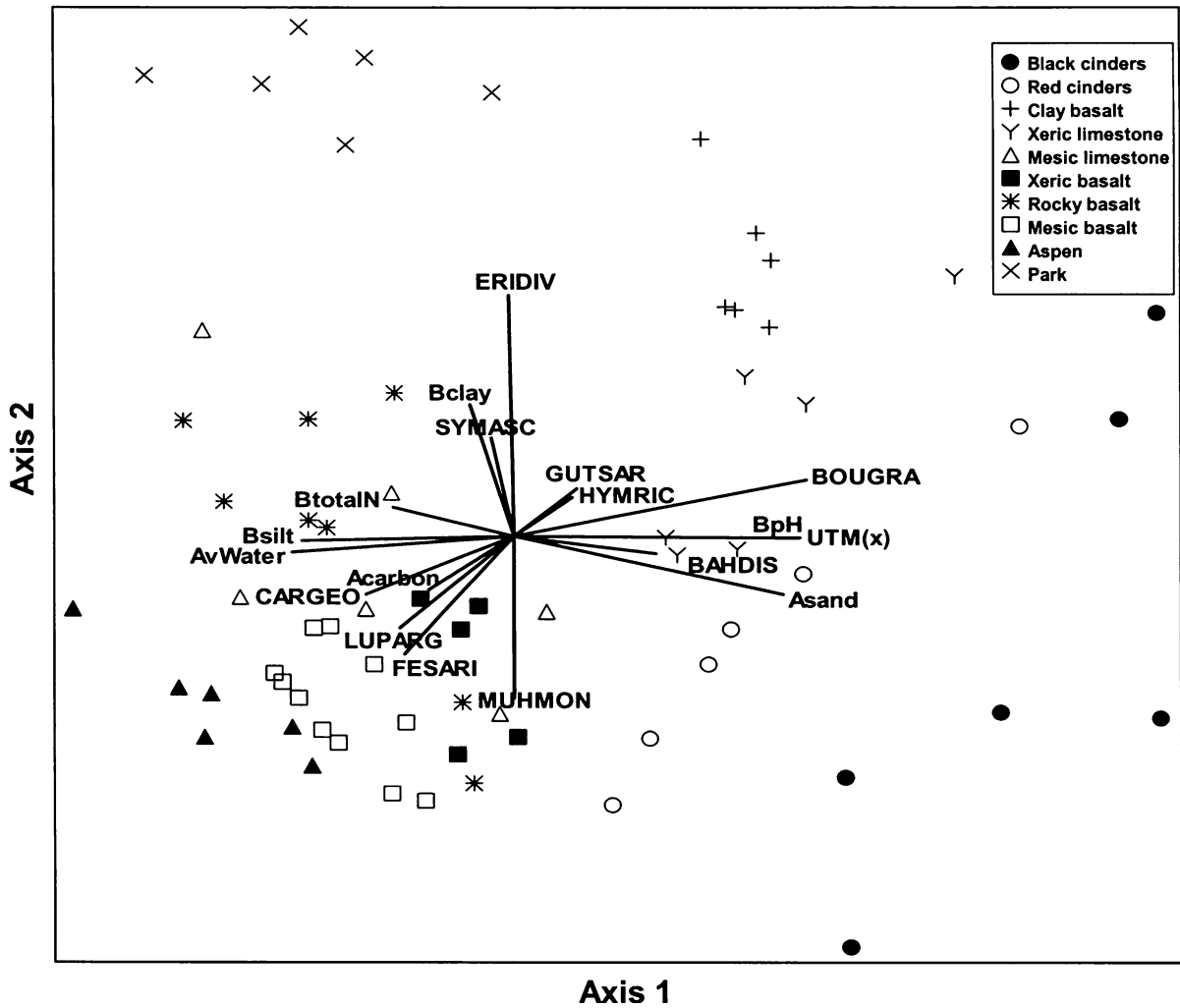


Figure 2. Non-metric multidimensional scaling ordination of a 66 plot \times 271 species importance value matrix for 10 ecosystem types of an Arizona *Pinus ponderosa* landscape. Vector lengths are proportional to correlations with community composition. Community composition was more closely related to soil properties reflecting parent materials than to topographic variables. For soil variables, A = 0–15 cm and B = 15–50 cm. UTM(x) = Universal Transverse Mercator easting and is partly correlated with a precipitation gradient. Vector abbreviations for species are as follows: BAHDIS = *Bahia dissecta*, BOUGRA = *Bouteloua gracilis*, CARGEO = *Carex geophila*, ERIDIV = *Erigeron divergens*, FESARI = *Festuca arizonica*, GUTSAR = *Gutierrezia sarothrae*, HYMRIC = *Hymenoxys richardsonii*, LUPARG = *Lupinus argenteus*, MUHMON = *Muhlenbergia montana*, and SYMASC = *Symphotrichum ascendens*.

six species along soil texture and fertility gradients (Figure 3). *Bahia dissecta*, for example, dominated plots sandier and lower in total N than did *Lupinus argenteus*. Occupying intermediate site conditions, *Pedicularis centranthera* Gray was important on plots containing 0.05–0.1% total N and 20–40% 15–50 cm sand. *Penstemon linarioides* Gray occurrences were not

soil-texture specific, but 0–15 cm pH exceeded 6.5 in 89% (8/9) of this species' occurrences. *Antennaria parvifolia* Nutt. and *Vicia americana* Muhl. ex Willd. exhibited similar distributions, occupying loam and silt loam sites of lower pH than *P. linarioides*. These similarities in single-species distributions form the basis for classifying ecological species groups.

Table 1. Discriminant functions predicting which one of four dominant grasses has the highest importance value at different levels of five environmental variables for an Arizona *Pinus ponderosa* landscape.

	<i>Bouteloua gracilis</i> n = 19 ^a	<i>Festuca arizonica</i> n = 17	<i>Muhlenbergia montana</i> n = 18	<i>Sporobolus interruptus</i> n = 5
	Discriminant functions			
Variable				
Constant	-1403	-1362	-1368	-1386
15–50 cm pH	17.61649	15.91682	15.787	8.74846
0–50 cm AWC ^b	1406	1575	1465	1478
0–15 cm clay (%)	0.83406	0.48799	0.66308	0.74321
