



Changes in forest vegetation and arbuscular mycorrhizae along a steep elevation gradient in Arizona

Marta A. Fisher¹, Peter Z. Fulé*

*School of Forestry and the Ecological Restoration Institute, Northern Arizona University,
PO Box 15018, Flagstaff, AZ 86011, USA*

Received 7 April 2004; received in revised form 2 July 2004; accepted 6 July 2004

Abstract

We assessed species composition, richness and abundance of understory vegetation, as well as arbuscular mycorrhizal (AM) inoculum potential on the San Francisco Peaks, tallest mountains in Arizona, crossing a steep, south-facing elevational gradient. These mountains have a high conservation value due to their rare habitats but previous vegetation studies have been limited. Because mature trees in the Pinaceae do not form associations with AM fungi, there may be more variation in plant community and AM fungal associations in coniferous forest than in ecosystems where all species associate with AM fungi. Differences in species composition between forest types reflected differences in the historical disturbance regimes. Species richness was highest in ponderosa pine forest (32.6 ± 1.4 per 1000 m² plot), although plant abundance was highest in aspen forest ($49.4 \pm 3.8\%$). Ponderosa pine and bristlecone pine forest were both high in species richness and contained species which were tolerant of frequent, low-intensity fire. Exotic species richness and abundance were highest in the lower elevations, which were also areas of high species richness and greater anthropogenic disturbance. Arbuscular mycorrhizal inoculum potential varied widely (1.2–80.1%), decreasing with increases in tree cover. We suggest indicator species that may be of use in monitoring these forests under changing climate and fire regimes.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Biodiversity; Disturbance; Soil ecology; Conservation; Wilderness; Arbuscular mycorrhizae

1. Introduction

By affecting temperature and precipitation, elevation gradients are important drivers of plant commu-

nity associations. Merriam (1890) used the San Francisco Peaks in Arizona to point out the similarities between high latitude and high altitude plant communities. His “life zones” concept implicitly agreed with the theory, later championed by Clements (1916), of communities as discrete units. Gleason (1926) argued for individualistic plant associations by pointing out that transition zones between vegetation types are wider where elevation gradients are more gradual. Neither Gleason’s nor Clements’s theories completely

* Corresponding author. Tel.: +1 928 523 1463;
fax: +1 928 523 0296.

E-mail address: pete.fule@nau.edu (P.Z. Fulé).

¹ Current address: Rocky Mountain Research Station, 507 25th St., Ogden, UT 84401, USA.

describe community distributions, but current theory retains elements from both (Shipley and Keddy, 1987; Callaway, 1997). Numerous studies of elevation gradients, such as those in the United States' Santa Catalina and Great Smoky Mountains and Israel's Mount Hermon, supported Gleason's argument by finding little overlap in plant species distributions (Whittaker, 1965; Whittaker and Niering, 1968; Auerbach and Shimda, 1993; Sagers and Lyon, 1997). However, dominant species may affect community composition by modifying the local environment (Collins et al., 1993; Hoagland and Collins, 1997). Furthermore, species can affect the distributions of other species even if their distributions are non-overlapping (Callaway, 1997; Callaway and Walker, 1997). A global study on plant interactions along elevation gradients found interactions between plants change from competition to facilitation as abiotic stress increases (Choler et al., 2001; Callaway et al., 2002), underscoring the importance of interactions between biotic as well as abiotic factors in determining species distributions (Callaway, 1997).

Changes in disturbance regimes across elevation have an important influence on plant communities (Harmon et al., 1983). Prior to settlement by Euro-Americans, fire was a frequent disturbance in the ponderosa pine forests of the southwestern United States; its exclusion is theorized to have caused dramatic changes including decreases in herbaceous production and decomposition rates and increases in tree density and fuel loads (Covington and Moore, 1994). Landscape biodiversity and abundance of native plants adapted to low-intensity fire may decline without fire disturbance (Keane et al., 2002; Beier and Maschinski, 2003; Korb and Springer, 2003). Fire exclusion is also a factor in decreasing aspen forests on the San Francisco Peaks and across the west, as old aspen stands become replaced by conifers (Kay, 1997; Turner et al., 2003).

Most previous gradient studies have compared plant communities solely to changes in the abiotic environment (Callaway, 1997), overlooking the role of arbuscular mycorrhizal fungi (AM), which form mutualistic to possibly parasitic associations with plants and affect plant fitness and competitive interactions (Allen and Allen, 1990; Johnson et al., 1997; Wilson and Hartnett, 1998; Hart et al., 2003). Almost all vascular plant species, with the notable exception

of mature (non-seedling) coniferous trees in the Pinaceae, can function as hosts for arbuscular mycorrhizal fungi (Mosse et al., 1981). AM are commonly known to assist host plants with phosphorous uptake, but may also provide other benefits including protection from fungal pathogens, assisting with the uptake of other nutrients such as nitrogen and copper, and improving water relations (Newsham et al., 1995). In return, AM fungi receive photosynthetic products from the host plant.

There is abundant evidence that AM fungi influence plant species composition and richness in grasslands (Grime et al., 1987; Gange et al., 1993; Wilson and Hartnett, 1997; Hartnett and Wilson, 1999). These studies have compared plants grown in the presence of AM fungi to the absence of AM fungi. However, AM fungi are thought to be ubiquitous in undisturbed grassland soils (Allen et al., 1995), therefore changes in AM species composition probably have greater ecological relevance in grasslands than AM presence alone (van der Heijden et al., 1998a, 1998b; Hart et al., 2003; Klironomos, 2003). In coniferous forests dominated by species in the Pinaceae, where the trees form associations almost exclusively with ectomycorrhizae, differences in AM inoculum could be more dramatic (Trappe, 1962; Ahlenslager, 1987; Benjamin et al., 1989). Although there are few studies of AM fungi in coniferous (Pinaceae) forest ecosystems, all have found decreasing colonization with increasing live tree cover (Kovacic et al., 1984; Korb et al., 2003b; Gildar et al., 2004) and AM colonization is low near alpine summits (Read and Haselwandter, 1981). If the presence of AM fungi alters the competitive balance between understory plants in coniferous forest, ecological implications could include changing the speed of plant community shifts under climate change scenarios or modifying the nutritive value of vegetation (McNaughton and Oosterheld, 1990; Perry et al., 1990).

In this study we assessed the herbaceous vegetation and AM inoculum potential on the San Francisco Peaks, crossing a steep, south-facing elevational gradient. Over 130 years after Merriam (1890) studies, the San Francisco Peaks remain a useful area to study vegetation distributions because they support representatives of all southwestern forest types arrayed along a steep elevation gradient. We expected that: (1) the species composition, richness, and abundance

of the understory vegetation would differ between forest types covering different elevational bands. Species richness was expected to decline with elevation, with the lowest species richness in bristlecone pine forest, except aspen vegetation was expected to have the highest species richness and species abundance. (2) Exotic plants were expected to be distributed in accordance with two hypotheses: first, communities with fewer natives would be the most heavily invaded; second, exotics would dominate where disturbance was more prevalent. Due to past management and modern recreation, there was more disturbance at the bottom of the San Francisco Peaks, so lower elevations were expected to have greater richness and abundance of exotic species. (3) AM inoculum potential was expected to decrease with increases in tree cover.

2. Study area

We conducted our study on the south face of the San Francisco Peaks within the Coconino National Forest in northern Arizona, centered on latitude 35°18', longitude 111°41' (Fig. 1). The "Peaks" are actually the caldera of a single extinct volcano. Three peaks around the caldera, Humphreys, Agassiz, and Fremont Peaks, are the highest points in Arizona (3851, 3766, and 3648 m respectively). Because of its volcanic origin, soil parent material is primarily andesite, rhyolite and basalt. Soils are chiefly inceptisols, alfisols, and mollisols (Terrestrial Ecosystems Survey, Anon, 1995). A weather station at 2240 m, slightly lower in elevation than our study area, records average annual precipitation of 56 cm. Average July maximum temperature is 27 °C and average January minimum temperature is -12 °C (Western Regional Climate Center, Anon, 2003). Over a 1000 m elevation increase on the San Francisco Peaks, precipitation increases by 11 cm while temperatures decrease by 6.89 °C (Pearson, 1920). Ponderosa pine, the most common forest type in northern Arizona and New Mexico, is found in the lowest elevations (Brown, 1994). Higher elevation forest types, rare in the Southwest, are remnant populations that have become isolated in the current interglacial period (Schaack, 1983; Brown, 1994). These forests include mixed conifer forest, dominated by Douglas-fir and limber pine, aspen stands, spruce/fir forest, and bristlecone pine

forest. Rocky Mountain bristlecone pine trees are found only in the highest elevations of Arizona, Colorado, and New Mexico (Brunstein and Yamaguchi, 1992). The San Francisco Peaks culminate in the only tundra vegetation in Arizona (Rominger and Paulik, 1983; Schaack, 1983; Brown, 1994).

Since Euro-American settlement (circa, 1876), the San Francisco Peaks were used for summer grazing of sheep and cattle starting in the 1870s, peaking around 1915 (Cline, 1994). Lower elevation ponderosa pine and mixed conifer forests were logged, though higher elevation forests were excluded from harvest because of the steep terrain. Since the Kachina Peaks Wilderness Area was established in 1984, it has received an increasing number of recreational visitors and a downhill ski area operates on 137 acres on the west side of the mountain (Aitchison, 1989).

3. Methods

We assessed plant community composition, site conditions, and overstory tree conditions on 121 plots located systematically on a 300 m grid that extended from ponderosa pine forest at 2442 m to timberline at 3569 m (Fig. 1). We were only examining the understory within the context of a forested overstory, so if a plot origin fell in a meadow or other unforested location, we attempted to relocate the plot 50 m to the N, E, W, or S. If these were also unforested we did not establish the plot.

Plot design was based on the National Park Service's Fire Monitoring protocol (National Park Service, 1992). Plots were 20 m × 50 m (1000 m²), with the longer axis oriented uphill to capture the elevation gradient and enable correction of the plot area for slope. Plot corners and center were permanently marked with iron stakes placed flush to the forest floor. We recorded the distance and direction from a tagged reference tree to the plot center and recorded GPS coordinates, slope, azimuth and elevation of the plot.

