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Habitat relationships and management implications for *Lesquerella filiformis* Rollins (Missouri bladderpod) on a xeric limestone prairie[1,2]

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Young, C. C. (National Park Service, Heartland Inventory and Monitoring Program, 6424 W. Farm Road 182, Republic, MO 65738), L. W. Morrison (National Park Service, Heartland Inventory and Monitoring Program, 6424 W. Farm Road 182, Republic, MO 65738 and Department of Biology, Missouri State University, Springfield, MO 65897), and J. L. Haack (National Park Service, Heartland Inventory and Monitoring Program, 6424 W. Farm Road 182, Republic, MO 65738). Habitat relationships and management implications for *Lesquerella filiformis* Rollins (Missouri bladderpod) on a xeric limestone prairie. J. Torrey Bot. Soc. 136: 233–241. 2009.—In xeric limestone prairies (XLPs, also known as "glades"), soil depth and fire are commonly posited to affect plant community composition and structure. Through mediating plant competition, these factors may explain plant distribution in XLPs, including mechanisms driving edaphic endemism. In a XLP in southwest Missouri, the abundance of *Lesquerella filiformis* Rollins (Missouri bladderpod), a rare winter annual, was higher in open sites, where competition was presumably low, than in *Juniperus virginiana* L. (eastern redcedar) or hardwood canopy cover types; *L. filiformis* density in the latter two cover types varied among years. Open, *J. virginiana*, and hardwood canopy cover types were distributed along an increasing soil depth gradient. During flowering of *L. filiformis* in April, photosynthetically active radiation was highest in open sites, intermediate below hardwood canopy (prior to leaf-out), and lowest below *J. virginiana* canopy. Removing *J. virginiana* was associated with greater increases in *L. filiformis* abundance between 2003 and 2005, and the basal area removed was positively associated with the magnitude of increase in plant abundance. These findings supported the hypothesis that interspecific competition, presumably at least partly for light, limited the distribution of *L. filiformis* in XLPs. While higher plant densities indicated that *L. filiformis* preferred open microhabitats, thinning *J. virginiana* provided a management option that increased *L. filiformis* density in marginal habitats subject to woody plant encroachment. Because factors affecting *L. filiformis* germination, establishment, growth, and survival likely vary along relatively fine-scale environmental gradients, (micro-) habitat specific management of XLP vegetation may assist in protecting rare edaphic endemic plant species, such as *L. filiformis*.

Key words: glade, *Juniperus virginiana*, *Lesquerella filiformis*, Ozarks, photosynthetically active radiation, soil depth gradient, xeric limestone prairie.

Patterns in plant community composition and structure in xeric limestone prairies (XLPs; sensu Baskin and Baskin 2000) are commonly attributed to two factors: soil depth and fire (Anderson et al. 1999, Jenkins and Jenkins 2006, Baskin et al. 2007). For example, *Sporobolus vaginiflorus* (Torr. ex A.Gray) Alph. Wood (poverty dropseed), a C_3 perennial grass, was locally dominant in shallow-soil (<10 cm) microhabitats in XLPs of central Kentucky, while the C_4 perennial grass, *Schizachyrium scoparium* (Michx.) Nash (little bluestem), was dominant over a wider range of soil depths (Lawless et al. 2006). As soil depths in XLPs range from a few cm (Kucera and Martin 1957) to over 1 m (Lawless 2006 et al.), periodic fire is likely required to prevent canopy closure in XLP microhabitats with depths sufficient to support tree establishment

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[2] Karola Mlekush assisted with plant identification. Tyler Cribbs, Karola Mlekush, and Melanie Weber assisted with field work. We thank Dawn Beaulac and Dr. Michael Kelrick for providing the 2003 plant density data.

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(Baskin and Baskin 2000). Effective fire control following European settlement (Guyette and McGinnes 1982) and overgrazing during the period of open-range in Missouri (Nelson 2005) may have promoted the dramatic increase in *Juniperus virginiana* L. (eastern redcedar) cover observed in XLPs (Kimmel and Probasco 1980, Lowell and Astroth 1989).