15–50 cm gravel (%)	1.7305	1.94237	1.83275	1.85903
UTM easting (m) ^c	0.0055	0.00538	0.00543	0.00556
Resubstitution accuracy ^d	% Classified into groups			
<i>Bouteloua gracilis</i>	74	0	16	11
<i>Festuca arizonica</i>	0	88	12	0
<i>Muhlenbergia montana</i>	17	6	56	22
<i>Sporobolus interruptus</i>	0	0	0	100
Cross-validation accuracy	63	88	50	80

^a Number of plots where a species exhibited the highest importance value among the four modeled species out of 59 plots where at least one of these species occurred.

^b AWC = available water capacity (Saxton et al. 1986).

^c UTM = Universal Transverse Mercator coordinates, partly correlated with a gradient of increasing precipitation from east to west across the study area (Jameson 1969).

^d Classification accuracy by resubstitution into the discriminant function. Values in bold are % correctly classified into a group. Overall classification accuracy using equal priors was 80% for resubstitution and 70% for cross-validation. Tabachnick and Fidell (1996) provide methodological details for discriminant analysis.

Ecological species groups

We classified 18 ecological species groups containing 52 of 271 total species detected in this study (Figure 4, Table 2). Similar to analyses at community and single-species levels, groups differentiated along soil texture and other gradients reflecting moisture and nutrient availability. The *Phacelia* group, for example, consisting of *Phacelia serrata* J. Voss, *Penstemon clutei* A. Nels., and *Physaria newberryi* Gray, was restricted to plots in black cinders/*Phacelia* ecosystems containing the driest surface soils in the study area. Upper 0–15 cm sand concentration averaged 92%, 15–50 cm organic C only 0.2%, and 15–50 cm total N only 0.02% in the three plots where the *Phacelia* group occurred. Similarly, *Erysimum capitatum* (Dougl. ex Hook.) Greene and *Hymenoxys subintegra* Cockerell comprising the *Erysimum* group were restricted to red cinders/*Bahia* ecosystems, and also indicated sandy sites low in organic C and total N. In contrast, the *Festuca* group, consisting of *Festuca arizonica*, *Lupinus argenteus*, and *Carex geophila*, indicated moist, loam-silt loam productive soils rich in C and N.