Each plot was measured once between the years 2000 and 2003. Sampling took 4 years because plots all had to be reached on foot, forests were closed to research in 2000 and 2002 due to extreme drought, and a wildfire in 2001 also closed the forest for several weeks. We do not believe the year a plot was sampled

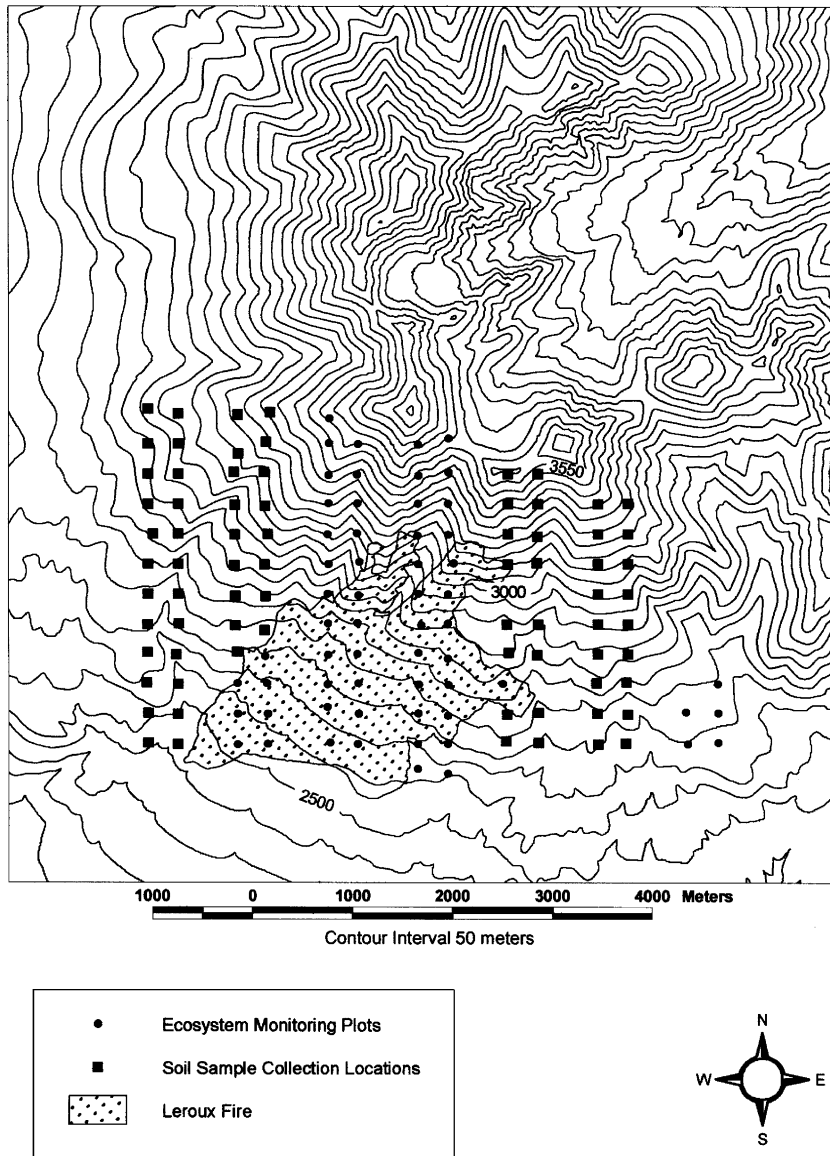


Fig. 1. Study sites on the San Francisco Peaks. Squares (■) show the permanent plots where we took soil samples. Dots (●) show the permanent plots where we did not take soil samples.

had a significant effect on our results, for the following reasons. First, representatives of all five forest types were sampled in 2000, 2001 and 2003. This meant that between-year sampling did not duplicate the results between forest types. In 2002, only three plots were sampled, all of which were bristlecone pine forest. This is a small proportion of the 21 bristlecone pine plots, and therefore should not sway the results.

Although climatic conditions differed between sampling years, all years were somewhat similar in that precipitation was below average. Finally, independent samples *t*-tests did not detect differences in species richness or composition between sampling years.

All trees on the 1000 m² plot with a diameter at breast height (dbh) greater than 15 cm were measured; trees with dbh 2.5–15 cm were measured on a 250 m²

subplot and trees < 2.5 cm dbh were measured on a 50 m² subplot. For each tree we recorded dbh, crown base height, total height, damage and decay class of snags (Thomas et al., 1979).

Herbaceous plant abundance was measured on two point-line intercept transects per plot, running along the 50 m plot boundaries. Every 30 cm we recorded all species encountered, height of the tallest species, and underlying substrate (litter, rock, etc.). To calculate plant abundance, we divided the number of plants encountered on each point-line intercept transect by 332, the total number of points sampled per plot. Since more than one plant could be encountered at a single point, it was possible for plant abundance to exceed one. We measured tree canopy cover by vertical projection every 3 m along each 50 m plot boundary. We recorded presence/absence of all vascular plant species on a belt transect (10 m × 50 m) centered on each point-line intercept transect.

Soil samples were collected in 2002 for measuring AM fungal inoculum potential on 75 of the 121 plots. We chose plots that were established no later than 2002, were not burned in a 2001 wildfire that covered part of the study area, were located in Fig. 1. Soil sampling plots ranged in elevation from 2442 to 3559 m, only 10 m less than the elevation range for the full study area.

Plant species can have significant effects on the fungal communities beneath them (Bever et al., 1996; Eom et al., 2000). Therefore, we chose to sample under grasses, rather than at random points on the plot, to confirm that any mycorrhizal differences we encountered were not an artifact of changes in the presence or abundance of certain species. We recorded the grass species under which the sample was taken. We collected soil by clearing away the organic layer, then pounding a 3.8 cm diameter pipe 15 cm into the ground. We took two soil cores from underneath the clump of grass closest to the center of each point-line intercept transect.

Roots from one of each of the paired soil samples were elutriated, dried, and weighed to estimate the root biomass available as a mycorrhizal inoculant. The other paired soil sample was transported to the lab in the soil corer for a corn bioassay to determine mycorrhizal inoculum potential (Johnson et al., 1999). The purpose of using an intact soil core was to retain root and AM hyphal networks substantially intact

(Klironomos and Hart, 2002). We covered the bottom of the corer with shade cloth to prevent soil loss but allow water drainage, and then planted a germinated corn seedling (*Zea mays*) in the soil core. After 6 weeks, we harvested the corn plants. To assess percent colonization by AM fungi, we harvested, stained, and scored the roots using the grid-line intersect method (Johnson et al., 1999).

To test for greenhouse contamination, we planted corn seedlings in steam-sterilized soil in five additional cores. AM colonization in the controls ranged between 0% and 5.5% (mean $2.8 \pm 1.0\%$). Therefore only about 2–4% of the colonization we observed could be due to greenhouse contamination. Any fungus we saw in the roots that could not be positively identified as AM was listed as non-mycorrhizal. *Olpidium* spp. and dark septate were noted in the roots, but as no trends were noted with those species they were all grouped together for analysis. All control plants were entirely free of non-AM fungi.

3.1. Data analysis

We categorized each plot into one of five forest types based on an importance value for each tree species calculated from the sum of the relative frequency (percent stems) and relative abundance (percent basal area) (Taylor, 2000). If the highest importance value on a given plot was *Pinus ponderosa*, *Populus tremuloides*, or *Pinus aristata*, we assigned it to the ponderosa pine, aspen, or bristlecone pine forest type, respectively. If the highest importance value was for *Pinus flexilis* or *Pseudotsuga menziesii* (limber pine or Douglas-fir), we assigned it to the mixed conifer forest type. If the highest importance value was for *Abies lasiocarpa* var. *arizonica* or *Picea engelmannii* (corkbark fir or Englemann spruce) we assigned it to the spruce/fir forest type. Henceforth in this paper, the scientific names are used to refer to individual tree species, while common names are used to refer to forest types (e.g., “ponderosa pine forest” or “spruce/fir forest”).

Due to the long sampling period and difficult access, it was not possible to conduct all the plant measurements under ideal phenological conditions. Some understory plants were difficult to identify in the field, so it was necessary to group certain taxa by genus for analysis (e.g., *Bromus anomalus* and *Bromus*

ciliatus were called *Bromus* spp.). For this reason, species richness and species diversity measures are underestimates.

Total plant abundance, exotic plant abundance, abundances of individual species and groups of species, and species diversity (Shannon's H') were calculated from point-line intercept data. We used the data from the belt transect to calculate species richness.

Multivariate community analyses were carried out with PC-Ord software (McCune and Mefford, 1999). We used nonmetric multidimensional scaling (NMDS) to visualize differences in plant community composition. In NMDS analyses, we used Sørensen distance with a random starting configuration and 40 runs with real data. We used 50 runs with randomized data in the Monte Carlo test. We choose the highest dimensionality that yielded a final stress lower than 95%. We decided our solution was sufficiently stable when we reached an instability <0.0001 or 500 iterations.

Differences in community composition were tested with multi-response permutation procedures (MRPP). MRPP creates a distance matrix between group members, then compares the within group distances and the between group distances of random permutations to the actual groups. MRPP output is composed of a P -value and the chance-corrected within-group agreement (A), a measure of effect size. Our MRPP analyses were done using Euclidean distance.

Indicator species analysis was used to identify species that were particularly faithful and/or exclusive to individual forest types (McCune and Grace, 2002). A comparison between the maximum indicator value of a species (ranging between 0 and 100) and randomized trials for the occurrence of that species (1000 randomizations in the Monte Carlo test) yields a P -value. To be a perfect indicator value, a species would need to be found on all plots in a forest type and not found on any plots of any other forest types. We accepted species with indicator values ≥ 25 and P -values ≤ 0.05 as indicator species.

We used Mantel tests to find correlations between different sets of data taken on the same set of plots. The output from a Mantel test is a standardized Mantel statistic (r) that indicates the strength of the correlation between the distance matrices of the two data sets and a P -value. We chose Mantel's asymptotic approximation to evaluate test statistics. SPSS for Windows (2002) was used for parametric and nonparametric

univariate analyses. All variables used in parametric tests were checked for normality and equal variance by confirming the Shapiro-Wilk's and Levene's test statistics were both >0.05 . Statistically significant differences between sampled populations were assessed with t -tests or ANOVA. Alpha level for all tests of statistical significance was 0.05. Individual means were compared following significant ANOVAs using Tukey's HSD post hoc test. Variables that did not meet the assumptions for parametric statistics were assessed with nonparametric methods of analysis. ANOVA's were replaced with Kruskal-Wallis tests and t -tests were replaced with Wilcoxon Signed Ranks tests. We used Pearson's correlations to look for relationships between factors. The N was consistent for all correlations because zero data values were not excluded.

