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# Canopy-tree influences along a soil parent material gradient in *Pinus ponderosa-Quercus gambelii* forests, northern Arizona

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ABELLA, S. R. (Public Lands Institute and School of Life Sciences, University of Nevada Las Vegas, Las Vegas, NV 89154-2040) AND J. D. SPRINGER (Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ 86011-5017). Canopy-tree influences along a soil parent material gradient in *Pinus ponderosa-Quercus gambelii* forests, northern Arizona. J. Torrey Bot. Soc. 135: 26–36. 2008.—The distribution of canopy trees can impose within-site patterns of soil properties and understory plant composition. At ten sites spanning a soil parent material gradient in northern Arizona *Pinus ponderosa-Quercus gambelii* forests, we compared soils and plant composition among five canopy types: openings, *Pinus ponderosa* single trees, *Quercus gambelii* single stems, dispersed clumps, and thickets. Soil texture on average did not differ significantly among canopy types, whereas Oi horizon thickness and weight, 0–15 cm soil loss-on-ignition, and gravimetric soil moisture differed significantly among three or more canopy types. Understory plant richness per 4 m<sup>2</sup> ranged from five species below *P. ponderosa* to 12 species in openings, with richness below *Q. gambelii* single stems significantly greater than below *Q. gambelii* thickets. C<sub>4</sub> graminoids (e.g., *Aristida purpurea*) inhabited openings, while C<sub>3</sub> species like *Poa fendleriana* also occurred below trees. The forbs *Thalictrum fendleri* and *Lathyrus laetivirens* were strongly associated with *Q. gambelii* dispersed clumps and thickets. We also conducted an experimental planting with *T. fendleri* that was consistent with these correlational results, with outplanted *T. fendleri* seedling survival 2–7 times greater when planted below *Q. gambelii* compared to openings. Previous research and our results suggest that understory species associated with *Q. gambelii* canopies vary regionally, but there are consistently some associated species. Canopy types affected understory vegetation similarly across soil parent materials, not supporting a hypothesis that positive plant interactions changed along soil gradients. Our results suggest that forest management that manipulates both the density and the pattern of trees, together with the growth forms of *Q. gambelii* trees, can induce within-site spatial patterns of soil properties and understory species.

Key words: *Lathyrus laetivirens*, *Pedicularis centranthera*, positive plant interactions, single-tree influences, *Thalictrum fendleri*, understory.

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Canopy-tree influences on soils and understory vegetation have long been studied in vegetation science (e.g., Ovington 1955, Barth and Klemmedson 1978, Crozier and Boerner 1984). Some authors have described savannas and forests as mosaics of single-tree influence circles where tree distributions constrain soil and understory compositional patterns (Zinke 1962, Wu et al. 1985, Boettcher and Kalisz 1990). In savannas of northwestern Kenya, for example, Weltzin and Coughenour (1990) found that aboveground herbaceous biomass averaged 260 g m<sup>-2</sup> under individual trees of *Acacia tortilis* (Forsskal) Hayne (Fabaceae), compared to only 95 g m<sup>-2</sup> in openings. Several plant species in that study were distributed according to distances from tree boles. Understory habitat below tree canopies differs from that of openings (Parker and Muller 1982, Leach and Givnish 1999). Habitat variables that may differ among

canopy types and between openings include: light, throughfall quantity and chemistry, soil moisture, litter thickness, allelopathy, organic matter, nutrients, pH, soil structure, herbivory, and invertebrate and animal communities (Scholes and Archer 1997, Økland et al. 1999). Single-tree influences have been detected by long-term studies tracking changes near individual trees (Quideau et al. 1996), chronosequence studies of different tree sizes and ages (Barth 1980, Everett et al. 1983), comparative studies among tree species and canopy openings (Jackson et al. 1990, Finzi et al. 1998), and resource manipulations or species additions and removals (Marañón and Bartolome 1993, Belsky 1994).

There has been increasing appreciation in vegetation science for positive, rather than only competitive, interactions between plants (Callaway 1995). Canopy-tree influences on understory plants can be negative, neutral, or positive, depending on the tree and the plant species or the environmental setting (Scholes and Archer 1997). Some authors have hypothesized that positive interactions intensify in stressful environments (e.g., Callaway 1997, Tewksbury and Lloyd 2001). Various studies have supported this hypothesis while others have not (Mordelet and Menaut 1995, Tewksbury and Lloyd 2001, Maestre et al. 2005). Outcomes can depend on several factors, including the plant community attributes examined (e.g., richness or composition; McClaran and Bartolome 1989, Maestre et al. 2005).

Using both correlational and experimental approaches, we undertook this study to evaluate canopy-tree influences of *Pinus ponderosa* P. & C. Lawson (Pinaceae) and *Quercus gambelii* Nutt. (Fagaceae) on soils and understory vegetation along a soil parent material gradient in semi-arid *P. ponderosa*-*Q. gambelii* forests in northern Arizona. *Quercus gambelii* is commonly the only deciduous tree in otherwise pure *P. ponderosa* forests (Harper et al. 1985). This clonal *Quercus* species has several different growth forms in *P. ponderosa* forests related to numbers and spacing of stems within clumps, also providing an opportunity to test whether different growth forms of the same species have different influences. Our hypotheses were that: (1) influences on soils and understory vegetation differ among *P. ponderosa* and *Q. gambelii* canopy types relative to openings, (2) *Q.*

*gambelii* exhibits the most positive associations with understory plant species by containing the greatest understory species richness, and (3) positive associations between tree and understory species increase along a soil parent material gradient from moist, nutrient-rich sites to dry, nutrient-poor sites.