On 13 plots where total importance of the *Festuca* group exceeded 30% (range = 30–51%), 0–15 cm silt averaged 52%, 15–50 cm organic C 1.5%, and 15–50 cm total N 0.13%. Although overlapping in distribution, the *Muhlenbergia* group typified by *Muhlenbergia montana* indicated sandier textures and lower soil-resource levels than the *Festuca* group. Upper 0–15 cm silt averaged 19% lower, and 15–50 cm organic C and total N were half as concentrated on the 13 plots where the *Muhlenbergia* group was most important (importance values = 26–43%) compared to the 13 plots where the *Festuca* group was most important.

Bouteloua gracilis, *Elymus elymoides* (Raf.) Swezey, and *Muhlenbergia wrightii* Vasey ex Coult. each exhibited unique distributions and were classified into single-species groups (Table 2). *Bouteloua gracilis*, for instance, dominated climatically dry ecosystems irrespective of soil parent material or texture. This species occurred with other dry-site groups such as the *Phacelia* or *Hymenopappus* groups in some ecosystems. However, *B. gracilis* was more widely distributed among dry ecosystems than were other dry-site species groups, which usually were most important

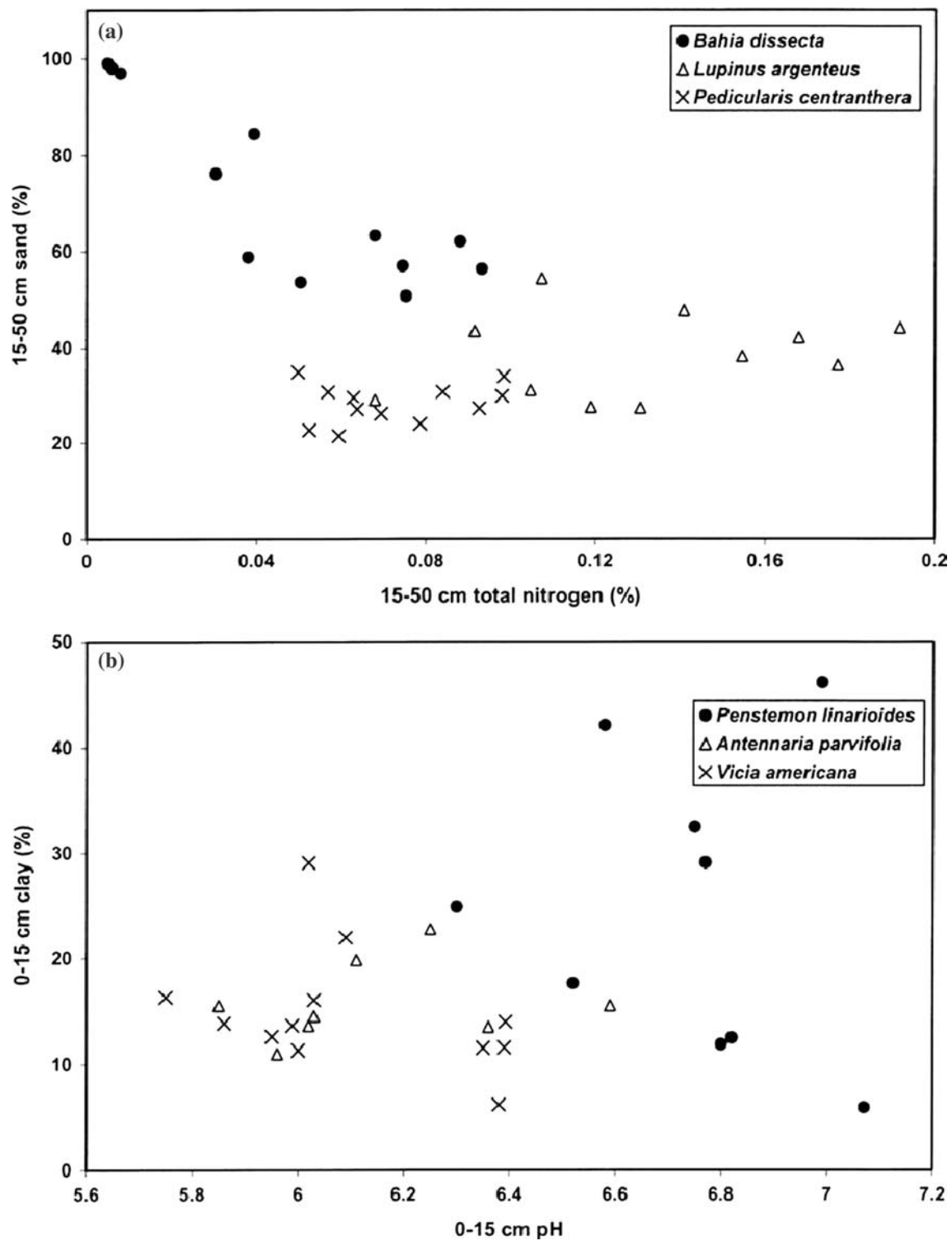


Figure 3. Distribution of six forbs along soil texture and fertility gradients on an Arizona *Pinus ponderosa* landscape. Distributions represent the 12 plots where a species was most important or all occurrences if a species occurred on fewer than 12 plots.

