



United States
Department
of Agriculture

Forest Service

Rocky Mountain
Research Station

Research Note
RMRS-RN-39

February 2009



Tree Canopy Types Constrain Plant Distributions in Ponderosa Pine-Gambel Oak Forests, Northern Arizona

Scott R. Abella

Abstract—Trees in many forests affect the soils and plants below their canopies. In current high-density southwestern ponderosa pine (*Pinus ponderosa*) forests, managers have opportunities to enhance multiple ecosystem values by manipulating tree density, distribution, and canopy cover through tree thinning. I performed a study in northern Arizona ponderosa pine-Gambel oak (*Quercus gambelii*) forests to measure the influences of tree canopy types on understory plant communities and soil properties. On ten 2.5-acre (1-ha) sites, I sampled five 43-ft² (4-m²) plots below each of the following five canopy types: openings; single ponderosa pine; and Gambel oak single stems, dispersed clumps, and thickets. Soil properties, species richness, plant cover, and the distribution of cool- and warm-season grasses were canopy-type specific. Openings contained the most species/plot, three to eight times greater plant cover than any tree canopy type, and warm-season grasses (for example, purple threeawn [*Aristida purpurea*]) that were infrequent below trees. In contrast, aspen pea (*Lathyrus laetivirens*) and Fendler's meadow-rue (*Thalictrum fendleri*) were most frequent below Gambel oak canopies. There were no species that were most frequent below ponderosa pine. Results suggest that canopy openings need to be reestablished and maintained on this landscape if understories are to be productive, diverse, and contain species dependent on these microsites.

Introduction

Two of the main variables in forest ecosystems that managers can manipulate are tree density and within-site distributions of trees. In southwestern ponderosa pine (*Pinus ponderosa*) forests, where small-diameter pine densities have irrupted, there is ample opportunity to manipulate tree density and distribution by mechanically thinning trees (Covington and others 1997, Naumburg and DeWald 1999). Tree patterns resulting from thinning can affect soils, plant communities, and other ecosystem components (Scholes and Archer 1997). Trees affect soil moisture, nutrients, microclimates, and other environmental variables on forest floors below their canopies (Barth 1980; Moir 1966; Parker and Muller 1982). These effects have been termed single-tree influences, and some authors have proposed that forests consist of mosaics of single-tree influences (Boettcher and Kalisz 1990).

To manage for multiple ecosystem values, managers need to understand the ecological effects of passively or

actively managing within-site tree patterns. This requires shifting focus away from the trees themselves to the ecosystem components that trees influence. In ponderosa pine forests, these ecosystem components include canopy openings, understory vegetation, soils, wildlife, hydrology, and others (Covington and others 1997). I performed a study on a northern Arizona landscape to measure the influence of canopy openings and ponderosa pine and Gambel oak (*Quercus gambelii*) trees on understory vegetation and soil properties. I isolated the biotic influences of trees from potentially confounding effects of abiotic variables by holding soil parent material constant within sites, supported by analyses indicating that soil texture did not differ among canopy types. This study's results, combined with previous research, provide insight into how different tree densities and distributions created by thinning may influence soils and understory vegetation in pine-oak forests.

Methods

Study Area

I conducted this study on ten ponderosa pine-Gambel oak sites on the northern half of the Coconino National Forest and on the Northern Arizona University Centennial Forest surrounding the city of Flagstaff in northern Arizona. Sites were separated by an average of 14 miles (23 km), with a maximum site-to-site distance of 26 miles (42 km; table 1). I selected these sites because they

Abella, Scott R. 2009. **Tree canopy types constrain plant distributions in ponderosa pine-Gambel oak forests, northern Arizona.** Res. Note RMRS-RN-39. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 7 p.

Scott R. Abella is Research Specialist, Sr., Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ. Present address: Assistant Research Professor, Public Lands Institute and Department of Environmental Studies, University of Nevada Las Vegas, Las Vegas, NV.

Table 1—Study site characteristics in northern Arizona ponderosa pine-Gambel oak forests.