4. Results

4.1. Vegetation distribution

The sampling grid included 26 ponderosa pine, 27 mixed conifer, 37 aspen, 10 spruce/fir and 21 bristlecone pine plots (Table 1). In a companion study, Coker (2004) showed that the sampling grid was representative of the actual proportions of each forest type in the study area, as measured by classified satellite imagery. Plant community composition differed between the five forest types (MRPP, $A = 0.08$, $P < 0.01$). Mixed conifer and aspen appeared to have the most similar community composition (Fig. 2). The vegetation types at opposite ends of the elevational gradient, ponderosa pine and bristlecone pine, shared traits of high species richness and low canopy cover. Plant community composition was correlated with the environmental variables canopy cover, elevation, exotic species richness, plant abundance, slope, Shannon's H' diversity index, species richness, and forest type (Mantel test, $r = 0.54$, $P < 0.01$).

Forest types were differentiated both by species richness (ANOVA, $F_{(4, 116)} = 7.29$, $P < 0.01$) and canopy cover (ANOVA, $F_{(4, 116)} = 11.749$, $P < 0.01$) (Table 1). Shannon's H' diversity index did not vary between vegetation types. Canopy cover and species richness were inversely related ($r = -0.48$, $P < 0.01$). Species richness in ponderosa pine forest (average

Table 1
Plot characteristics by forest type

	Ponderosa pine	Mixed conifer	Aspen	Spruce/fir	Bristlecone pine
Elevation (m)	2595 (15)	2778 (25)	2875 (27)	3224 (31)	3308 (32)
Slope (%)	16.1 (1.6)	31.6 (2.7)	31.0 (2.2)	41.1 (3.0)	52.9 (2.0)
Tree canopy cover (%)	51.5 (3.4)	69.9 (2.8)	65.7 (2.9)	57.0 (4.8)	40.1 (4.6)
Species richness	32.6 (1.4)	26.0 (1.4)	24.5 (1.0)	25.8 (2.4)	28.7 (1.1)
Shannon's H' diversity index	1.6 (0.1)	1.7 (0.1)	1.8 (0.1)	1.5 (0.2)	1.7 (0.1)
Exotic species richness	1.9 (0.4)	0.6 (0.2)	1.0 (0.2)	0.7 (0.2)	1.0 (0.2)
Understory plant cover (%)	31.8 (5.6)	22.3 (2.9)	49.4 (3.8)	16.6 (4.6)	27.4 (3.5)
Non-plant cover (%)					
LICH	3.6 (0.9)	2.6 (0.9)	2.8 (0.7)	8.6 (1.8)	5.33 (1.4)
LITT	57.2 (4.9)	55.7 (2.5)	34.3 (3.4)	55.1 (4.2)	47.0 (3.8)
ROCK	3.1 (0.9)	5.4 (1.2)	2.8 (0.5)	8.2 (2.4)	8.3 (1.9)
SOIL	0.7 (0.3)	0.4 (0.1)	1.1 (0.2)	0.6 (0.3)	6.95 (2.6)
WOOD	3.1 (0.5)	6.8 (0.6)	8.4 (0.7)	7.2 (1.8)	4.2 (0.7)
AM colonization (%)	23.6 (5.1)	20.7 (2.2)	23.0 (2.0)	15.3 (3.7)	28.4 (4.6)
Non-AM colonization (%)	3.6 (1.0)	2.6 (0.6)	2.0 (0.5)	0.7 (0.3)	3.92 (1.2)
Ten most common species	<i>Carex</i> spp.	<i>Carex</i> spp.	<i>Lathyrus/Vicia</i> spp.	<i>Lathyrus lanszwertii</i> var. <i>leucanthus</i>	<i>Carex</i> spp.
	<i>Festuca arizonica</i>	<i>Lathyrus lanszwertii</i> var. <i>leucanthus</i>	<i>Carex</i> spp.	<i>Carex</i> spp.	<i>Poa fendleriana</i>
	<i>Muhlenbergia Montana</i>	<i>Bromus</i> spp.	<i>Lathyrus lanszwertii</i> var. <i>leucanthus</i>	<i>Bromus</i> spp.	<i>Arenaria lanuginosa</i> ssp. <i>saxosa</i>
	<i>Lathyrus/Vicia</i> spp.	<i>Pteridium aquilinum</i>	<i>Festuca arizonica</i>	<i>Lathyrus/Vicia</i> spp.	<i>Bromus</i> spp.
	<i>Elymus elymoides</i>	<i>Lathyrus/Vicia</i> spp.	<i>Bromus</i> spp.	<i>Mertensia franciscana</i>	<i>Lathyrus lanszwertii</i> var. <i>leucanthus</i>
	<i>Poa fendleriana</i>	<i>Muhlenbergia montana</i>	<i>Muhlenbergia montana</i>	<i>Solidago</i> spp.	<i>Solidago</i> spp.
	<i>Cirsium</i> spp.	<i>Poa fendleriana</i>	<i>Poa fendleriana</i>	<i>Pseudocymopterus montanus</i>	<i>Muhlenbergia montana</i>
	<i>Lupinus</i> spp.	<i>Festuca arizonica</i>	<i>Pteridium aquilinum</i>	<i>Ribes montigenum</i>	<i>Hymenoxys hoopseii</i>
	<i>Pteridium aquilinum</i>	<i>Elymus elymoides</i>	<i>Elymus elymoides</i>	<i>Hymenoxys hoopseii</i>	<i>Taraxacum officinale</i>
	<i>Ceanothus fendleri</i>	<i>Solidago</i> spp.	<i>Senecio eremophilus</i>	<i>Erigeron</i> spp.	<i>Festuca arizonica</i>

Standard errors are shown in parentheses.

32.6 species/1000 m² plot) was significantly higher than all forest types except bristlecone pine. Bristlecone pine and ponderosa pine, the two forest types with least canopy cover, differed from the two forest types with greatest cover, aspen and mixed conifer.

Plant abundance also varied between forest types (Kruskal-Wallis, $\chi^2_{(4)} = 29.46$, $P < 0.01$) and was not correlated with richness. Plant abundance was 36% higher in aspen than in ponderosa pine, the forest type with the next highest plant abundance. *Populus tremuloides* was the only tree species whose basal area was positively associated with plant abundance ($r =$

0.49, $P < 0.01$). Nitrogen fixing plants were more abundant on plots with high *P. tremuloides* basal area (N fixers: $r = 0.72$, $P < 0.01$).

Pinus ponderosa basal area and plant abundance were negatively related ($r = -0.23$, $P = 0.01$). In particular, high *P. ponderosa* basal area was associated with low abundances of nitrogen fixing plants and shrubs (N fixers: $r = -0.32$, $P < 0.01$; shrub: $r = -0.22$, $P = 0.01$). Plant abundance was inversely related to basal area of *Pseudotsuga menziesii* and both tree species associated with spruce/fir forest (*P. menziesii*: $r = -0.24$, $P = 0.01$; *Picea engelmannii*: $r =$

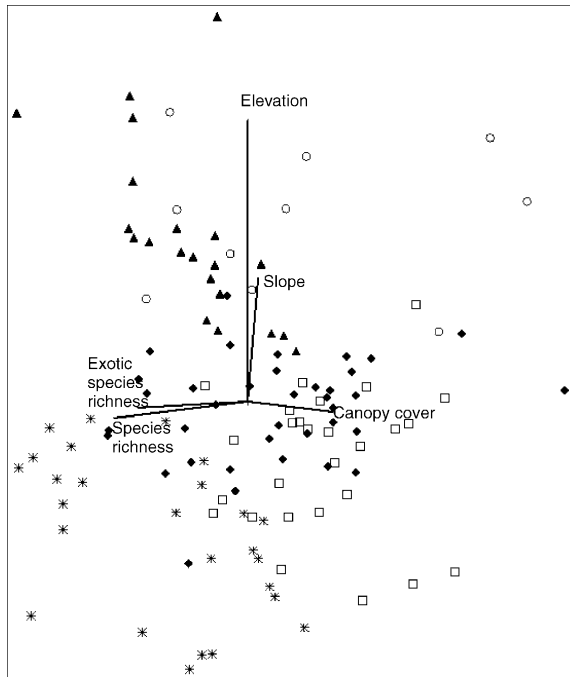


Fig. 2. NMDS ordination comparing plots by forest type. Tree species were not included in this ordination. Ponderosa pine plots are indicated by stars (*), mixed conifer by open boxes (□), aspen plots by closed diamonds (◆), spruce/fir by open circles (○), and bristlecone pine by closed triangles (▲). The final result required 500 iterations to achieve final stress of 18.41 and final instability of 0.0048 ($P = 0.02$).

-0.24 ; $P = 0.01$; *Abies lasiocarpa*: $r = -0.22$, $P = 0.02$). *Pinus aristata* was the only species to be significantly positively associated with shrub abundance ($r = 0.55$, $P < 0.01$).

Fourteen indicator species were identified for ponderosa pine forest, four for mixed conifer, none for aspen, two for spruce/fir, and eight for bristlecone pine forest (Table 2). Abundances of all three grasses that were ponderosa pine indicator species were positively correlated with species richness (*Muhlenbergia Montana*: $r = 0.54$, $P < 0.01$; *Elymus elymoides*: $r = 0.36$, $P < 0.01$; *Festuca arizonica*: $r = 0.35$, $P < 0.01$). There were also positive correlations between the abundances of ponderosa pine indicator species and species richness of N-fixing plants (*E. elymoides*: $r = 0.52$, $P < 0.01$; *F. arizonica*: $r = 0.47$, $P < 0.01$; *M. Montana*: $r = 0.45$, $P < 0.01$; *Lupinus* spp.: $r = 0.25$, $P < 0.01$). Of the mixed conifer indicator species, *Mahonia repens* was associated with plots that had high canopy cover

($r = 0.23$, $P = 0.01$). Two bristlecone pine indicator species were more abundant on plots with high species richness (*Festuca ovina*: $r = 0.21$, $P = 0.02$; *Erigeron* spp.: $r = 0.21$, $P = 0.02$). There was an inverse relationship between the abundances of bristlecone pine indicator species and richness of nitrogen fixing species (*Ribes montigenum*: $r = -0.33$, $P < 0.01$; *Penstemon whippleanus*: $r = -0.33$, $P < 0.01$; *Festuca ovina*: $r = -0.27$, $P < 0.01$). *Penstemon whippleanus* abundance was correlated with the percent cover of soil ($r = 0.21$, $P = 0.02$).