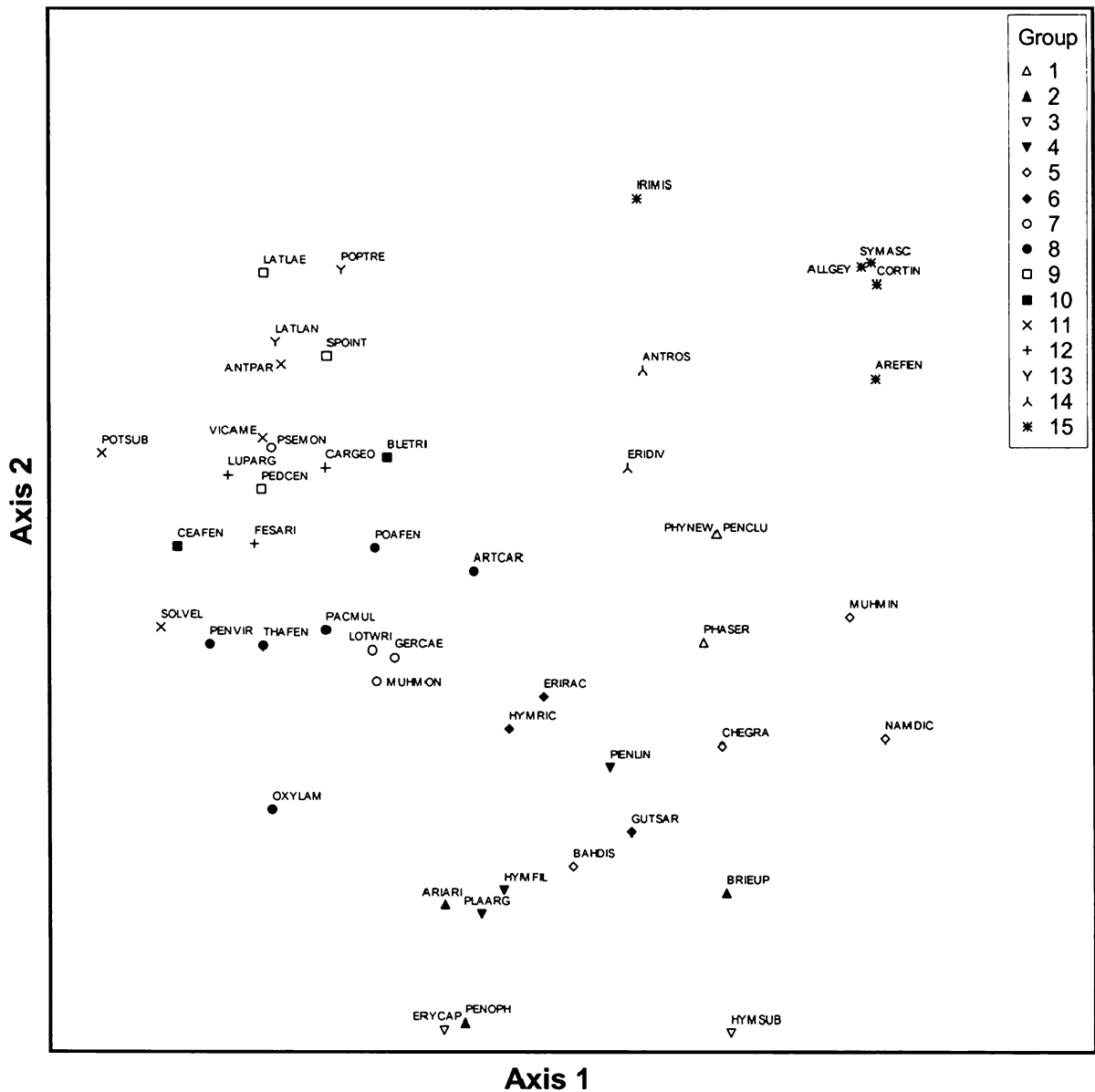


Figure 4. R-mode non-metric multidimensional scaling ordination of 49 species constituting 15 ecological species groups of an Arizona *Pinus ponderosa* landscape. Three species (*Bouteloua gracilis*, *Elymus elymoides*, and *Muhlenbergia wrightii*) forming single-species groups are not shown. Species are abbreviated by the first three letters of each of the genus and species names, and their full names and group identities are given in Table 2.

in only one or two dry ecosystems. Classifying *B. gracilis* into an existing dry-site group would weaken the indicator value of that group and misrepresent *B. gracilis*'s distribution. Several previous species-group classifications also have contained some single-species groups (Bergeron and Bouchard 1984; Simpson et al. 1990; Meilleur et al. 1992).

Our results on this semi-arid landscape support several general species group principles chiefly developed on temperate landscapes (e.g., Spies and Barnes 1985; Grabherr et al. 2003; Kashian et al. 2003). For example, authors in eastern USA forests have concluded that while some species groups are restricted to only one ecosystem type, most groups occur in several ecosystems but are

Table 2. Summary of ecological species groups and their environmental affinities for an Arizona *Pinus ponderosa* landscape between 1920 and 2660 m elevations.

Dry-site groups