Site	Parent material	Texture ^b	Elevation (ft)	Location	Ponderosa pine		Gambel oak	
					Trees/ac	BA ^c ft ² /ac	Trees/ac	BA ft ² /ac
Turkey Hills – 513 ^a	Red volcanic cinders	Sandy loam	6819	35°14'N, 111°31'E	— ^d	—	—	—
Garjon Tank – 536	Limestone/chert	Sandy loam	7118	35°08'N, 111°53'E	222	150	53	19
Campbell Mesa – 500	Limestone/sandstone	Sandy loam	6793	35°12'N, 111°33'E	25	31	68	13
Pine Grove – 586	Basalt	Silt loam	7137	34°59'N, 111°29'E	—	—	—	—
Railroad Draw – 582	Basalt	Loam	6845	35°07'N, 111°55'E	276	99	75	14
Little Horse Park – 585	Basalt	Clay loam	6973	34°57'N, 111°35'E	—	—	—	—
Coulter Cabin – 585	Basalt	Loam	7252	35°02'N, 111°36'E	—	—	—	—
Howard Mountain – 585	Basalt	Loam	7186	35°03'N, 111°39'E	288	114	50	20
Dry Lake – 570	Benmoreite	Loam	7380	35°11'N, 111°45'E	94	86	30	15
Fisher Tank – 570	Benmoreite	Loam	7446	35°11'N, 111°46'E	412	127	83	21

^a Terrestrial ecosystem survey type on the Coconino National Forest (Miller and others 1995).

^b 0- to 6-inch (0- to 15-cm) mineral soil.

^c Basal area.

^d Not measured.

contained pine-oak forests, spanned a range of soil parent materials and terrestrial ecosystem survey types (Miller and others 1995), and were studied in previous research (Abella and Covington 2006). Among sites, 0- to 6-inch (0- to 15-cm) soil texture ranged from sandy to clay loam, pH from 5.6 to 6.8, and loss-on-ignition (2 hours at 572 °F [300 °C]) in open-area soils from 1.5 to 5.6 percent. Loss-on-ignition in this study is used as a surrogate for organic carbon (Abella and Zimmer 2007). Sites also encompassed a range of stand structures, from dense stands exceeding 400 pine + oak/acre (1,000/ha) to open stands containing fewer than 100 pine + oak/acre (250/ha; fig. 1). Annual precipitation across the study area averages 17 to 22 inches (42 to 56 cm) based on three weather stations (Western Regional Climate Center, Reno, NV).

Field and Laboratory Procedures

On a 2.5-acre (1-ha) grid on each site, I randomly selected five of each of the following canopy types for sampling: openings; Gambel oak single trees, dispersed clumps, or thickets; and ponderosa pine single trees (fig. 1). This canopy-type classification was based on previous research and is articulated with examples and photos in Kruse (1992) and Abella and Springer (2008). Canopies were able to be randomly selected for sampling by using existing stem maps of the grids (Abella and Springer 2008) and enumerating all of the individual canopies. Openings were free of tree canopy cover and typically 0.025 to 0.25 acres (0.01 to 0.1 ha) in size. Diameters at breast height of sampled oak single stems ranged from 3 to 30 inches (7 to 77 cm). Compared to thickets, oak dispersed clumps usually contained stems larger in diameter with greater stem spacing. Oak thickets contained closely spaced stems usually of small diameter (< 6 inches [15 cm]). Sampled ponderosa pine ranged in

diameter from 11 to 32 inches (29 to 81 cm) and 80 percent were greater than 20 inches (50 cm) in diameter.