**Materials and Methods.** **STUDY AREA.** We performed this study at ten *Pinus ponderosa*-*Quercus gambelii* sites on the Northern Arizona University Centennial Forest and on the northern half of the Coconino National Forest surrounding the city of Flagstaff. The mean distance between sites was 23 km, with an extent of 42 km (Table 1). We selected these sites, based on previous research, to span a range of soil parent materials and soil properties (Abella and Covington 2006a, 2006b). Based on three weather stations, precipitation across the study area averages 42–56 cm/yr, snowfall from 152–233 cm yr<sup>-1</sup>, and maximum daily temperatures from 15.7–17.5°C (Western Regional Climate Center, Reno, NV). Elevations at the study sites range from 2071–2270 m, and slope gradients are < 5%. Soil taxonomic units vary among sites, with major soil subgroups including Typic and Mollic Eutroboralfs and Typic Ustorthents (Miller et al. 1995). Sites span a textural gradient from 25–60% sand (0–15 cm mineral soil) and 40–75% silt + clay, a pH gradient from 5.6–6.8, and a loss-on-ignition (LOI; 300°C, 2 hr) gradient in open-area soils from 1.5–5.6%. Understory composition differs among sites, but is dominated by graminoids and forbs including *Elymus elymoides* (Raf.) Swezey (Poaceae), *Poa fendleriana* (Steud.) Vasey (Poaceae), and *Erigeron divergens* Torr. & Gray (Asteraceae).

**PLOT LAYOUT.** On a 1 ha (100 × 100 m) grid at each site, we randomly selected for sampling five each of the following five canopy types: openings, *Pinus ponderosa* single trees, *Quercus gambelii* single stems, dispersed clumps, and thickets (Fig. 1). We sampled a 4-m<sup>2</sup> circular plot below each canopy because this plot area fits within typical drip lines of the tree canopies (Gill et al. 2000). There were a total of 25 plots per grid (5 canopy types × 5 canopies of each type). Tree boles were plot centers for single trees, with plot radii corrected for bole area to maintain plot sizes of 4 m<sup>2</sup> excluding boles. Plots were located in the

Table 1. Study site characteristics in *Pinus ponderosa-Quercus gambelii* forests, northern Arizona.

Site	Parent material	Texture <sup>a</sup>	Elevation (m)	UTM (mE, mN) <sup>b</sup>	<i>Pinus ponderosa</i>		<i>Quercus gambelii</i>	
					Trees/ha	BA <sup>c</sup> m <sup>2</sup> ha <sup>-1</sup>	Trees/ha	BA m <sup>2</sup> ha <sup>-1</sup>
Turkey Hills	Red volcanic cinders	Sandy loam	2079	452715, 3898173	— <sup>d</sup>	—	—	—
Garjon Tank	Limestone/chert	Sandy loam	2170	419288, 3887985	549	34.3	130	4.4
Campbell Mesa	Limestone/sandstone	Sandy loam	2071	449215, 3894994	63	7.2	167	2.9
Pine Grove	Basalt	Silt loam	2176	456397, 3871387	—	—	—	—
Little Horse Park	Basalt	Clay loam	2126	446770, 3866823	—	—	—	—
Railroad Draw	Basalt	Loam	2087	417081, 3885511	681	22.6	185	3.2
Coulter Cabin	Basalt	Loam	2211	445788, 3877037	—	—	—	—
Howard Mountain	Basalt	Loam	2191	441402, 3877861	712	26.1	124	4.5
Dry Lake	Benmoreite	Loam	2250	431605, 3893383	232	19.7	75	3.4
Fisher Tank	Benmoreite	Loam	2270	430602, 3893052	1019	29.1	204	4.7

<sup>a</sup> 0–15 cm mineral soil.

<sup>b</sup> Universal Transverse Mercator coordinates (zone 12, North American Datum 1983).

<sup>c</sup> Basal area.

<sup>d</sup> Not measured.

centers of openings and of *Q. gambelii* clumps and thickets. Sampling occurred between June 8–30, 2004.

**SOIL SAMPLING AND ANALYSIS.** We randomly selected one plot of each canopy type on each grid for soil sampling. We collected a 0–15 cm mineral soil sample ( $\approx$  1 kg field moist including coarse fragments) about 0.5 m from boles of single trees and from plot centers of other canopy types. We analyzed the < 2 mm fraction for texture (hydrometer method; Dane and Topp [2002]), pH (1:1 soil:water; Sparks [1996]), and LOI (300°C, 2 hr; Abella and Zimmer [2007]). Repeated measurements of every tenth sample indicated that measurement error averaged < 5%. We also measured Oi weight by collecting samples in 0.25-m<sup>2</sup> frames and oven drying samples at 70°C for 24 hr. We measured soil moisture on three randomly selected plots of each canopy type on each grid by collecting a 207-cm<sup>3</sup> core of the 0–15 cm mineral soil and oven drying the sample at 105°C for 24 hr.