Phacelia group: Restricted to dry, gravelly, black cinder soils of the Sunset Crater volcanic field low in organic C and total N (BC)^a

Phacelia serrata, *Penstemon clutei*, *Physaria newberryi*

Aristida group: Characteristic of dry, gravelly, sandy or sandy loam black or red cinder soils on or near cinder cones (BC, RC)

Aristida arizonica, *Brickellia eupatorioides*, *Penstemon ophianthus*

Erysimum group: Characteristic of dry, sandy loam red cinder soils on or near cinder cones (RC)

Erysimum capitatum, *Hymenoxys subintegra*

Hymenopappus group: Most abundant on climatically dry limestone or basalt soils (XL, CB)

Hymenopappus filifolius, *Plantago argyraea*, *Penstemon linarioides*

Bouteloua group: Climatically dry sites on soils with various parent materials (BC, RC, XL, CB)

Bouteloua gracilis

Bahia group: Most abundant on red and black cinder soils and less abundant on basalt or limestone soils (BC, RC)

Bahia dissecta, *Nama dichotomum*, *Chenopodium graveolens*, *Muhlenbergia minutissima*

Gutierrezia group: Frequent on climatically dry limestone or basalt soils (XL, CB)

Gutierrezia sarothrae, *Hymenoxys richardsonii*, *Eriogonum racemosum*

Dry-moist groups

Muhlenbergia group: Dry-moist soils including black and red cinders, limestone, and basalt (most dominant in XB)

Muhlenbergia montana, *Geranium caespitosum*, *Pseudocymopterus montanus*, *Lotus wrightii*

Oxytropis group: Diverse group of dry-moist soils of a variety of parent materials (several ecosystems)