I sampled a 43-ft² (4-m²) circular plot below each of the five randomly selected canopies of each of the five canopy types on each grid (5 plots/canopy × 5 canopy types = 25 plots/grid). I selected the 43-ft² plot size to fit within the typical drip lines of the tree canopies (Gill and others 2000). Tree boles were the plot centers for single trees, and I located plots in the centers of openings and Gambel oak clumps and thickets. On each plot, I categorized the areal cover of each plant species rooted in the plot following cover classes modified from Peet and others (1998): 1 = < 0.1 percent, 2 = 0.1 to 1 percent, 3 = 1 to 2 percent, 4 = 2 to 5 percent, 5 = 5 to 10 percent,



Figure 1—Example of stand structure in a low-density ponderosa pine-Gambel oak forest sampled on Campbell Mesa, 2 miles (3 km) east of Flagstaff, Arizona, in the Coconino National Forest. Plots were sampled below canopy openings; Gambel oak single trees, dispersed clumps, and thickets; and single ponderosa pine. Photo by S.R. Abella, June 16, 2004 (35°11'48"N, 111°33'23"W).

6 = 10 to 25 percent, 7 = 25 to 50 percent, 8 = 50 to 75 percent, 9 = 75 to 95 percent, and 10 = 95 to 100 percent. I included Gambel oak seedlings and sprouts shorter than breast height in these measurements. Estimates of total plant cover were comparable to total cover estimated by summing cover of individual species, so I report total plant cover summed from individual species. I assessed reproducibility of cover categorizations by remeasuring every fifth plot. Repeated measurement errors averaged < 1 cover class and 0.5 species/plot. Two specimens, both forbs, with insufficient material for accurate identification to species were deleted from the data set. Sampling occurred in June 2004 and represents pre-monsoon summer sampling. Nomenclature followed NRCS (2004). I classified graminoids (grasses and sedges) based on their photosynthetic pathway as cool-season (C_3) or warm-season (C_4) following Waller and Lewis (1979).

On one randomly selected plot of each canopy type on each grid, I collected a 0- to 6-inch (0- to 15-cm) soil sample that weighed about 2.2 pounds (1 kg) including coarse fragments. I analyzed the <0.08-inch (2-mm) fraction for texture (hydrometer method), pH (1:1 soil:water), and loss-on-ignition (2 hours at 572 °F [300 °C]) following Sparks (1996) and Dane and Topp (2002). I also measured Oi horizon (litter) weight by oven drying a 2.7-ft² (0.25-m²) sample at 158 °F (70 °C) for 24 hours. I estimated 0- to 6-inch (0- to 15-cm) gravimetric soil moisture on three randomly selected plots of each canopy type on each grid by oven drying a 13-inch³ (207-cm³) core at 221 °F (105 °C) for 24 hours.

Data Analysis

I averaged all plant community measures on a grid basis for statistical analyses. I compared the following understory variables among canopy types: the sum of species percent cover excluding Gambel oak cover, total average species richness per plot (43 ft² [4 m²]), and cool- and warm-season graminoid richness per plot. Texture, pH, loss-on-ignition, Oi horizon weight, and gravimetric moisture constituted the soil variables. With the exception of species richness, I compared variables among canopy types using one-way analysis of variance, with grids (sites) serving as blocks and Fisher's least significant difference for mean separation. I compared the three richness variables among canopy types using a Kruskal-Wallis test followed by a pairwise Wilcoxon test with Bonferroni adjustment. I used a non-parametric test for richness because these data were originally count data. JMP software (SAS Institute 2002) was used to perform analysis of variance, and R (<http://www.r-project.org/>) was used for the Kruskal-Wallis test.

Results

Plant Community Cover and Richness

Understory plant cover, excluding Gambel oak cover, averaged about three to eight times greater in openings than below tree canopies (fig. 2). Plant cover was intermediate below oak canopies and least below pine where cover averaged less than 4 percent. Oak seedlings and sprouts shorter than breast height constituted about half of the plant cover below oak and ponderosa pine canopies, while herbaceous plants predominated in openings.

Average plant species richness/43 ft² (4 m²) ranged from 12 species below openings to 5 species below ponderosa pine (fig. 3). Among oak canopy types, richness increased in the order: thickets < dispersed clumps < single stems. Richness of cool-season graminoids was lowest below pine, but did not differ significantly among other canopy types. In contrast, warm-season graminoids were more than twice as rich in openings compared to single oaks, the next richest canopy type.