4.2. Exotic species

Native plant community composition on plots with exotic species differed from native plant composition on plots without exotics (MRPP, $A = 0.01$, $P < 0.01$). Plots with exotic species tended to be those with low canopy cover and high species richness (Fig. 3). Exotic species richness differed between forest types

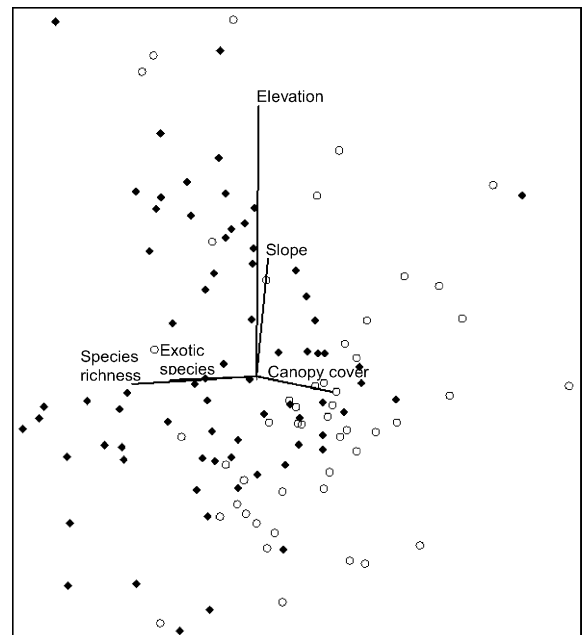


Fig. 3. NMDS ordination comparing native species composition on plots with and without exotic species. Plots that had no exotic species are shown by the open circles (○). Plots where exotic species were present are shown by closed diamonds (◆). The final result required 500 iterations to achieve final stress of 17.92 and final instability of 0.0048 ($P = 0.02$).

Table 2
Indicator species for each forest type

Ponderosa Pine			Mixed conifer			Aspen			Spruce/fir			Bristlecone pine		
Species	IV	P	Species	IV	P	Species	IV	P	Species	IV	P	Species	IV	P
<i>Cirsium</i> spp.	52.2	<0.01	<i>Thalictrum fendleri</i>	34.0	<0.01	No indicator species			<i>Pyrola</i> spp.	54.3	<0.01	<i>Festuca ovina</i>	48.1	<0.01
<i>Hieracium fendleri</i>	48.6	<0.01	<i>Pteridium aquilinum</i>	32.0	<0.01				<i>Aquilegia</i> spp.	25.2	<0.01	<i>Mertensia franciscana</i>	40.5	<0.01
<i>Packeria multilobata</i>	48.4	<0.01	<i>Holodiscus dumosus</i>	31.1	<0.01							<i>Monardella glauca</i>	38.1	<0.01
<i>Astragalus rusbyi</i>	36.5	<0.01	<i>Mahonia repens</i>	29.2	<0.01							<i>Penstemon whippleanus</i>	37.5	<0.01
<i>Lotus</i> spp.	34.8	<0.01										<i>Hymenoxys hoopesii</i>	35.3	<0.01
<i>Oxytropis lambertii</i>	34.6	<0.01										<i>Potentilla</i> spp.	32.5	<0.01
<i>Ceanothus fendleri</i>	34.3	<0.01										<i>Ribes montigenum</i>	31.7	<0.01
<i>Verbascum thapsus</i>	32.6	<0.01										<i>Erigeron</i> spp.	26.8	0.01
<i>Antennaria parviflora</i>	30.9	<0.01												
<i>Elymus elymoides</i>	29.1	<0.01												
<i>Astragalus humistratus</i>	26.9	<0.01												
<i>Festuca arizonica</i>	26.9	<0.01												
<i>Lupinus</i> spp.	26.6	0.03												
<i>Muhlenbergia Montana</i>	25.0	<0.01												

IV is the indicator value. A perfect indicator value would be 100.

(Kruskal-Wallis $\chi^2_{(4)} = 9.84$, $P = 0.04$). Mean exotic species richness was nearly twice as high in ponderosa pine as in bristlecone pine and aspen forests, which had the next highest exotic species richness (Table 1). Exotic species richness was positively correlated with both native species richness and native plant abundance (native richness: $r = 0.46$, $P < 0.01$; native abundance: $r = 0.41$, $P < 0.01$). However, exotic species richness was inversely related to canopy cover and elevation (canopy: $r = -0.39$, $P < 0.01$; elevation: $r = -0.19$, $P = 0.04$).

Abundance of exotic species showed similar trends to exotic species richness and the two variables were positively correlated ($r = 0.58$, $P < 0.01$). Exotic plant abundance was positively correlated with native plant abundance and native species richness (native abundance: $r = 0.54$, $P < 0.01$; native richness: $r = 0.20$, $P = 0.03$). Exotic plant abundance also decreased with increasing canopy cover ($r = -0.18$, $P = 0.05$). Exotics accounted for no more than 6% of plant encounters on any given plot.

Of the 200 different species encountered in this study there were 11 exotic species, 187 native species, and two which we could only identify to genus making us uncertain of their origin. The exotic species were *Bromus inermis*, *B. tectorum*, *Dactylis glomerata*, *Lactuca serriola*, *Linaria dalmatica*, *Poa compressa*, *P. pratensis*, *Sanguisorba minor*, *Taraxacum officinale*, *Tragopogon dubius*, and *Verbascum thapsus*. We also found a *Chenopodium* that may be the exotic *C. album* or the native *C. berlandieri*. We counted this *Chenopodium* as a native species in our analysis.

The patterns of distribution of individual exotic species varied with elevation (Fig. 4). *Taraxacum officinale* was the only exotic species we encountered frequently enough (37% of belts) to analyze its individual abundance. *T. officinale* was more abundant on plots high in abundance of both exotic and native species (exotic abundance: $r = 0.56$, $P < 0.01$; native abundance: $r = 0.33$, $P < 0.01$) and was positively correlated with exotic species richness and native species richness (exotic richness: $r = 0.58$, $P <$

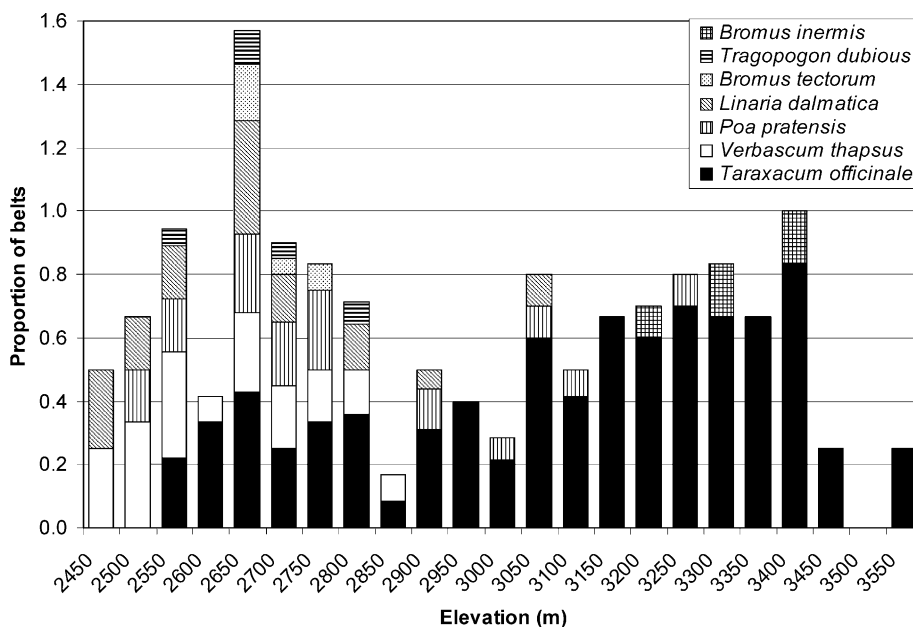


Fig. 4. Proportion of belt plots with each exotic species. Only species which were found on >1% of plots are shown.

0.01; native richness: $r = 0.32$, $P < 0.01$). Plots with little canopy cover also had more *T. officinale* ($r = -0.24$, $P = 0.01$). *T. officinale* was the most common (or only) exotic species in the higher elevation sites (Fig. 4). Excluding *T. officinale* from exotic species richness resulted in a larger negative correlation with elevation (excluding *T. officinale*: $r = -0.34$, $P < 0.01$; including *T. officinale*: $r = -0.19$, $P = 0.04$).

Nine native species were indicators for plots with exotic species and six native species indicated plots without exotics (Table 3). Abundance of indicator species for plots with exotic species was positively

correlated with native species richness and abundance as well as exotic species richness and abundance (Table 4).

4.3. Arbuscular mycorrhizal colonization

A total of 135 soil samples were collected: 14 in ponderosa pine, 33 in mixed conifer, 59 in aspen, 10 in spruce/fir, and 19 in bristlecone pine forest. We sampled soil under eight species of plants: the C_3 grasses *Bromus* spp., *Elymus elymoides*, *Festuca arizonica*, *Pascopyrum smithii*, and *Poa fendleriana*, and

Table 3
Indicator species for plots with and without exotic species

Plots with exotics			Plots with no exotics		
Species	IV	P	Species	IV	P
<i>Poa fendleriana</i>	52.8	<0.01	<i>Populus tremuloides</i>	46.9	<0.01
<i>Arenaria lanuginosa</i> ssp. <i>saxosa</i>	50.5	<0.01	<i>Pteridium aquilinum</i>	43.5	0.03
<i>Muhlenbergia Montana</i>	50.3	0.03	<i>Mahonia repens</i>	39.6	<0.01
<i>Festuca arizonica</i>	48.7	0.05	<i>Pseudotsuga menziesii</i>	36.9	0.03
<i>Pseudocymopterus montanus</i>	41.8	0.01	<i>Thalictrum fendleri</i>	35.5	0.02
<i>Agoseris glauca</i>	36.9	<0.01	<i>Corallorrhiza maculata</i>	32.1	<0.01
<i>Achillea millefolium</i>	32.8	<0.01			
<i>Hymenoxys hoopesii</i>	29.5	<0.01			
<i>Potentilla</i> spp.	28.2	<0.01			

IV is the indicator value. A perfect indicator value would be 100.