Oxytropis lambertii, *Artemisia carruthii*, *Penstemon virgatus*, *Packera multilobata*, *Thalictrum fendleri*, *Poa fendleriana*

Elymus group: Widespread species occurring on 97% of plots and consistently of medium-high abundance (all ecosystems)

Elymus elymoides

Intermediate and moist-site groups

Sporobolus group: Characteristic of loamy or clay loam basalt soils with high (> 10%) surface rock cover (RB)

Sporobolus interruptus, *Lathyrus laetivirens*, *Pedicularis centranthera*

Blepharoneuron group: Provisional group with both species most abundant on moist basalt and limestone soils (RB, MB, ML)

Blepharoneuron tricholepis, *Ceanothus fendleri*

Solidago group: Common on limestone and moist basalt soil (ML, MB)

Solidago velutina, *Potentilla subviscosa*, *Antennaria parvifolia*, *Vicia americana*

Festuca group: Dominant on moist, loam-silt loam basalt soils with high organic C and total N (MB, AN)

Festuca arizonica, *Lupinus argenteus*, *Carex geophila*

Lathyrus group: Restricted to aspen ecosystems containing moist, loamy soils with high organic C and total N (AN)

Lathyrus lanszwertii, *Populus tremuloides*

Erigeron group: Occupied all soils except cinder soils but most abundant in two ecosystem types (CB, PK)

Erigeron divergens, *Antennaria rosulata*

Muhlenbergia wrightii group: Abundant in treeless parks but also occurred on limestone and basalt forested soils (PK, ML, MB)

Muhlenbergia wrightii

Symphotrichum group: Dominant in parks containing deep, primarily clay loam soils (PK)

Symphotrichum ascendens, *Allium geyeri*, *Arenaria fendleri*, *Coreopsis tinctoria*, *Iris missouriensis*

^a Ecosystem types where species groups were most characteristic are given in parenthesis: AN = aspen/*Lathyrus*, BC = black cinders/*Phacelia*, CB = clay basalt/*Gutierrezia*, MB = mesic basalt/*Festuca*, ML = mesic limestone/mixed flora, PK = park/*Symphotrichum*, RB = rocky basalt/*Sporobolus*, RC = red cinders/*Bahia*, XB = xeric basalt/*Muhlenbergia*, and XL = xeric limestone/*Bouteloua*.

quantitatively most important in only a few (Archambault et al. 1989; Abella and Shelburne 2004). Our findings concur with this principle because only a few groups, such as the *Phacelia* and *Erysimum* groups, were restricted to one ecosystem type. Furthermore, distributions of closely related groups like the *Festuca* and *Muhlenbergia* groups were only distinguishable quantitatively (Table 2). Species groups also are reported to more strongly

indicate environmental complexes than single-factor gradients (Spies and Barnes 1985; Archambault et al. 1989; Meilleur et al. 1992), which also agrees with our results. While a soil texture gradient corresponded with the *Bahia* group's distribution, for example, most other groups could not be differentiated along single-factor gradients. This point is exemplified by the *Hymenopappus* group, which occurred on a range of soil textures