**VEGETATION SAMPLING.** In all 25 plots on each grid, we categorized *Quercus gambelii* litter (Oi horizon) cover and aerial cover of understory plant species rooted in plots using cover classes modified from Peet et al. (1998):

1 = < 0.1%, 2 = < 1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100%. Nomenclature and lifeform and U.S. nativity classifications followed U.S. Natural Resources Conservation Service (2007). We measured *Pinus ponderosa* and *Quercus gambelii* percent canopy cover using a densitometer (Geographic Resource Solutions, Arcata, CA) and Oi thickness at four equally spaced locations on each plot (0.5 m from boles of single trees). For all *Q. gambelii* canopies, we also measured heights of canopy bottoms, which could affect shading and litter redistribution (Scholes and Archer 1997).

We recorded diameter at 1.4 m (breast height) and mapped all living trees > 1 cm diameter on six of the 1 ha grids. We divided grids into 100, 10 × 10 m cells and mapped stems to the nearest 0.1 m. Repeated measurement errors averaged < 0.15 m for x,y stem coordinates.

**EXPERIMENTAL PLANTING.** To test the hypothesis that plant survival differs among *Quercus gambelii* canopy types and openings, we outplanted six-month-old, greenhouse-grown seedlings of *Thalictrum fendleri* Engelm. ex Gray (Ranunculaceae) and *Penstemon virgatus* Gray (Scrophulariaceae). Seed-

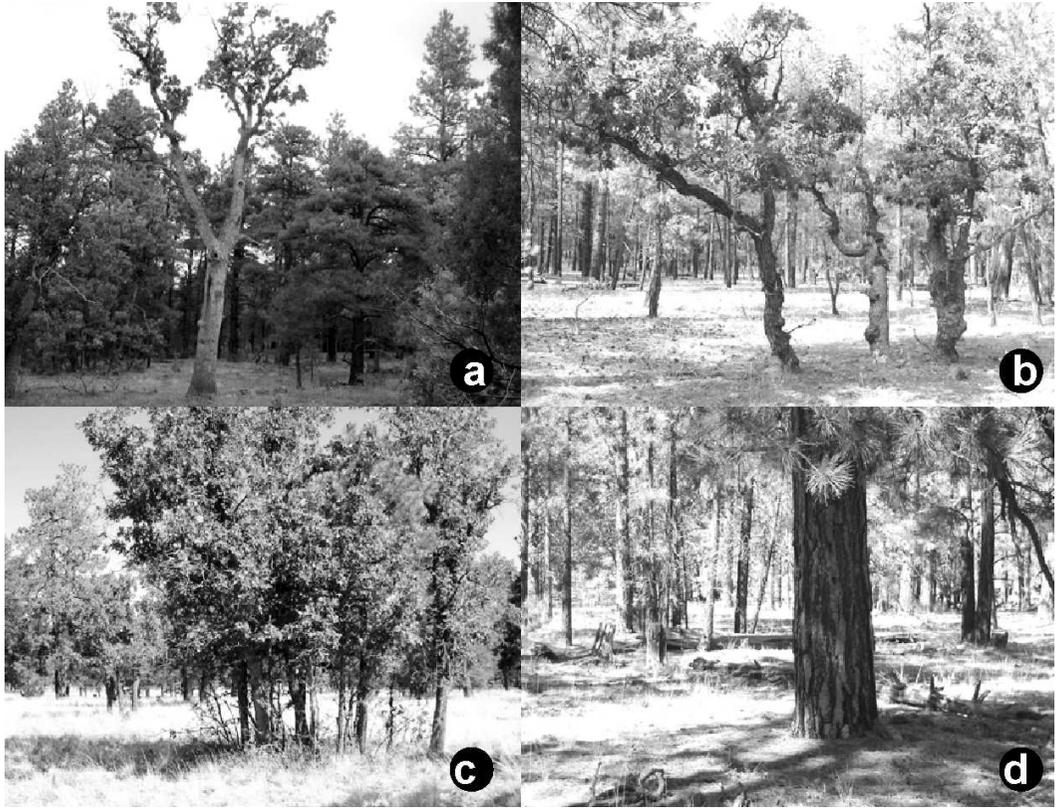


FIG. 1. Examples of *Quercus gambelii* and *Pinus ponderosa* canopy types, northern Arizona. Sampled (a) *Q. gambelii* single trees ranged in diameter from 7–77 cm. Maximum diameters of *Q. gambelii* stems within clumps were 62 cm for (b) dispersed clumps and 74 cm for (c) thickets. Sampled (d) *P. ponderosa* single trees ranged in diameter from 29–81 cm, with 80% greater than 50 cm diameter.

lings were purchased from a local grower (Flagstaff Native Plant and Seed, Flagstaff, AZ). We chose these species based on our correlational field data to include a species with an affinity for *Q. gambelii* (*T. fendleri*) and for openings (*Penstemon virgatus*). We stored seedlings outdoors for two months before outplanting on 21 November 2005 near the Dry Lake site (Table 1). Three seedlings each of *T. fendleri* and *P. virgatus* were planted below three each of three *Q. gambelii* canopy types (single stems, dispersed clumps, and thickets) and in openings 12 m away from trees paired with each *Q. gambelii* canopy. Thus, there were a total of nine *Q. gambelii* canopies and nine openings, for a total of 54 seedlings planted for each of *T. fendleri* and *P. virgatus*. We planted seedlings in a 1 m<sup>2</sup> circular area below each canopy or in openings. We recorded plant survival on 9 September 2006, approximately 10 months after planting.