Species Composition

While understory composition varied among sites, several species showed affinities for three or fewer canopy types within sites (table 2). For example, the warm-season grass purple threeawn (*Aristida purpurea*) occurred in 43 percent of plots in openings on the six sites this species occupied. The only tree canopy type that threeawn

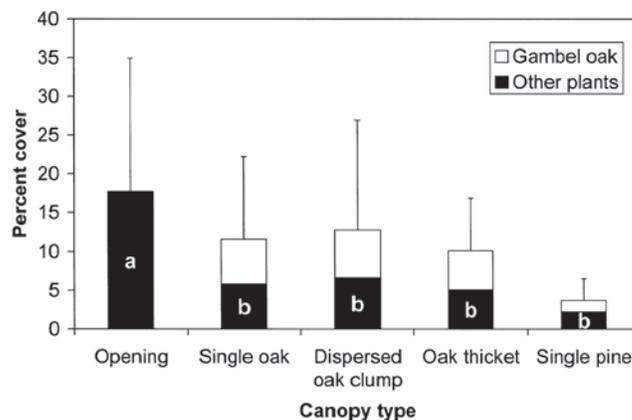


Figure 2—Understory plant cover among five canopy types in northern Arizona ponderosa pine-Gambel oak forests. Canopy openings contained significantly greater plant cover than occurred below any tree canopy. Means without shared letters for the other plants category (all plants excluding Gambel oak) differ among canopy types ($F = 6.3$, $P < 0.01$). Error bars are 1 standard deviation for mean total cover.

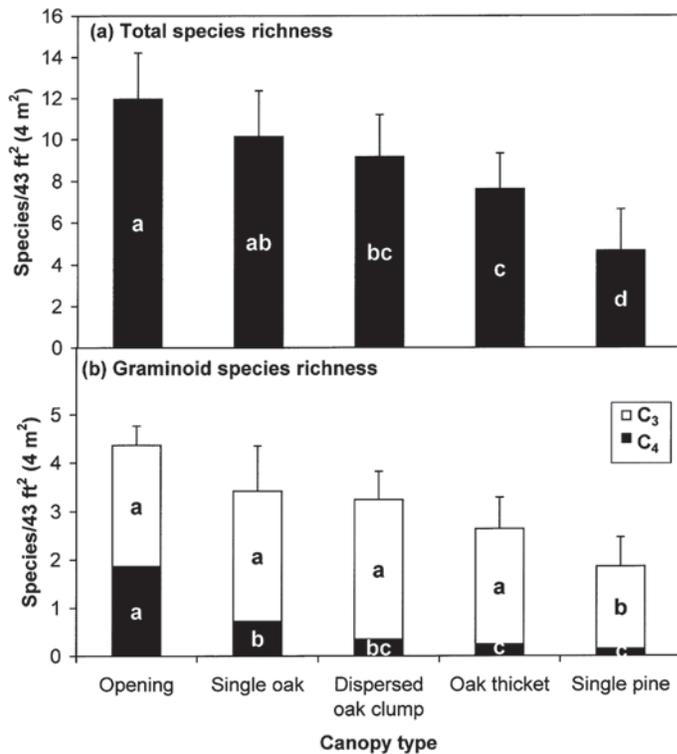


Figure 3—(a) Average total understory plant richness and (b) graminoid (grass and sedge) richness by photosynthetic pathway (C_3 = cool-season, C_4 = warm-season) among five canopy types in ponderosa pine-Gambel oak forests, northern Arizona. Means without shared letters differ among canopy types (a: Kruskal-Wallis χ^2 statistic = 78.1, $P < 0.01$; b warm-season: $\chi^2 = 104$, $P < 0.01$; b cool-season: $\chi^2 = 25.9$, $P < 0.01$). Error bars are 1 standard deviation for mean totals.