Table 4
Correlations with indicator species for plots with and without exotic species

	Species	Exotic abundance		Exotic richness		Native abundance		Native richness	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Plots with exotics	<i>Achillea millefolium</i>	0.54	<0.01	0.50	<0.01	0.47	<0.01	0.26	<0.01
	<i>Arenaria lanuginosa</i> ssp. <i>saxosa</i>		ns		ns		ns	0.24	0.01
	<i>Festuca arizonica</i>	0.44	<0.01	0.51	<0.01	0.66	<0.01	0.28	<0.01
	<i>Muhlenbergia montana</i>	0.24	0.01	0.58	<0.01	0.38	<0.01	0.48	<0.01
	<i>Poa fendleriana</i>	0.35	<0.01	0.46	<0.01	0.52	<0.01	0.38	<0.01
No exotics	<i>Pseudocymopterus montanus</i>	0.60	<0.01	0.30	<0.01	0.49	<0.01		ns
	<i>Mahonia repens</i>		ns	−0.23	0.01		ns		ns
	<i>Populus tremuloides</i>		ns		ns	0.41		<0.01	ns
	<i>Pteridium aquilinum</i>	0.26	<0.01		ns		ns	0.59	<0.01

No significant correlation is indicated by “ns”.

the C₄ grasses *Blepharoneuron tricholepis*, *Muhlenbergia montana*, and *M. virescens*. Only two samples were collected under *Pascopyrum smithii* and three under *Blepharoneuron tricholepis*. This was insufficient to provide an adequate idea of the variation within those species, so they were not included in the analysis by species.

Plots with high understory plant abundance had higher AM fungal colonization (Table 1), although this accounted for only a small amount of the variability (regression, $F_{(1, 134)} = 4.87$, $P = 0.03$, $r^2 = 0.04$). Percentage AM fungal colonization was positively associated with high species richness and low basal area (species richness: $r = 0.18$, $P = 0.04$; basal area: $r = -0.20$, $P = 0.02$). Neither the richness nor abundance of exotic species was related to AM colonization. AM fungal colonization and non-AM fungal colonization were also positively correlated ($r = 0.40$, $P < 0.01$). Root biomass available as inoculant was not related to percent AM colonization.

AM colonization differed based on the grass it was collected under (ANOVA $F_{(5, 124)} = 2.90$, $P = 0.02$). AM colonization was highest in corn plants grown in soil from under *Muhlenbergia virescens* ($38.4 \pm 11.8\%$). This was 240% higher than AM colonization of corn grown in *Bromus* spp. soil ($16.1 \pm 1.9\%$) and 300% higher than corn grown in *Poa fendleriana* soil ($12.8 \pm 2.5\%$).

Bromus spp., *M. montana*, and *F. arizonica* were the only three grass species under which we collected more than ten soil samples (23, 39, and 49 samples,

respectively). Soil samples from under each of these species spanned an elevation range greater than 850 m and were occurred in all five forest types. In soil collected under *M. montana*, AM colonization increased with elevation (regression, $F_{(1, 37)} = 7.37$, $P = 0.01$, $r^2 = 0.17$). AM colonization did not change with elevation from soil collected under *Bromus* spp., *F. arizonica*, or when soil samples were not separated by grass species.

5. Discussion

5.1. Plant community differences

Our hypothesis that species richness would differ between forest types was supported, although it did not follow the pattern that we expected. Brown (1994) claimed that the richness of the aspen understory is an important wildlife resource; therefore, we expected that aspen forest would have the highest species richness. We also expected an overall decrease in species richness with elevation. Instead we found that aspen forest had the lowest species richness and species richness was low in the middle elevations and high in ponderosa and bristlecone pine forest, the highest and lowest elevation forests. The low canopy cover in bristlecone and ponderosa pine forest may explain the high species richness, as species richness was negatively correlated with canopy cover. In 1876, as reconstructed by Cocke (2004), 15% of the

current ponderosa pine forest plots were nearly unfor-ested, with total tree basal areas less than 3 m²/ha. The current high species richness in ponderosa pine forest may be a relict from when these plots were less forested. However, there have also been substantial increases in the basal area of current aspen plots over the past century (Cocke, 2004), but aspen plots had the lowest species richness.

The pattern of high species richness in the low and high elevation forest, with lower species richness in the middle elevations was also reported by Allen et al. (1991) in the southern Rocky Mountains. Although the plot size in their study was similar to ours, their overall species richness was between 5% and 65% larger than what we found on the San Francisco Peaks. The isolation of the high elevation forest on the Peaks may explain the discrepancy. However, Allen et al. (1991) also reported a positive correlation between species richness and site moisture. Average yearly precipitation in northern Arizona (56 cm) is similar to that at their wettest site (Rocky Mountain National Park, 53 cm). However, we sampled during 2000–2003, when precipitation throughout the Southwest averaged 5.1 cm/year below normal (Lawrimore, 2004). Allen et al. (1991) sampled during 1985–1986, when precipitation was 5.8 and 8.0 cm above normal, respectively (Lawrimore, 2004). The drought may have resulted in low species richness in our study area, as it has in other parts of the Southwest (Fulé et al., 2002).

Although we found differences in species richness, we did not find differences in Shannon's H' diversity index, which accounts for how evenly abundance is distributed among species as well the number of species present. The lack of difference in Shannon's H' may indicate abundance was more evenly distributed among all species in the plots with low species richness. Alternatively, methodological problems may have obscured differences in diversity between forest types. The point-line intercept method tends to underestimate species richness and overestimate cover, compared to quadrat methods (Korb et al., 2003a). As a consequence, any species diversity index calculated from point-line intercept data should be low. We believe comparisons based on the point-line intercept method are still valuable because Korb et al. (2003a) showed that the error was fairly consistent over a wide range of plant abundance. Therefore comparisons of

both species diversity and cover should still reflect differences between forest types.

We confirmed our hypothesis that plant abundance differed between forest types and was highest in aspen forest. Abundance of herbaceous plants could be higher in aspen forest because aspen litter is more nutritious than acidic, low-nitrogen conifer litter (Fisher and Binkley, 2000). The extra light available in the spring before aspen leaves emerge could also be important to understory plants.

Species composition differed between forest types with ecological links between indicator species and historical patterns of disturbance regime and forest structure. Our results agree with Naumburg and DeWald (1999) who found species composition was related to disturbance history.

Ponderosa pine forests are adapted to a fire regime of frequent low-intensity fire, associated with historically open, grassy stands (Cooper, 1960; Swetnam and Baisan, 2003). *Astragalus rusbyi*, *Ceanothus fendleri*, *Cirsium* spp., *Elymus elymoides*, *Lupinus* spp., *Muhlenbergia montana*, and *Verbascum thapsus*, all indicator species for ponderosa pine forest, are well-adapted to surviving or recolonizing after fire (Walsh, 1995; Simonin, 2001; Beier and Maschinski, 2003; Hull-Sieg et al., 2003; Korb and Springer, 2003). Four ponderosa pine indicators, *Antennaria parviflora*, *Elymus elymoides*, *Festuca arizonica* and *Muhlenbergia montana*, grow poorly in shaded conditions (Matthews, 1993; Walsh, 1995; Naumburg and DeWald, 1999; Naumburg et al., 2001; Simonin, 2001). Ponderosa pine was also characterized by high diversity of nitrogen fixing species, although they were not necessarily abundant. Six of the 14 ponderosa pine indicator species were nitrogen fixers (*Astragalus humistratus*, *A. rusbyi*, *Ceanothus fendleri*, *Lotus* spp., *Lupinus* spp., and *Oxytropis lambertii*). Both NH_4^+ and NO_3^- are lower in ponderosa pine forests than most other forest types and may be more limiting than in other forest types (Stark and Hart, 1997).

Despite ponderosa pine and mixed conifer forest being adjacent to each other in elevation and similar in historical fire regime (Heinlein, 1996), there was little overlap in species composition between the two forest types (Fig. 2). Three of the four mixed conifer indicator species are adapted to surviving either with or without fire. *Holodiscus dumosus* colonizes disturbed and burned areas well, but is also considered indicative

of late seral communities (McMurray, 1987). *Mahonia repens* can survive fire and exists in both shade and full sun, although in our study it was encountered more frequently in more shaded areas (Walkup, 1991). *Pteridium aquilinum* requires fire for regeneration by spores, but more often regenerates vegetatively (Crane, 1990).

We found no indicator species for aspen forest. However, there were correlations between *Populus tremuloides* and abundance of nitrogen fixing plants. In particular, two legumes, *Lathyrus lanszwertii* var. *leucanthus* and *Lathyrus* or *Vicia* spp., were between 2 and 25 times more abundant on aspen plots than in other forest types. However, both species were found on 85% of all plots and one or both of them were among the most common species encountered in all five forest types (Table 1). We used the presence or absence of species to determine indicator species, so a species that is present in a variety of forest types, but notably abundant in one, would not emerge in the analysis.

Basal area in spruce/fir forest is more than 20% greater than any other forest type on the San Francisco Peaks (Cocke, 2004). The two indicators for spruce/fir forest are both taxa commonly associated with moist, shady areas. Neither indicator species disperses widely, consistent with a stand-replacing fire regime in spruce/fir. The widest variation in species composition occurred in spruce/fir forest (Fig. 2). This may be because of variation in species composition between the dense stands of trees that characterize spruce/fir forest, and unforested openings where most herbaceous species are concentrated (Brown, 1994).