**DATA ANALYSIS.** We compared soil variables and species richness per 4 m<sup>2</sup> and diversity among canopy types with sites serving as blocks using analysis of variance (ANOVA) and Fisher's least significant difference for mean separation. Analyses were performed with the software JMP (SAS Institute 2002). To avoid pseudoreplication (Hurlbert 1984), we averaged all variables on a site basis for ANOVA that had the following degrees of freedom: whole model = 13, error = 36, site = 9, and canopy type = 4. We calculated diversity based on relative cover class as Shannon's Diversity Index in the software PC-ORD (McCune and Mefford 1999). We ordinated combinations of soil variables using principal components analysis (correlation matrix) to examine if canopy influences on species richness changed along multivariate soil gradients. For these analyses, we relativized richness site means of tree canopies by subtracting from open canopy site means. We

analyzed categorical (alive or dead) survival data from the experimental planting using a generalized linear model with binomial error terms. The factors in this model were *Quercus gambelii* canopy type (three levels: single stems, dispersed clumps, or thickets), habitat (two levels: below *Q. gambelii* or in openings), and planted species (two levels: *Thalictrum fendleri* or *Penstemon virgatus*). To avoid pseudoreplication, we used the fraction of the individuals of each planted species that survived (out of three) from each planting for a particular *Q. gambelii* canopy or opening as the raw data. Due to overdispersion in the data, we used the *F* statistic, rather than the chi-square, to assess statistical significance at  $\alpha = 0.05$ . We used R software (<http://www.r-project.org/>) to perform this analysis.

**Results.** Although 0–15 cm gravel concentration tended to be 8–17% lower below openings than below tree canopies, gravel and soil texture were not significantly different among canopy types (Table 2). Soil pH below *Pinus ponderosa* tended to be 0.2–0.4 units lower than below other canopy types, but pH of *Quercus gambelii* canopy types did not appreciably differ from openings. Loss-on-ignition below *Q. gambelii* canopies consistently exceeded that of openings, increasing in the order: openings < *P. ponderosa* < single *Q. gambelii* < *Q. gambelii* thickets < *Q. gambelii* dispersed clumps. Oi weight and thickness were greatest below *P. ponderosa*, averaging about 3–4 times heavier and 2–3 times thicker than below *Q. gambelii* canopies. Gravimetric soil moisture ranged from 7–13%, increasing in the order: openings < single *Q. gambelii* < *Q. gambelii* dispersed clumps < *P. ponderosa* < *Q. gambelii* thickets.

Understory plant richness per 4 m<sup>2</sup> ranged from 4.7 species below *Pinus ponderosa* to 12.0 species in openings (Fig. 2). Richness was intermediate below *Quercus gambelii* canopy types, with richness below thickets averaging 2.5 species fewer than below single *Q. gambelii* stems. Shannon's diversity index ranged from 1.2 below *P. ponderosa* to 2.3 in openings and exhibited multiple comparisons identical to those for species richness. There was a slight trend for greater richness of annuals and biennials below open canopies and single *Q. gambelii*, but canopy types overall were dominated by perennials. Forbs on average composed 64% of richness in openings, 51–

Table 2. Mean soil characteristics below five canopy types averaged for ten sites across a soil parent material gradient in *Pinus ponderosa*-*Quercus gambelii* forests, northern Arizona. Means without shared letters differ at  $P < 0.05$ .

Variable <sup>a</sup>	Canopy type <sup>b</sup>			Canopy <sup>c</sup>			Site		
	Open	SQ	DQC	QT	SP	F	P	F	P
Gravel (% wt.)	26 ± 10	34 ± 14	37 ± 20	43 ± 24	40 ± 20	2.31	0.08	5.58	< 0.01
Sand (% wt.)	37 ± 16	40 ± 17	37 ± 12	37 ± 11	41 ± 16	1.10	0.37	28.73	< 0.01
Silt (% wt.)	41 ± 8	39 ± 11	44 ± 9	42 ± 8	40 ± 12	1.15	0.35	9.59	< 0.01
Clay (% wt.)	22 ± 12	20 ± 10	19 ± 6	20 ± 6	19 ± 5	0.55	0.70	5.30	< 0.01
pH	6.1 ± 0.3	6.2 ± 0.5	6.1 ± 0.5	6.0 ± 0.5	5.8 ± 0.5	2.55	0.06	11.36	< 0.01
LOI (% wt.) <sup>d</sup>	3.6 ± 1.4c	5.9 ± 2.9ab	7.5 ± 3.2a	6.7 ± 3.6a	4.8 ± 1.6bc	6.09	< 0.01	5.30	< 0.01
Oi wt. (g m <sup>-2</sup> )	82 ± 69c	1159 ± 789b	921 ± 475b	1461 ± 751b	4049 ± 1212a	45.94	< 0.01	1.91	0.08
Oi thickness (cm)	0.1 ± 0.2c	1.9 ± 1.5b	1.8 ± 0.7b	3.2 ± 1.5b	5.7 ± 3.0a	15.88	< 0.01	1.28	0.28
Moisture (% wt.) <sup>e</sup>	7.3 ± 3.9d	9.3 ± 3.6c	11.2 ± 4.4bc	13.1 ± 5.2a	12.3 ± 6.2ab	10.10	< 0.01	12.58	< 0.01

<sup>a</sup> All soil variables except for Oi variables are for 0–15 cm mineral soil.