Table 2—Distributions of 17 prevalent plant species (of 123 total detected species) among five canopy types in northern Arizona ponderosa pine-Gambel oak forests. Values in bold represent canopy types under which a species most frequently occurred.

Species	No. sites ^b	Canopy type ^a				
		Open	SO	DC	OT	SP
----- Percent frequency ^c -----						
Warm-season grasses						
<i>Aristida purpurea</i>	6	26	2	0	0	0
<i>Bouteloua gracilis</i>	6	42	12	6	0	0
<i>Sporobolus interruptus</i>	6	26	8	4	8	2
<i>Blepharoneuron tricholepis</i>	6	32	14	2	2	0
<i>Muhlenbergia montana</i>	8	42	36	22	14	12
Cool-season graminoids						
<i>Carex geophila</i>	9	48	58	62	46	22
<i>Poa fendleriana</i>	10	66	70	78	60	50
<i>Elymus elymoides</i>	10	74	94	86	94	64
Forbs						
<i>Erigeron divergens</i>	10	64	24	14	8	0
<i>Lithophragma tenellum</i>	5	10	14	6	0	0
<i>Heliomeris multiflora</i>	8	26	20	12	10	0
<i>Symphotrichum falcatum</i>	6	32	16	10	4	2
<i>Lupinus kingii</i>	6	36	24	10	12	10
<i>Eriogonum racemosum</i>	9	42	28	24	26	24
<i>Pedicularis centranthera</i>	6	6	18	28	14	4
<i>Thalictrum fendleri</i>	6	0	2	16	16	2
<i>Lathyrus laetivirens</i>	5	0	4	16	22	2

^a SO = single Gambel oak, DC = dispersed oak clump, OT = oak thicket, and SP = single ponderosa pine.

^b Number of sites ($n = 10$ total) on which a species occurred.

^c Frequencies represent presence or absence in fifty 43-ft² (4-m²) plots for each canopy type (five canopies of each type sampled at each of 10 sites).

occurred below was single oaks. As a group, warm-season graminoids sharply declined with increasing tree canopy cover. Cool-season graminoids, in contrast, were more evenly distributed among canopy types. The forbs aspen pea (*Lathyrus laetivirens*) and Fendler's meadow-rue (*Thalictrum fendleri*) were associated with oak clumps and thickets. Dwarf lousewort (*Pedicularis centranthera*) also had an affinity for oak.

Soils

On average, percent sand, silt, or clay did not differ significantly among canopy types (F - statistic < 1.2 , $P > 0.35$). Soil pH also did not differ significantly among canopy types ($F = 2.55$, $P = 0.06$) but tended to be 0.2 to 0.4 units lower below pine compared to other canopies. In contrast, Oi horizon weight sharply differed among canopy types. Oi horizons weighed 18 tons/acre ($4,000 \text{ g/m}^2$) below pine compared to 4 to 6 tons/acre ($900 \text{ to } 1,500 \text{ g/m}^2$) below oak and less than one ton/acre (200 g/m^2) in openings (fig. 4). Loss-on-ignition was greatest below oak canopy types and least in openings. Soil moisture was also lowest in openings and greatest below oak thickets.

Discussion

The distribution of tree canopy types constrained within-site patterns of understory plant cover, richness, and composition. These within-site patterns probably arise from the biotic influences of trees on soils and microclimates (Boettcher and Kalisz 1990), because soil parent material was homogeneous within sites and soil texture did not differ among canopy types. This study's findings, such as greater loss-on-ignition in soils below tree canopies, are also consistent with tree influences reported in many experimental studies that manipulated tree cover (Scholes and Archer 1997).