We were surprised by the number of shared characteristics between bristlecone pine forest and ponderosa pine forest. Some bristlecone pine plots were more similar to ponderosa pine plots than spruce/fir plots; even though mean elevation in spruce/fir and bristlecone pine forest differs by only 84 m (Fig. 2). Bristlecone and ponderosa pine forests were high in species richness and low in canopy cover. Mean species richness in these two forest types was 30.9 ± 0.9 , compared to 25.0 ± 0.8 in all other forest types. Canopy cover for bristlecone and ponderosa pine forest was $45.9 \pm 2.9\%$, but $66.3 \pm 1.9\%$ in all other forest types. They were also the only forest types that had grasses as indicator species. Germination of one bristlecone pine indicator, *Ribes montigenum*, is

thought to be enhanced by low-intensity fire (Marshall, 1995). Bristlecone pine forest differed from ponderosa pine forest in having a high density of shrubs and low richness of N-fixing species. Soil cover was seven times greater in bristlecone pine forest than in any other forest type. One bristlecone pine indicator, *Penstemon whippleanus*, was associated with a high occurrence of bare soil.

Bristlecone pine indicator species on the San Francisco Peaks were similar to species associated with *Pinus aristata* in the Rocky Mountains. Both *Penstemon whippleanus* and *Festuca ovina* were common in one of the six bristlecone pine associations identified by Ranne et al. (1997) and *Ribes montigenum* was common in two. In addition, both studies found species of *Erigeron* and *Mertensia* were indicative of bristlecone pine forest.

The mycorrhizal dependencies of the great majority of the species encountered in this study have been poorly documented, so we made no attempt to create a list of mycorrhizal/non-mycorrhizal status. However, at least two of the most common taxa (Table 1: *Carex* spp. and *Lupinus* spp.) and several indicator species (Table 2: *Lupinus* spp., *Verbascum thapsus*, *Pyrola* spp.) are widely considered non-mycorrhizal.

5.2. Exotics and susceptibility to invasion

The most invaded communities were the ones with the highest native species richness and abundance, contradicting our hypothesis. This was supported by univariate correlations, multivariate ordinations and correlations between indicator species for plots with exotic species with native species richness and abundance (Table 4). Theory, supported by greenhouse experiments, predicts that high biodiversity areas should more completely use available resources, making them more resistant to invasion by new species (Naeem et al., 2000). However, observational studies often show greater richness or abundance of exotic species in areas with higher native species richness (Stohlgren et al., 1999, 2001). Site characteristics, such as water availability and soil fertility, usually vary in observational studies but are held constant in experiments and may account for the discrepancy (Naeem et al., 2000).

Our hypothesis of lower exotic species richness in higher elevations was confirmed although exotic spe-

cies abundance did not vary with elevation. This suggests exotic species do not face barriers to growth, but may face barriers to dispersal. Roads, campgrounds, and livestock grazing can facilitate invasion by providing a dispersal vector into an area (Knapp, 1996; Allen and Hansen, 1999). However, since the exotic species most frequently encountered in high elevations, *Taraxacum officinale*, has wind dispersed seeds, disturbance should minimally influence its spread.

Alternatively, high-elevation forests on the San Francisco Peaks may have experienced relatively little invasion because seed sources for exotic species well-adapted to boreal forest are not available due to the rarity of this forest type in the Southwest. Stohlgren et al. (2000) hypothesized low temperatures limited exotic species in the higher elevations of Rocky Mountain National Park. Even though successful invaders often have wide ecological tolerances or can adapt quickly to new conditions (Bazzaz, 1986; Parker et al., 2003), generalist species have ecological limits. Species such as *Bromus tectorum*, *Linaria dalmatica*, and *Verbascum thapsus* that are known invaders of lower elevation ecosystems may have encountered ecological limitations above ponderosa pine forest (Knapp, 1996; Jacobs and Sheley, 2003; Parker et al., 2003).

Exotic species do not yet appear to be a major portion of the plant community on the San Francisco Peaks. On average, exotic species accounted for only $3.5 \pm 3.8\%$ of the total species richness per plot and $0.5 \pm 1.2\%$ of the total plant abundance per plot. Exotic species never composed more than 14.3% of the species richness and 6.0% of the abundance. No exotic species were found on 40% of plots and exotic species were not abundant enough to be detected on the point-line transect of an additional 37%. However, plant species composition on plots with exotic species differed from those which had none. Unfortunately, our study design does not allow us to distinguish whether exotic species change the plant community as whole or whether some plant communities are more easily invaded than others.

It is important to identify which exotic species may pose future threats to native vegetation (Parker et al., 1999). We believe *Linaria dalmatica* has the most invasive potential because it is already known to be noxious in this area, responds positively to fire, and

seeds are still viable after relatively long-term storage (Jacobs and Sheley, 2003; Zouhar, 2003b). *Verbascum thapsus* is a noxious weed in Arizona, frequently encountered in burned areas (Crawford et al., 2001), but it declines in the absence of recurring soil disturbance (Hull-Sieg et al., 2003). *Taraxacum officinale* has been assumed to be a poor competitor with later seral plants (Esser, 1993). However, our results agree with others who found *T. officinale* is able to invade previously undisturbed areas (Weaver et al., 1990).

Although *Bromus inermis*, *Poa compressa* and *P. pratensis* are not listed as noxious weeds in Arizona, exotic grasses, such as *P. pratensis*, can be the most commonly encountered exotic species (Weaver et al., 1990, 2001; Hull-Sieg et al., 2003). In particular, *P. pratensis* was the second most widely distributed exotic species in our study. *Bromus tectorum* has altered many areas of sagebrush steppe so it can no longer support native plant communities (Knapp, 1996; Zouhar, 2003a). *B. tectorum* does not grow well under low-light conditions or under a large organic layer, making it a less severe a threat to forest vegetation (Pierson and Mack, 1990; Pierson et al., 1990). However, it is well-adapted to fire and other disturbances (Knapp, 1996; Zouhar, 2003a).

5.3. Arbuscular mycorrhizal colonization

Levels of AM inoculum potential that we found are consistent with other studies with corn bioassays in coniferous forest, though this may be a coarse comparison because of differences in AM species composition and methodologies. Gildar et al. (2004) and Korb et al. (2003b) reported AM inoculum potential in ponderosa pine forest varied between 6–24% and 18–45%, respectively, depending on the fire history and tree density. Although AM inoculum potential has been assumed low in forests where trees do not associate with AM fungi (Newman and Reddell, 1988), our corn bioassay results report inoculum potentials comparable to those found in other ecosystems. For example, Johnson et al. (1991) recorded AM inoculum potential in a prairie varied between 1% and 20%, while Gehring et al. (2002) reported AM inoculum potential of between 12% and 19% in a tropical rainforest.

Our hypothesis of negative correlation between AM colonization and basal area was supported, agree-

ing with findings of researchers in other forest types (Benjamin et al., 1989; Johnson et al., 1991). Benjamin et al. (1989) hypothesized AM colonization was low under forest canopy due to inhibition from the ectomycorrhizal fungi colonizing tree roots. Newman and Reddell (1988) used a similar explanation to account for a positive correlation between herbaceous species richness and the abundance of trees capable of associating with AM fungi. If this were true, we would expect AM colonization to be highest in aspen-dominated plots because aspen can form associations with both AM and ectomycorrhizae, while most coniferous trees can only form associations with ectomycorrhizae (Trappe, 1962; Mosse et al., 1981; Neville et al., 2002). Our results did not support this theory because AM colonization was no higher in aspen forest than in any other forest type.

Our results showing that plots with high AM colonization also tended to have high species richness agree with a number of other researchers' findings, though some previous studies compared mycorrhizal presence/absence rather than mycorrhizal abundance (Grime et al., 1987; Newman and Reddell, 1988; Moora and Zobel, 1996). However, there were no correlations between AM inoculum and exotic species richness or abundance. In some cases AM fungi may encourage the establishment of native over exotic species (Reeves et al., 1979; Korb, 2001). However, this may vary depending on the specific exotic species in question, the native species with which it interacts, and the mycorrhizal dependency of both species (Knapp, 1996; Marler et al., 1999).

Changes in AM fungi across landscape gradients are a fertile area of study (Reynolds et al., 2003), but we suspect AM colonization levels are affected by microsite differences that were not adequately addressed in a study of this scale. Percent AM colonization varied with the plant the soil was taken under, consistent with the host species effect noted by Eom et al. (2000). Canopy cover, tree basal area, soil nutrients, soil moisture, and ecotypes within species also affect the AM community (Anderson et al., 1984, 1994; Benjamin et al., 1989; Johnson et al., 1991; Schultz et al., 2001). Changes in elevation are necessarily tied with changes in soil moisture, temperature, slope, tree stand structure, vegetation and soil nutrients (Austin, 1999). Important differences in AM inoculum potential may have been lost in these inter-

acting variables. For example, we only found an increase in AM colonization with elevation when we exclusively compared samples collected under *Muhlenbergia montana*. Future studies comparing AM fungi across landscape level gradients would also be improved by examining AM species composition (van der Heijden et al., 1998a; Klironomos, 2003).

5.4. Community change

Communities are stable over a range of environmental conditions, but can rapidly change toward a new steady state if threshold conditions are exceeded (Gosz, 1992). Ecosystem stability is increased by the presence of many functional groups (Naeem et al., 1999). The richness of the functional groups that we identified did not vary across forest types. Having several species within a functional group can be important for the resilience of that community as environmental conditions change (Walker, 1995; Naeem, 1998; Walker et al., 1999). N-fixing plants in ponderosa pine forest are species rich, which could help preserve the functioning of the community as climate changes. Only two leguminous taxa, *Lathyrus lanszwertii* var. *leucanthus* and *Lathyrus* or *Vicia* spp., were found in all other forest types on the San Francisco Peaks. Since these two species are common in all forest types, they appear to have broad ecological tolerances (Table 1). If these species encounter problems migrating under changing climate, however, the missing functional group could result in ecosystem failure (Naeem, 1998).

Perry et al. (1990) suggested low abundance of AM fungi in coniferous forests could hinder migration of plants that associate chiefly with AM fungi. Our research showed AM inoculum is present in forests and should be available to facilitate species migrations. However, changes associated with climate change such as elevated CO₂, increasing temperatures, and decreased water availability may affect the colonization abilities of AM fungi (Monz et al., 1994).