<sup>b</sup> SQ = single *Quercus gambelii* tree, DQC = dispersed *Q. gambelii* clump, QT = *Q. gambelii* thicket, and SP = single *Pinus ponderosa*.

<sup>c</sup> *F*-statistic and probability of  $a > F$  for a randomized block analysis of variance testing canopy type effects with sites serving as blocks.

<sup>d</sup> Loss-on-ignition (300°C, 2 hr).

<sup>e</sup> Gravimetric soil moisture.

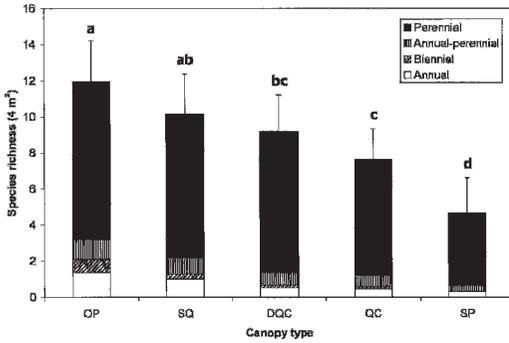


FIG. 2. Species richness below five canopy types in *Pinus ponderosa*-*Quercus gambelii* forests, northern Arizona. Error bars (1 SD) and comparisons of means are for total mean richness. Means without shared letters differ at  $P < 0.05$ . Richness did not differ significantly among sites ( $F = 0.45$ ,  $P = 0.90$ ). Canopy types are abbreviated as follows: SQ = single *Quercus gambelii* tree, DQC = dispersed *Q. gambelii* clump, QT = *Q. gambelii* thicket, and SP = single *Pinus ponderosa*.

56% below *Q. gambelii* canopy types, and 42% below *P. ponderosa*. Less than 5.3% of mean richness below all five canopy types consisted of exotic species.

Several species occurred more frequently below two or fewer canopy types (Table 3). The  $C_4$  grass *Aristida purpurea* Nutt. (Poaceae), for instance, occurred in 43% of plots in openings on the six grids this species occupied, but was absent below *Pinus ponderosa* and *Quercus gambelii* dispersed clumps and thickets. Compared to  $C_3$  species,  $C_4$  grasses occurred more frequently below openings and to a lesser extent single *Q. gambelii* than below other canopy types. In contrast, the forbs *Thalictrum fendleri* and *Lathyrus laetivirens* Greene ex Rydb. (Fabaceae) occurred most frequently below *Q. gambelii* dispersed clumps and thickets. *Pedicularis centranthera* Gray (Scrophulariaceae) also was most frequent below *Q. gambelii* canopies. No species was most frequent below *P. ponderosa*, although *Poa fendleriana* and *Elymus elymoides* maintained frequencies  $\geq 50\%$  below *P. ponderosa*.

For single *Quercus gambelii*, species richness was weakly correlated with *Q. gambelii* diameter (Pearson  $r = 0.41$ ,  $n = 50$ ), but there was large variation in richness for a given diameter (e.g., 4–16 species per 4 m<sup>2</sup> for 26 cm diameters). On the six 1-ha stem-mapped grids, richness in *Q. gambelii* dispersed clumps and thickets was negatively correlated with *Q.*

*gambelii* stem density within clumps ( $r = -0.34$ ,  $n = 60$ ) but positively correlated with basal area ( $r = 0.32$ ,  $n = 60$ ). Richness was negatively correlated with Oi thickness for *Q. gambelii* dispersed clumps and thickets ( $r = -0.48$ ,  $n = 100$ ), a relationship that strengthened when single *Q. gambelii* were included ( $r = -0.62$ ,  $n = 150$ ). Across *Q. gambelii* canopy types, richness was not correlated with mean *Q. gambelii* canopy cover ( $r = 0.06$ ,  $n = 150$ ).

Correlations between soil variables and species richness site means of *Quercus gambelii* canopy types provided little support for the hypothesis that *Q. gambelii* influence on richness changed along soil gradients (Fig. 3). Richness of *Q. gambelii* dispersed clumps, for instance, was not strongly correlated with pH ( $r = 0.05$ ,  $n = 10$ ), sand concentration ( $r = 0.11$ ), or soil moisture ( $r = -0.36$ ). One exception for *Pinus ponderosa*, however, was that richness more closely approached that of open canopy richness with increasing soil pH. Results of principal components analysis were consistent with these bivariate findings, with little relationship between multivariate combinations of soil variables and richness of canopy types (Fig. 4).

In the experimental planting, planting habitat (below *Quercus gambelii* or in openings) and planted species interacted significantly ( $F_{1,26} = 12.1$ ,  $P < 0.01$ ). *Thalictrum fendleri* survival was significantly greater below *Q. gambelii* compared to openings ( $F_{1,17} = 18.3$ ,  $P < 0.01$ ), whereas survival of *Penstemon virgatus* did not differ significantly between habitats ( $F_{1,17} = 27.6$ ,  $P = 0.58$ ). *Thalictrum fendleri* survival was constant among *Q. gambelii* canopy types, and averaged 2–7 times greater below *Q. gambelii* than in openings (Fig. 5).