Canopy openings contained greater understory plant cover, richness, and warm-season grass abundance than occurred below Gambel oak and pine canopies. This finding was consistent across the sampled soil parent materials and terrestrial ecosystem types. Many previous studies in ponderosa pine forests have also highlighted the importance of canopy openings for understory communities (Arnold 1950; Covington and others 1997; Moir 1966). The greater abundance of warm-season grasses that I found in openings compared to below trees concurs with predictions that warm-season species are most competitive in sunnier, drier environments (Sage and Monson 1999). In addition to warm-season grasses, spreading fleabane (*Erigeron divergens*), white prairie aster (*Symphotrichum falcatum*), and several other forbs were most frequent in

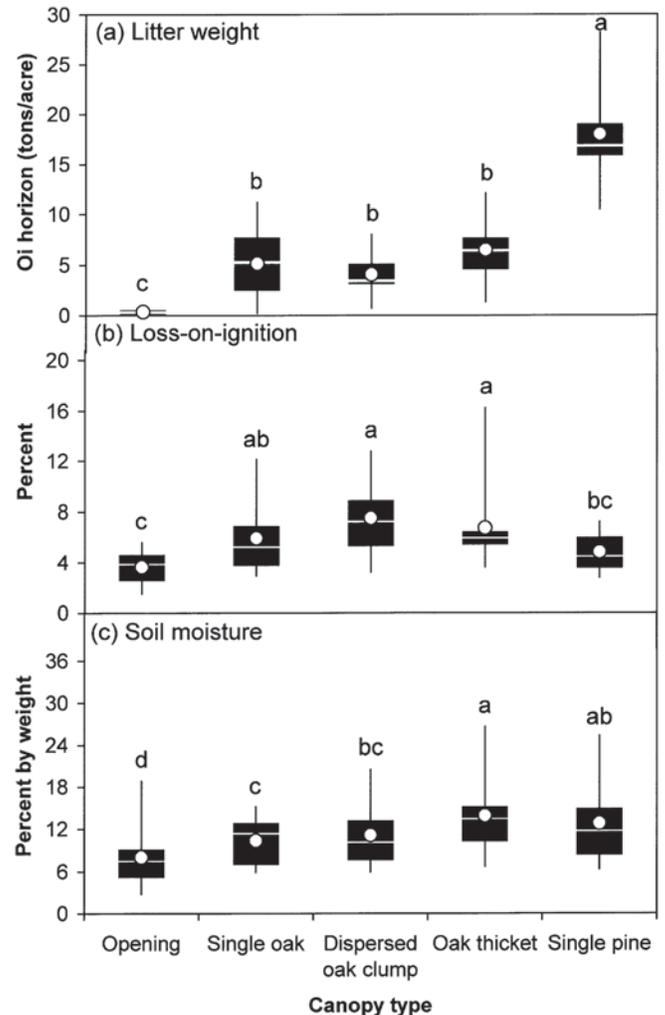


Figure 4—Variation in soil properties among five canopy types in northern Arizona ponderosa pine-Gambel oak forests. Averages without shared letters differ among canopy types (a: $F = 45.9$, $P < 0.01$; b: $F = 6.1$, $P < 0.01$; c: $F = 10.1$, $P < 0.01$). Averages = circles, medians = white horizontal lines, first quartiles = lower boxes, third quartiles = upper boxes, and minimums/maximums = vertical lines.

openings (table 2). Affinities for openings by these species could be related to greater resource availability (for example, light or nutrients) in openings (Moir 1966) or thinner litter layers that facilitate seedling establishment (Evenson and others 1980).

While plant cover and richness was lower below Gambel oak canopies than it was in openings, three forbs (aspen pea, Fendler's meadow-rue, and dwarf lousewort) were more frequent below oaks than in openings (table 2). Studies in other parts of Gambel oak's range also found that certain plant species are most prevalent below oak canopies. For example, Brown (1958) found that Geyer's

sedge (*Carex geyeri*) biomass in western Colorado averaged 204 pounds/acre (229 kg/ha) below Gambel oak compared to only 25 pounds/acre (28 kg/ha) in openings. In northern Utah, Evenson and others (1980) reported that Geyer's sedge and tuber starwort (*Pseudostellaria jamesiana*) were most abundant below oak. It appears that oak commonly constitutes key habitat for certain plant species, but these species vary with regional floras.