The indicator species that we identified may be valuable in monitoring changes throughout the San Francisco Peaks. Five indicator species were found in many forest types, but most reliably in one forest type, making them faithful but not exclusive indicators. They were *Elymus elymoides*, *Festuca arizonica*, *Lupinus* spp., and *Muhlenbergia montana* from ponderosa pine forest and *Pteridium aquilinum* from

mixed conifer forest. Species, such as these, whose habitat extends into ecotones might be better able to migrate under changing climatic conditions (Stohlgren et al., 2000). The remaining indicator species are more limited to the forest type in which they are indicators, but are not reliably found on every example of that forest type. Since this later group of indicator species are restricted to one forest type, they could be useful in monitoring the health of specific Arizona forest types (Carignan and Villard, 2002). Several non-indicator species were common in multiple forest types and could be predisposed to being successful migrants (Malcolm et al., 2002). *Arenaria lanuginosa* ssp. *saxosa*, *Lathyrus lanszwertii* var. *leucanthus*, *Poa fendleriana*, *Pseudocymopterus montanus*, and *Senecio eremophilus* were found in all five forest types and were found on more than 20 belts in three or more forest types. *Frasera speciosa*, *Maianthemum stellatum*, and *Penstemon barbatus* were found in all five forest types and were found on more than 10 belts in two or more forest types.

Acknowledgements

Thanks to the Rocky Mountain Research Station (U.S. Department of Agriculture), especially Dr. Carl Edminster and Sheila Sandusky, and the Bureau of Land Management (U.S. Department of Interior) for funding. The comments of Margaret Moore, Catherine Gehring, Nancy Johnson, and two anonymous reviewers were valuable. We are also grateful to the hardworking and dedicated staff and students of the Ecological Restoration Institute. The Coconino National Forest and Arizona Snowbowl provided logistical assistance.

References

- Anon, 1995. Terrestrial Ecosystems Survey of the Coconino National Forest, United States Department of Agriculture, Forest Service, Southwestern Region, Albuquerque, NM.
- Anon, 2003. Western Regional Climate Center. <http://www.wrcc.dri.edu/index.html>. Accessed 3/4/2004
- Ahlenslager, K., 1987. *Pinus aristata*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/tree/pinari/index.html>. Accessed 5/1/2002.
- Aitchison, S.W., 1989. Wilderness areas of the Colorado Plateau. Plateau 60 [4]. Museum of Northern Arizona, Flagstaff, AZ.
- Allen, E.B., Allen, M.F., 1990. The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace, J.B., Tilman, D. (Eds.), *Perspectives on Plant Competition*, Academic Press, Inc, San Diego, pp. 367–389.
- Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J.M., Molina, R., Rincon, E., 1995. Patterns and regulation of mycorrhizal plant and fungal diversity. In: Collins, H.P., Robertson, G.P., Klug, M.J. (Eds.), *The Significance and Regulation of Soil Biodiversity*, Kluwer Academic Publishers, Netherlands, pp. 47–62.
- Allen, K., Hansen, K., 1999. Geography of exotic plants adjacent to campgrounds, Yellowstone National Park. *USA Great Basin Nat.* 59, 315–322.
- Allen, R.B., Peet, R.K., Baker, W.L., 1991. Gradient analysis of latitudinal variation in southern Rocky Mountain forests. *J. Biogeogr.* 18, 123–139.
- Anderson, R.C., Hetrick, B.A.D., Wilson, G.W.T., 1994. Mycorrhizal dependence of *Andropogon gerardii* and *Schizachyrium scoparium* in two prairie soils. *Am. Midl. Nat.* 132, 366–376.
- Anderson, R.C., Liberta, A.E., Dickman, L.A., 1984. Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisture–nutrient gradient. *Oecologia* 64, 111–117.
- Auerbach, M., Shimda, A., 1993. Vegetation change along an altitudinal gradient of Mt. Hermon, Israel—no evidence for discrete communities. *J. Ecol.* 81, 25–33.
- Austin, M.P., 1999. The potential contribution of vegetation ecology to biodiversity research. *Ecography* 22, 465–484.
- Bazzaz, F.A., 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. In: Mooney, H.A., Drake, J.A. (Eds.), *Ecology of Biological Invasions of North America and Hawaii*, Springer-Verlag, New York, pp. 96–110.
- Beier, P., Maschinski, J., 2003. Threatened, endangered, and sensitive species. In: Friederici, P. (Ed.), *Ecological Restoration of Southwestern Ponderosa Pine Forests*, Island Press, Washington, DC, pp. 306–327.
- Benjamin, P.K., Anderson, R.C., Liberta, A.E., 1989. Vesicular-arbuscular mycorrhizal ecology of little bluestem across a prairie-forest gradient. *Can. J. Bot.* 67, 2678–2685.
- Bever, J.D., Morton, J.B., Antonovics, J., Schultz, P.A., 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *J. Ecol.* 84, 71–82.
- Brown, D.E., 1994. *Biotic Communities of the Southwestern United States and Northwestern Mexico*, University of Utah Press, Salt Lake City.
- Brunstein, F.C., Yamaguchi, D.K., 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.). *Arctic Alpine Res.* 24, 253–256.
- Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112, 143–149.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848.

- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Carignan, V., Villard, M.-A., 2002. Selecting indicator species to monitor ecological integrity: a review. *Environ. Monit. Assess.* 78, 45–61.
- Choler, P., Michalet, R., Callaway, R.M., 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82, 3295–3308.
- Clements, F.E., 1916. *Plant Succession: An Analysis of the Development of Vegetation*, Carnegie Institution of Washington, Washington, DC.
- Cline, P., 1994. *Mountain Town: Flagstaff's First Century*, Northland Publishing Co, Flagstaff, AZ.
- Cocke, A., 2004. *Fire Exclusion and Burn Severity on the San Francisco Peaks*, Northern Arizona University, Arizona.
- Collins, S.L., Glenn, S.M., Roberts, D.W., 1993. The hierarchical continuum concept. *J. Veg. Sci.* 4, 149–156.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* 30, 129–164.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- Crane, M.F., 1990. *Pteridium aquilinum*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/fern/pteaqu/index.html>. Accessed 12/17/2003.
- Crawford, J.A., Wahren, C.-H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *J. Veg. Sci.* 12, 261–267.
- Eom, A.-H., Hartnett, D.C., Wilson, G.W.T., 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. *Oecologia* 122, 435–444.
- Esser, L.L., 1993. *Taraxacum officinale*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/forb/taroff/index.html>. Accessed 11/8/2003.
- Fisher, R.F., Binkley, D., 2000. *Ecology and Management of Forest Soils*, John Wiley and Sons Inc, New York.
- Fulé, P.Z., Covington, W.W., Smith, H.B., Springer, J.D., Heinlein, T.A., Huisinga, K.D., Moore, M.M., 2002. Comparing ecological restoration alternatives Grand Canyon, Arizona. *For. Ecol. Manage.* 170, 19–41.
- Gange, A.C., Brown, V.K., Sinclair, G.S., 1993. Vesicular-arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. *Funct. Ecol.* 7, 616–622.
- Gehring, C.A., Wolf, J.E., Theimer, T.C., 2002. Terrestrial vertebrates promote arbuscular mycorrhizal fungal diversity and inoculum potential in a rain forest soil. *Ecol. Lett.* 5, 540–548.
- Gildard, C.N., Fulé, P.Z., Covington, W.W., 2004. Plant community variability in ponderosa pine forest has implications for reference conditions. *Nat. Areas J.* 24, 101–111.
- Gleason, H.A., 1926. The individualistic concept of the plant association. *B. Torrey Bot. Club.* 53, 7–26.
- Gosz, J.R., 1992. Gradient analysis of ecological change in time and space: implications for forest management. *Ecol. Appl.* 2, 248–261.
- Grime, J.P., Mackey, J.M.L., Hillier, S.H., Read, D.J., 1987. Floristic diversity in a model system using experimental microcosms. *Nature* 328, 420–422.
- Harmon, M.E., Bratton, S.P., White, P.S., 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio* 55, 129–139.
- Hart, M.M., Reader, R.J., Klironomos, J.N., 2003. Plant coexistence mediated by arbuscular mycorrhizal fungi. *Trends Ecol. Evol.* 18, 418–423.
- Hartnett, D.C., Wilson, G.W.T., 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80, 1187–1195.
- Heinlein, T.A., 1996. *Fire Regimes and Forest Structure in Lower Mixed Conifer Forests: San Francisco Peaks Arizona*, Northern Arizona University, Flagstaff, AZ.
- Hoagland, B.W., Collins, S.L., 1997. Gradient models, gradient analysis, and hierarchical structure in plant communities. *Oikos* 78, 23–30.
- Hull-Sieg, C., Phillips, B.G., Moser, L.P., 2003. Exotic Invasive Plants. In: Friederici, P. (Ed.), *Ecological Restoration of Southwestern Ponderosa Pine Forests*, Island Press, Washington, DC, pp. 251–267.
- Jacobs, J.J., Sheley, R.L., 2003. Prescribed fire effects on dalmatian toadflax. *J. Range Manage.* 56, 193–197.
- Johnson, N.C., Graham, J.H., Smith, F.A., 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* 135, 575–585.
- Johnson, N.C., O'Dell, T.E., Bledsoe, C.S., 1999. Methods for ecological studies of mycorrhizae. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollin, P. (Eds.), *Standard Soil Methods for Long-Term Ecological Research*, Oxford University Press, New York, pp. 378–412.
- Johnson, N.C., Zak, D.R., Tilman, D., Pflieger, F.L., 1991. Dynamics of vesicular-arbuscular mycorrhizae during old field succession. *Oecologia* 86, 349–358.
- Kay, C.E., 1997. The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: implications for ecological integrity. *Can. Field Nat.* 111, 607–616.
- Keane, R.E., Ryan, K.C., Veblen, T.T., Allen, C.D., Logan, J., Hawkes, B., 2002. Cascading Effects of Fire Exclusion in Rocky Mountain Ecosystems: A Literature Review. United States Department of Agriculture, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-96, Ft. Collins, CO.
- Klironomos, J.N., 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84, 2292–2301.
- Klironomos, J.N., Hart, M., 2002. Colonization of roots by arbuscular mycorrhizal fungi using different sources of inoculum. *Mycorrhiza* 12, 181–184.
- Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. *Global Environ. Chang.* 6, 37–52.
- Korb, J.E., 2001. Understory Plant Community Dynamics in Southwestern Ponderosa Pine Forest Restoration, Northern Arizona University, Flagstaff, AZ.