**Discussion. SOILS.** Inferences were strengthened in this study for isolating tree influences from within-site abiotic variation because soil texture did not differ significantly among canopy types (Boettcher and Kalisz 1986). While tree canopies can reduce throughfall (Anderson et al. 1969), more soil moisture below trees compared to openings could be the result of several factors. Loss-on-ignition was greater below trees, suggesting increased organic matter that probably increased moisture-holding capacity (Saxton et al. 1986). Hydraulically lifted water from tree roots also

Table 3. Distributions of 17 prevalent understory species (of 123 total species) among five canopy types in *Pinus ponderosa*-*Quercus gambelii* forests, northern Arizona. Values in bold represent canopy types under which a species most frequently occurred.

Species <sup>b</sup>	No. sites <sup>c</sup>	Canopy type <sup>a</sup>				
		Open	SQ	DQC	QT	SP
% frequency when present on site						
C <sub>4</sub> graminoids						
<i>Aristida purpurea</i>	6	<b>43</b>	3	0	0	0
<i>Bouteloua gracilis</i>	6	<b>70</b>	20	10	0	0
<i>Sporobolus interruptus</i>	6	<b>43</b>	13	7	13	3
<i>Blepharoneuron tricholepis</i>	6	<b>53</b>	<b>23</b>	3	3	0
<i>Muhlenbergia montana</i>	8	<b>53</b>	<b>45</b>	<b>28</b>	18	15
C <sub>3</sub> graminoids						
<i>Carex geophila</i>	9	<b>53</b>	<b>64</b>	<b>69</b>	<b>51</b>	24
<i>Poa fendleriana</i>	10	<b>66</b>	<b>70</b>	<b>78</b>	<b>60</b>	<b>50</b>
<i>Elymus elymoides</i>	10	<b>74</b>	<b>94</b>	<b>86</b>	<b>94</b>	<b>64</b>
Forbs						
<i>Erigeron divergens</i>	10	<b>64</b>	<b>24</b>	14	8	0
<i>Lithophragma tenellum</i>	5	<b>20</b>	<b>28</b>	12	0	0
<i>Heliomeris multiflora</i>	8	<b>33</b>	<b>25</b>	15	13	0
<i>Symphyotrichum falcatum</i>	6	<b>53</b>	<b>27</b>	17	7	3
<i>Lupinus kingii</i>	6	<b>60</b>	<b>40</b>	17	20	17
<i>Eriogonum racemosum</i>	9	<b>47</b>	<b>31</b>	<b>27</b>	<b>29</b>	<b>27</b>
<i>Pedicularis centranthera</i>	6	10	<b>30</b>	<b>47</b>	<b>23</b>	7
<i>Thalictrum fendleri</i>	6	0	3	<b>27</b>	<b>27</b>	3
<i>Lathyrus laetivirens</i>	5	0	8	<b>32</b>	<b>44</b>	4

<sup>a</sup> SQ = single *Quercus gambelii* tree, DQC = dispersed *Q. gambelii* clump, QT = *Q. gambelii* thicket, and SP = single *Pinus ponderosa*.

<sup>b</sup> Photosynthetic pathways compiled from Waller and Lewis (1979).

<sup>c</sup> Number of sites ( $N = 10$  total) on which a species occurred. Percent frequencies are calculated based only on sites on which a species occurred and represent presence or absence in 4 m<sup>2</sup> plots below canopy types.

could have increased soil moisture (Horton and Hart 1998). Furthermore, thicker Oi horizons combined with shading below trees likely affected microclimates and reduced evaporation (Parker and Muller 1982). For example, Evenson et al. (1980) found that light intensity in summer was 48% lower below *Pinus ponderosa* canopies and 69% lower below *Quercus gambelii* canopies relative to openings in northern Utah. At a 7.5 cm depth in the mineral soil in June–July, Boyle et al. (2005) reported that temperatures were approximately 0.5–2°C cooler below canopies of old *P. ponderosa* than in openings in northern Arizona.

Consistent with Klemmedson (1987), *Quercus gambelii* did not affect mineral soil pH. Klemmedson (1987) found that pH of freshly fallen *Q. gambelii* leaves was 4.9 (less than our measured mineral soil pH values; Table 2) compared to 3.9 for *Pinus ponderosa* needles. Stand-level pH of only the Oi+e horizon increased in his study with increasing *Q. gambelii* relative to *P. ponderosa*. While all three *Q. gambelii* canopy types in our study consistently increased LOI, absolute amounts

occurring under a given canopy type strongly depended on the site. Loss-on-ignition below *Q. gambelii* thickets, for instance, ranged from 4% on dry limestone/chert soils at the Garjon Tank site, to 16% on loamy benmoreite soils at Fisher Tank. These changes were approximately proportional to changes in open canopy LOI along the gradient, however, suggesting that *Q. gambelii* effects on measured soil properties did not change along the sampled soil gradient.