This study supports previous findings in ponderosa pine (Klemmedson 1987; Moir 1966; Naumburg and DeWald 1999) and other forest types (Barth 1980; Boettcher and Kalisz 1990; Scholes and Archer 1997) that trees induce fine-scale patterns in soil properties and understory plant communities. This study's results also reinforce recommendations by previous authors (for example, Laughlin and others 2006) that maintaining or creating canopy openings is critical for sustaining understory plant diversity in ponderosa pine forests.

Management Implications

- Results suggest that passively or actively managing both the density and distribution of trees affects within-site patterns of plant communities and soil properties in ponderosa pine-Gambel oak forests.
- Compared to below pine, canopy openings contained eight times more plant cover, three times more species/43 ft² (4 m²), and 13 times greater frequencies of warm-season grasses. Creating canopy openings when thinning ponderosa pine forests is critical if these forests are to contain diverse understory plant communities.
- Specific growth forms of Gambel oak — single stems, dispersed clumps, or dense thickets — exhibited different effects on soils and understory richness and composition. Single oaks had the highest species richness, while clumps and thickets constituted habitat for Fendler's meadow-rue and aspen pea on about half of the study sites. Maintaining areas of these different growth forms increases plant community diversity and is probably also important for some wildlife species.
- Trees are dominant structures in pine-oak forests that affect other ecosystem components, including soils and plant communities. The growing space occupied by trees influences the living space available to other organisms, and such influences warrant consideration when managing forests for multiple ecosystem values.
- The tradeoffs of leaving large numbers of pine after thinning operations include fewer canopy openings, heavier fuel loads, more acidic soils, and depauperate understories.

Acknowledgments

I thank Judy Springer and Mark Daniels (Ecological Restoration Institute) for help with fieldwork; Wally Covington (Ecological Restoration Institute) for discussions and guidance on disseminating summaries of research results; Jim Fowler (Rocky Mountain Research Station), Charlie Denton and Dennis Lund (Ecological Restoration Institute), and Kristi Coughlon (Rocky Mountain Research Station) for reviewing the manuscript; and David Turner (Rocky Mountain Research Station) and Cheryl Vanier (University of Nevada Las Vegas) for providing statistical reviews and help with statistical analyses. Funding was provided by the U.S. Forest Service and the Ecological Restoration Institute.

References

- Abella, Scott R.; Covington, W. Wallace. 2006. Forest ecosystems of an Arizona *Pinus ponderosa* landscape: multifactor classification and implications for ecological restoration. *Journal of Biogeography*. 33:1368-1383.
- Abella, Scott R.; Zimmer, Brian W. 2007. Estimating organic carbon from loss-on-ignition in northern Arizona forest soils. *Soil Science Society of America Journal*. 71:545-550.
- Abella, Scott R.; Springer, Judith D. 2008. Canopy-tree influences along a soil parent material gradient in *Pinus ponderosa-Quercus gambelii* forests, northern Arizona. *Journal of the Torrey Botanical Society*. 135:26-36.
- Arnold, Joseph F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry*. 48:118-126.
- Barth, R.C. 1980. Influence of pinyon pine trees on soil chemical and physical properties. *Soil Science Society of America Journal*. 44:112-114.
- Boettcher, S.E.; Kalisz, P.J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology*. 74:1365-1372.
- Brown, Harry E. 1958. Gambel oak in west-central Colorado. *Ecology*. 39:317-327.
- Covington, W. Wallace; Fule, Peter Z.; Moore, Margaret M.; Hart, Stephen C.; Kolb, Thomas E.; Mast, Joy N.; Sackett, Stephen S.; Wagner, Michael R. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry*. 95:23-29.
- Dane, Jacob H.; Topp, G. Clarke, eds. 2002. *Methods of soil analysis. Part 4. Physical methods*. Madison, WI: Soil Science Society of America. 1692 p.
- Evenson, William E.; Brotherson, Jack D.; Wilcox, Richard B. 1980. Relationship between environmental and vegetational parameters for understory and open-area communities. *Great Basin Naturalist*. 40:167-174.
- Gill, Samantha J.; Biging, Gregory S.; Murphy, Edward C. 2000. Modeling conifer tree crown radius and estimating canopy cover. *Forest Ecology and Management*. 126:405-416.
- Klemmedson, James O. 1987. Influence of oak in pine forests of central Arizona on selected nutrients of forest floor and soil. *Soil Science Society of America Journal*. 51:1623-1628.
- Kruse, William H. 1992. Quantifying wildlife habitats within Gambel oak/forest/woodland vegetation associations in Arizona. In: Ffolliott, Peter F.; Gottfried, Gerald J.; Bennett, Duane A.; C. Hernandez, Victor Manuel; Ortega-Rubio, Alfredo; Hamre, R.H., tech. coords. *Ecology and management of oaks and associated woodlands: perspectives in the southwestern United States and*