- Korb, J.E., Covington, W.W., Fulé, P.Z., 2003a. Sampling techniques influence understory plant trajectories after restoration: an example from ponderosa pine restoration. *Restor. Ecol.* 11, 504–515.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2003b. Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments. *J. Appl. Ecol.* 40, 101–110.
- Korb, J.E., Springer, J.D., 2003. Understorey Vegetation. In: Friederici, P. (Ed.), *Ecological Restoration of Southwestern Ponderosa Pine Forests*, Island Press, Washington, DC, pp. 233–250.
- Kovacic, D.A., St. John, T.V., Dyer, M.I., 1984. Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine forest. *Ecology* 65, 1755–1759.
- Lawrimore, J., 2004. National Climatic Data Center-U.S. Regional Analysis. <http://www.ncdc.noaa.gov/oa/climate/research/cag3/regional.html>. Accessed 1/20/2004.
- Malcolm, J.R., Markham, A., Neilson, R.P., Garaci, M., 2002. Estimated migration rates under scenarios of global climate change. *J. Biogeogr.* 29, 835–849.
- Marler, M.J., Zabinski, C.A., Callaway, R.M., 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* 80, 1180–1186.
- Marshall, K.A., 1995. *Ribes montigenum*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/shrub/ribmon/index.html>. Accessed 1/28/2004.
- Mathews, R.F., 1993. *Antennaria parviflora*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/forb/antpar/index.html>. Accessed 12/17/2003.
- McCune, B., Mefford, M.J., 1999. PC-Ord for Windows, MjM Software, Gleneden Beach, OR.
- McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities, MjM Software Design, Gleneden Beach, OR.
- McMurray, N.E., 1987. *Holodiscus dumosus*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/shrub/holdum/index.html>. Accessed 12/17/2003.
- McNaughton, S.J., Oesterheld, M., 1990. Extramatrix mycorrhizal abundance and grass nutrition in a tropical grazing ecosystem, the Serengeti National Park, Tanzania. *Oikos* 59, 92–96.
- Merriam, C.H., 1890. Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado Arizona. U.S. Government Printing Office, Washington, DC.
- Monz, C.A., Hunt, H.W., Reeves, F.B., Elliott, E.T., 1994. The response of mycorrhizal colonization to elevated CO₂ and climate change in *Pascopyrum smithii* and *Bouteloua gracilis*. *Plant Soil* 165, 75–80.
- Moora, M., Zobel, M., 1996. Effect of arbuscular mycorrhizae on inter- and intraspecific competition of two grassland species. *Oecologia* 108, 79–84.
- Mosse, B., Stribley, D.P., LeTacon, F., 1981. Ecology of mycorrhizae and mycorrhizal fungi. In: Alexander, M. (Ed.), *Advances in Microbial Ecology*, Plenum Press, New York, pp. 137–210.
- Naeem, S., 1998. Species redundancy and ecosystem reliability. *Conserv. Biol.* 12, 39–45.
- Naeem, S., Knops, J.M., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91, 97–108.
- Naeem, S., Tjossem, S.F., Byers, D., Bristow, C., Li, S., 1999. Plant neighborhood diversity and production. *Ecoscience* 6, 355–365.
- National Park Service, 1992. Western Region Fire Monitoring Handbook. San Francisco, CA.
- Naumburg, E., DeWald, L.E., 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presences and abundance. *For. Ecol. Manage.* 124, 205–215.
- Naumburg, E., DeWald, L.E., Kolb, T.E., 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. *Can. J. Bot.* 79, 1001–1009.
- Neville, J., Tessier, J.L., Morrison, I., Scarratt, J., Canning, B., Klironomos, J.N., 2002. Soil depth distribution of ecto- and arbuscular mycorrhizal fungi associated with *Populus tremuloides* within a 3-year-old boreal forest clear-cut. *Appl. Soil Ecol.* 19, 209–216.
- Newman, E.I., Reddell, P., 1988. Relationship between mycorrhizal infection and diversity in vegetation: evidence from the Great Smoky Mountains. *Funct. Ecol.* 2, 259–262.
- Newsham, K.K., Fitter, A.H., Watkinson, A.R., 1995. Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends Ecol. Evol.* 10, 407–411.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B.M.P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions* 1, 3–19.
- Parker, I.M., Rodriguez, J., Loik, M.E., 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and the general-purpose genotypes in the weed *Verbascum thapsus*. *Conserv. Biol.* 17, 59–72.
- Pearson, G.A., 1920. Factors controlling the distribution of forest types, Part I. *Ecology* 1, 139–159.
- Perry, D.A., Borchers, J.G., Borchers, S.L., Amaranthus, M.P., 1990. Species migrations and ecosystem stability during climate change: the belowground connection. *Conserv. Biol.* 4, 266–274.
- Pierson, E., Mack, R.N., 1990. The population biology of *Bromus tectorum* in forests: effect of disturbance, grazing, and litter on seedling establishment and reproduction. *Oecologia* 84, 526–533.
- Pierson, E., Mack, R.N., Black, R.A., 1990. The effect of shading on photosynthesis, growth, and regrowth following defoliation for *Bromus tectorum*. *Oecologia* 84, 534–543.
- Ranne, B.M., Baker, W.L., Andrews, T., Ryan, M.G., 1997. Natural variability of vegetation, soils, and physiography in the bristlecone pine forests of the Rocky Mountains. *Great Basin Nat.* 57, 21–37.
- Read, D.J., Haselwandter, K., 1981. Observations on the mycorrhizal status of some alpine plant communities. *New Phytol.* 88, 341–352.

- Reeves, F.B., Wagner, D., Moorman, T., Kiel, J., 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *Am. J. Bot.* 66, 6–13.
- Reynolds, H.L., Packer, A., Bever, J.D., Clay, K., 2003. Grassroots ecology: plant–microbe–soil interactions as drivers of plant community structure and dynamics. *Ecology* 84, 2281–2291.
- Rominger, J.M., Paulik, L.A., 1983. A floristic inventory of the plant communities of the San Francisco Peaks Research Natural Area. United States Department of Agriculture, Rocky Mountain Research Station, General Technical Report RMRS-GTR-91, Ft. Collins, CO.
- Sagers, C.L., Lyon, J., 1997. Gradient analysis in a riparian landscape: contrasts among forest layers. *For. Ecol. Manage.* 96, 13–26.
- Schaack, C.G., 1983. The alpine vascular flora of Arizona. *Madroño* 30, 79–88.
- Schultz, P.A., Miller, R.M., Jastrow, J.A., Rivetta, C.V., Bever, J.D., 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (Poaceae) to high- and low-nutrient prairies. *Am. J. Bot.* 88, 1650–1656.
- Shipley, B., Keddy, P.A., 1987. The individualistic and community-unit concepts as falsifiable hypotheses. *Vegetatio* 69, 47–55.
- Simonin, K.A., 2001. *Elymus elymoides*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/graminoid/elyely/index.html>. Accessed 12/17/2003.
- SPSS for Windows, 2002. SPSS Inc., Chicago, IL.
- Stark, J.M., Hart, S.C., 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385, 61–64.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., Son, Y., 1999. Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* 69, 25–46.
- Stohlgren, T.J., Otsuki, Y., Villa, C.A., Lee, M., Belnap, J., 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. *Biol. Invasions* 3, 37–51.
- Stohlgren, T.J., Owen, A.J., Lee, M., 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. *Biodivers. Conserv.* 9, 65–86.
- Swetnam, T.W., Baisan, C.H., 2003. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and Southwestern United States. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*, Springer-Verlag, New York, pp. 158–195.
- Taylor, A.H., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. *J. Biogeogr.* 27, 87–104.
- Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L., 1979. Snags. In: Parker, J.L. (Ed.), *Wildlife habitat in managed forests—the Blue Mountains of Oregon and Washington*, USDA Agricultural Handbook, Washington, DC, pp. 60–77.
- Trappe, J.M., 1962. Fungus associates of ectotrophic mycorrhizae. *Bot. Rev.* 28, 538–606.
- Turner, M.G., Romme, W.H., Reed, R.A., Tuskan, G.A., 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecol.* 18, 127–140.
- van der Heijden, M.G.A., Boller, T., Wiemken, A., Sanders, I.R., 1998a. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79, 2082–2091.
- van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998b. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396, 69–72.
- Walker, B., 1995. Conserving biological diversity through ecosystem resilience. *Conserv. Biol.* 9, 747–752.
- Walker, B., Kinzig, A., Langridge, J., 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113.
- Walkup, C.J., 1991. *Mahonia repens*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/shrub/mahrep/index.html>. Accessed 12/17/2003.
- Walsh, R.A., 1995. *Muhlenbergia montana*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/graminoid/muhmon/introductory.html>. Accessed 12/17/2003.
- Weaver, T., Gustafson, D., Lichthardt, J., 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). *West. N. Am. Naturalist* 61, 417–427.
- Weaver, T., Lichthardt, J., Gustafson, D., 1990. Exotic invasion of timberline vegetation, northern Rocky Mountains, USA. In: Wyman C. Schmidt, Kathy J. McDonald (Eds.), *Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource*, Ogden, UT. United States Department of Agriculture, Forest Service, Intermountain Research Station, pp. 208–213.
- Whittaker, R.H., 1965. Dominance and diversity in land plant communities. *Science* 147, 250–260.
- Whittaker, R.H., Niering, W.A., 1968. Vegetation of the Santa Catalina Mountains, Arizona. III. Species distribution and floristic relations on the north slope. *J. Ariz. Acad. Sci.* 5, 3–21.
- Wilson, G.W.T., Hartnett, D.C., 1997. Effects of mycorrhizae on plant growth and dynamics in experimental tallgrass prairie microcosms. *Am. J. Bot.* 84, 478–482.
- Wilson, G.W.T., Hartnett, D.C., 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. *Am. J. Bot.* 85, 1732–1738.
- Zouhar, K., 2003a. *Bromus tectorum*, Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/graminoid/brotec/index.html>. Accessed 3/25/1911a.
- Zouhar, K., 2003b. *Linaria* spp., Fire Effects Information System. Fire Sciences Laboratory, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <http://www.fs.fed.us/database/feis/plants/forb/linspp/index.html>. Accessed 11/25/2003b.