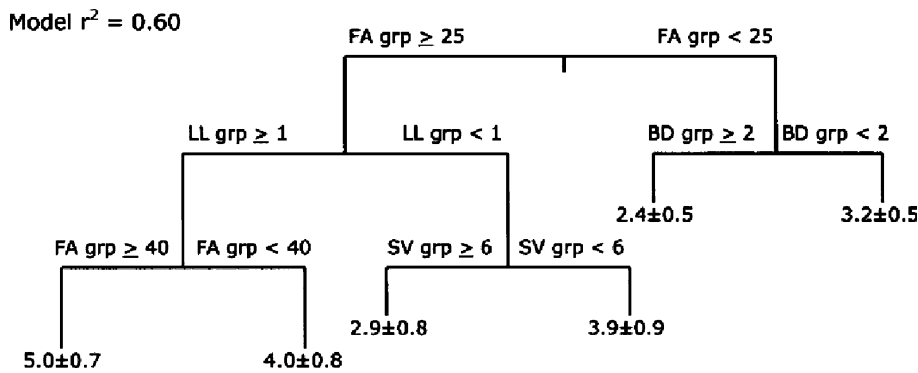


Figure 5. Regression tree estimating diameter growth of old, open-grown *Pinus ponderosa* based on species group importance values. Terminal nodes represent predicted mean *P. ponderosa* diameter increment in mm/year (predicted value \pm standard deviation). The model does not include plots in treeless park/*Symphytotrichum* ecosystems or plots in black cinders/*Phacelia* ecosystems because of unusually high tree growth variability. Species-group abbreviations are as follows: FA = *Festuca arizonica*, BD = *Bahia dissecta*, LL = *Lathyrus lanszwertii*, and SV = *Solidago velutina*.

illustrated by *Penstemon linarioides*'s distribution (Figure 3). High importance of this group, however, was indicative of dry soils, often of xeric limestone/*Bouteloua* or clay basalt/*Gutierrezia* ecosystems. Dry soils of these ecosystems resulted from multifactor gradients of clayey or sandy textures, low precipitation, and low-moderate organic C concentrations.

Species groups are based on the theory, derived from voluminous literature, that species are confined to environmental complexes where they are best adapted (Mueller-Dombois and Ellenberg 1974; Pregitzer and Barnes 1982; Kashian et al. 2003). The strong associations we observed between environmental variables and species distributions support this theory (e.g., Figures 2, 3). However, disturbance and other factors should not be overlooked for their role in governing species distributions. It is particularly difficult to disentangle environmental and disturbance factors when a given distinct environmental complex, or ecosystem type, also has a distinct disturbance regime (Host and Pregitzer 1992). Park/*Symphytotrichum* ecosystems from our data set illustrate this point. These ecosystems contain an unique environment (Abella 2005), but also are intensively grazed by ungulates (Clary 1975). Several species of the *Symphytotrichum* (e.g., *Arenaria fendleri* Gray) and *Erigeron* (*Erigeron divergens* Torr. & Gray, *Antennaria rosulata* Rydb.) groups are relatively unpalatable (Clary 1975). This could partly explain why these species thrived in the heavily grazed park ecosystems, making causal

relationships of these species with environmental factors less certain. These observations underscore a research need in *Pinus ponderosa* forests to better understand the relative roles and interactions of environmental factors and past and present disturbances on species distributions.

Estimating tree growth

We applied the species groups by predicting past diameter growth of old, open-grown *Pinus ponderosa* based on species-group importance values using a regression tree (Figure 5). Increasing importance of the *Festuca* and *Lathyrus* moist-site groups indicated rapid *P. ponderosa* growth. In contrast, increasing importance of the *Bahia* group, often in the red cinders/*Bahia* ecosystem, signified slow growth. Growth differences were substantial, ranging from 5.0 mm/year when the moist-site groups were important, to 2.4 mm/year when importance of the *Bahia* group equaled or exceeded two. Other groups generally indicative of slow tree growth included the *Sporobolus* group occupying rocky sites with clayey subsoils, and the *Bouteloua* group inhabiting climatically dry sites. Daubenmire (1961) and Stansfield et al. (1991) also found that plant distributions predicted tree growth fairly reliably in *P. ponderosa* forests. These findings are consistent with understory plants serving as phytometers useful for indicating environmental site conditions, which affect trees

and other ecosystem components (Kashian et al. 2003).

Conclusion

Species groups classified in this study are initial multivariate hypotheses about which species often grow together and have similar environmental requirements. Site conditions and *Pinus ponderosa* growth can be reasonably estimated on this landscape by observing plant species distributions. We believe that studies of communities and individual species combined with classifications of ecological species groups provide a stronger understanding of vegetation-environment relationships than studying either one alone. For example, our analysis of *Lupinus argenteus*'s distribution found that this species dominated plots containing the most soil N (Figure 3). Correspondingly, the *Festuca* group, of which *L. argenteus* was a member, dominated high soil N plots. Additional research could clarify whether *L. argenteus*'s N-fixing ability was a causal factor increasing soil N concentrations and affecting the distribution of the whole *Festuca* group. Several forms of vegetation-environment research will likely prove useful for furthering our understanding of species distributions on environmentally diverse *P. ponderosa* landscapes.

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