- northern Mexico; 1992 April 27-30; Sierra Vista, AZ. Gen. Tech. Rep. RM-218. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 182-186.
- Laughlin, Daniel C.; Moore, Margaret M.; Bakker, Jonathan D.; Casey, Cheryl A.; Springer, Judith D.; Fulé, Peter Z.; Covington, W. Wallace. 2006. Assessing targets for the restoration of herbaceous vegetation in ponderosa pine forests. *Restoration Ecology*. 14:548-560.
- Miller, Greg; Ambos, Norm; Boness, Pat; Reyher, Deanna; Robertson, George; Scalzone, Ken; Steinke, Rory; Subirge, Tom. 1995. Terrestrial ecosystems survey of the Coconino National Forest. U.S Department of Agriculture, Forest Service, Southwestern Region. 405 p.
- Moir, William H. 1966. Influence of ponderosa pine on herbaceous vegetation. *Ecology*. 47:1045-1048.
- Naumburg, Elke; DeWald, Laura E. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. *Forest Ecology and Management*. 124:205-215.
- NRCS [U.S. Department of Agriculture, Natural Resources Conservation Service]. 2004. The PLANTS database. Baton Rouge, LA: National Plant Data Center. <http://plants.usda.gov/>.
- Parker, V.T.; Muller, C.H. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist*. 107:69-81.
- Peet, Robert K.; Wentworth, Thomas R.; White, Peter S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea*. 63:262-274.
- Sage, Rowan F.; Monson, Russell K., eds. 1999. *C₄ plant biology*. New York: Academic Press. 596 p.
- SAS Institute. 2002. *JMP user's guide*. Cary, NC: SAS Institute, Inc. 263 p.
- Scholes, R.J.; Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*. 28:517-544.
- Sparks, D.L., ed. 1996. *Methods of soil analysis*. Part 3. Chemical methods. Madison, WI: Soil Science Society of America and American Society of Agronomy. 1390 p.
- Waller, S.S.; Lewis, J.K. 1979. Occurrence of C₃ and C₄ photosynthetic pathways in North American grasses. *Journal of Range Management*. 32:12-28.

You may order additional copies of this publication by sending your mailing information in label form through one of the following media. Please specify the publication title and number.

Publishing Services

Telephone (970) 498-1392

FAX (970) 498-1122

E-mail rschneider@fs.fed.us

Web site <http://www.fs.fed.us/rmrs>

Mailing Address Publications Distribution
Rocky Mountain Research Station
240 West Prospect Road
Fort Collins, CO 80526



The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of the National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals. Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

Station Headquarters

Rocky Mountain Research Station
 240 W. Prospect Road
 Fort Collins, CO 80526
 (970) 498-1100

Research Locations

Flagstaff, Arizona	Reno, Nevada
Fort Collins, Colorado	Albuquerque, New Mexico
Boise, Idaho	Rapid City, South Dakota
Moscow, Idaho	Logan, Utah
Bozeman, Montana	Ogden, Utah
Missoula, Montana	Provo, Utah

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, DC 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.