**SPECIES RICHNESS AND DIVERSITY.** While all tree canopies reduced understory species richness and diversity relative to openings, *Quercus gambelii* effects depended on canopy type (Fig. 2). Different growth forms of *Q. gambelii* differentially affected richness. While there might be a minimum diameter (and age) below which *Q. gambelii* does not affect species richness (Everett et al. 1983), richness for single *Q. gambelii* was not strongly correlated with stem diameter across our range of sampled diameters (7–77 cm). Based on *Q. gambelii* diameter-age regressions developed from Fulé et al. (1997) within the study area,

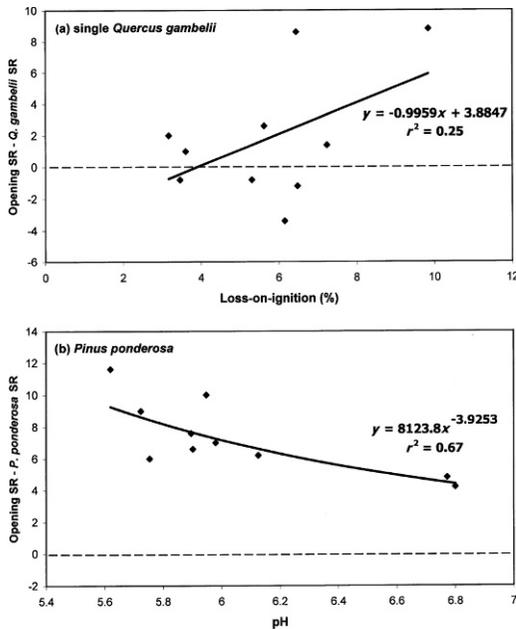


FIG. 3. Bivariate examples of influences of (a) single *Quercus gambelii* and (b) *Pinus ponderosa* on understory plant species richness (SR; 4 m<sup>2</sup>) along soil gradients in *P. ponderosa-Q. gambelii* forests, northern Arizona. Tree influences are relativized for each site by subtracting from open-area SR, and soil variables represent site means averaged among canopy types. To support the hypothesis that positive tree influences on richness changed along these soil gradients, relativized SR would be near zero or negative at a soil extreme.

estimated ages of our sampled single *Q. gambelii* ranged from 66–377 yr. *Quercus gambelii* clones, however, may be older than the oldest living stem (Harper et al. 1985). Differing from our results, Everett et al. (1983) found that tree size and age affected understory composition in northern Nevada *Pinus monophylla* Torr. & Frém. (Pinaceae) woodlands. Consistent with our results, however, Haworth and McPherson (1994) reported that diameters of *Quercus emoryi* Torr. (Fagaceae; ranging from 12–48 cm diameter) did not affect understory plant composition in south-eastern Arizona *Quercus* woodlands.

Stem density and basal area were not strongly correlated with understory richness for *Quercus gambelii* dispersed clumps and thickets. Differences in richness between these canopy types instead could be partly related to stem spacing, with the closely spaced stems in thickets resulting in reduced richness. Variations in herbivory or wildlife habitat also

could have contributed to these differences (Scholes and Archer 1997).

**SPECIES COMPOSITION.** Within-site tree distribution in *Pinus ponderosa-Quercus gambelii* forests constrains distributions of understory plant species. All five prevalent C<sub>4</sub> grasses occurred more frequently in openings than under any tree canopy, while three C<sub>3</sub> graminoids were relatively frequent under both openings and tree canopies (Table 3). These data support the theory that C<sub>4</sub> species are most competitive in warm, dry environments (Sage and Monson 1999). While not exclusively occurring below *Q. gambelii*, the forbs *Thalictrum fendleri*, *Lathyrus laetivirens*, and to a lesser extent *Pedicularis centranthera*, were strongly associated with *Q. gambelii*. Similar to differential influences of *Q. gambelii* canopy types on species richness, *T. fendleri* and *L. laetivirens* were more prevalent below *Q. gambelii* dispersed clumps and thickets than under single *Q. gambelii*. Apparently these species are fairly shade tolerant, and their positive association with these canopy types could result from shading or favorable moisture or nutrient regimes (Table 2; Klemmedson 1987). Greater survival of *T. fendleri* below *Q. gambelii* than in openings in the experimental planting supported the correlational finding of *T. fendleri* being more prevalent below *Q. gambelii* (Fig. 5). However, *T. fendleri* survival did not differ among *Q. gambelii* canopy types in the experimental planting, as its distribution did in the correlational findings. Inferences could be strengthened in a future experimental planting, however, by including additional sites and attempting to more closely isolate potential reasons for differences in survival, such as controlling for animal activity which may differ between openings and below trees (Scholes and Archer 1997).

Our study supports previous investigations in other parts of *Quercus gambelii*'s range that have found positive associations between *Q. gambelii* and some understory species. In western Colorado, Brown (1958) reported that *Carex geyeri* Boott (Cyperaceae) biomass averaged 229 kg/ha below *Q. gambelii* compared to only 28 kg/ha in openings. Evenson et al. (1980) in Utah also found that *C. geyeri* was abundant below *Q. gambelii*, in addition to *Pseudostellaria jamesiana* (Torr.) W.A. Weber & R.L. Hartman (Caryophyllaceae).

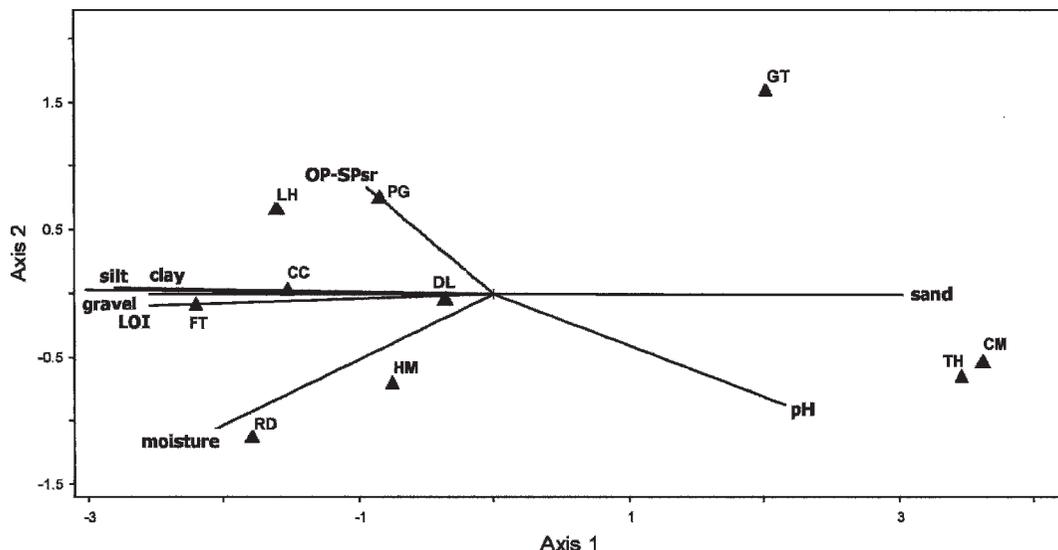


FIG. 4. Principal components analysis ordination of site soil means for ten sites along a soil parent material gradient in *Pinus ponderosa-Quercus gambelii* forests, northern Arizona. Component 1 extracted 73% of variance and component 2 extracted 10%. Vectors are soil variables and relativized effects of canopy types on species richness. With the possible exception of a pH  $\times$  species richness interaction for *P. ponderosa* canopies, data did not provide strong evidence that influences of canopy types on richness changed along multivariate soil gradients. Vector abbreviations are as follows: moisture = gravimetric soil moisture, LOI = loss-on-ignition, and OP-SPsr = relativized open canopy species richness minus *P. ponderosa* species richness. Site abbreviations represent the first two words of site names given in Table 1.

Apparently associated species vary regionally, but a few species occur most frequently below *Q. gambelii* in several regions within its range.

PLANT-PLANT INTERACTIONS ALONG ENVIRONMENTAL GRADIENTS. Research has been conflicting in evaluating the hypothesis that positive plant-plant interactions (e.g., nurse plants) are more prevalent in stressful environments within landscapes (Mordelet and Menaut 1995). Our study sites span fairly wide soil texture, pH, and productivity gradients within this regional climate (Fig. 4), a conclu-

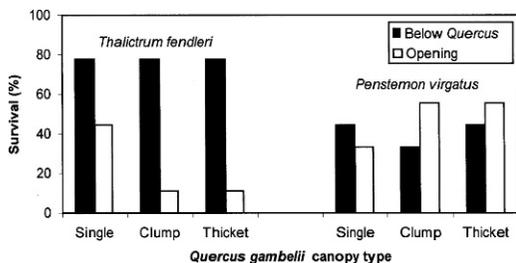


FIG. 5. Survival of *Thalictum fendleri* and *Penstemon virgatus* outplanted below three *Quercus gambelii* canopy types and in openings, northern Arizona.

sion supported by significant statistical differences among sites (Table 2). However, we did not find strong evidence that *Quercus gambelii*'s influence on soils or species richness or composition was more intense on dry sites or changed in detectable ways along our sampled gradient. For example, *Thalictum fendleri* was associated with *Q. gambelii* on both the lowest and highest soil pH sites (5.6 at Fisher Tank and 6.8 at Campbell Mesa). However, we did not sample *Q. gambelii* in riparian areas or canyons in the study area, which may affect the perceived length of our sample gradient (Callaway 1997). Also, *Q. gambelii* is infrequent on some productive basalt and limestone soils in the study area that do support *T. fendleri*. Experimentally testing for positive interactions using species removals or additions across environmental gradients may contribute further insights about canopy-tree influences along environmental gradients in these forests (Moir 1966). The experimental planting that we conducted at one site, for example, could be extended to additional sites.

MANAGEMENT IMPLICATIONS. *Pinus ponderosa-Quercus gambelii* forests consist of mosaics

of tree influences inducing within-site soil and understory plant patterns (Zinke 1962, Finzi et al. 1998). Results suggest that manipulating tree densities and spatial patterns will affect distributions of soil properties and understory species. For *Q. gambelii* canopy types, dispersed clumps seem to provide a compromise between maintaining fairly high species richness (Fig. 2), while providing habitat for the three plant species associated with *Q. gambelii* in our study (Table 3). *Quercus gambelii* thickets exhibited depressed species richness, probably because of their dense, closely spaced stems, many of which are small diameter (< 15 cm). Densities of small-diameter *Q. gambelii* and *P. ponderosa* trees are thought to have sharply increased in *P. ponderosa*-*Q. gambelii* forests beginning in the late 1800s after human exclusion of frequent fires (Fulé et al. 1997). Thinning dense *Q. gambelii* thickets may increase understory richness below them. Thinning *P. ponderosa* to create canopy openings probably improves habitat for C<sub>4</sub> grasses that we did not find growing below *P. ponderosa*. Our study suggests that manipulating not only *P. ponderosa* and *Q. gambelii* densities, but also the specific growth form of *Q. gambelii*, affects the richness, composition, and distribution of understory species.

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