Like many winter annual plants, the edaphic endemic *Lesquerella filiformis* Rollins (Brassicaceae) grows in sparsely vegetated, shallow-soil microhabitats in XLPs (Thomas 1996). A commonly held concept of plant species distribution in XLPs may also explain the distribution of *L. filiformis*: small-statured plants, such as winter annuals, tolerate or avoid environmental stresses associated with shallow-soil microhabitats, while plants with superior competitive abilities colonize deeper-soil microhabitats and effectively exclude shallow-soil specialists (Ware 1969, Baskin et al. 1972, Sharitz and McCormick 1973 cited in Ware 2002). High inter-annual variability in *L. filiformis* population sizes (Morrison et al. 2008) that presumably reflects environmentally-controlled, density-independent demographic change circumstantially corroborates this view (Thomas 1996). Growth over a range of substrate conditions, combined with findings of low competitive abilities in greenhouse studies and photosynthetic rates that indicate strong shade intolerance, suggest that high light requirements account for edaphic endemism in numerous plant species of rock outcrops (Baskin and Baskin 1988). Winter annuals, including *L. filiformis* (pers. obs.), grow occasionally in deeper soils of XLPs, often prior to leaf-out or where biomass of perennial plants is removed (Baskin and Baskin 1985). To mimic such disturbances, land managers use cutting and prescribed fire to reduce *Juniperus virginiana* canopy cover in XLPs, which may increase habitat suitability for plant species such as *L. filiformis* (Nelson 2005).

While reducing competition is expected to benefit edaphic endemic plant species in areas with deeper soils, this mechanism is rarely explicitly tested in XLPs. In this study, we provide evidence for mechanisms driving edaphic specialization. We correlate changes in the abundance and habitat of *Lesquerella filiformis* along a soil depth gradient and evaluate the response of *L. filiformis* to *Juniperus virginiana* removal. Specifically, we tested the following hypotheses: 1) density of *L. filiformis* is highest in areas of shallow soil, where interspecific competition is presumably low, 2) in contrast to *J. virginiana*- and hardwood-dominated forests, open habitats are correlated with relatively shallow soil depths and high insolation, and 3) removal of *J. virginiana* increases *L. filiformis* abundance.

Materials and Methods. POPULATION AND STUDY AREA. *Lesquerella filiformis* Rollins—the Missouri bladderpod—is an outcrop-endemic, winter annual plant found in southwestern Missouri to west-central Arkansas (Yatskievych 2006). *Lesquerella filiformis* germinates in late summer to autumn, overwinters as a rosette, and flowers, sets seed, and senesces in spring or early summer. XLPs in the Ozarks region are often referred to as "glades" and, due to the prominence of *Juniperus virginiana* near such outcrops, also as "cedar glades". Despite this common usage, Baskin and Baskin (2000) recommend the term "xeric limestone (or dolomite) prairie" to differentiate these Ozarks plant communities from "cedar glades" of the southeastern United States. Distinguishing characteristics of XLPs include dominance of C_3 forbs and C_4 perennial grasses (particularly *S. scoparium*), periodic disturbances that maintain open site conditions, paucity of primary successional seres of cryptogams and annual forbs, and highly variable soil depths (Lawless et al. 2006, Baskin et al. 2007). As soil depth in Ozarks XLPs increases from bare rock to deeper soils, vegetation generally shifts from 1) cryptogams to 2) winter annuals and small succulents to 3) summer annual dicots and annual grasses to 4) perennial dicots and grasses to 5) *J. virginiana* (eastern redcedar) woodland (Ware 2002). Deeper soils on the XLP periphery support *J. virginiana*, hardwood, or mixed forests.

Bloody Hill Glade (hereafter BHG) is a 3.4-ha limestone XLP in Wilson's Creek National Battlefield, Republic, Missouri (37.10N, 93.41W) that supports a relatively large *Lesquerella filiformis* population (Thomas 1996). Populations on the Springfield Plateau, such as the one studied at the battlefield, occur on calcareous outcrops associated with the Burlington-Keokuk formation of the Mississippian period (Nelson and Ladd 1983, Nelson 2005). These outcrops typically support narrow, small-patch communities on steep slopes, compared to the more expansive dolomite

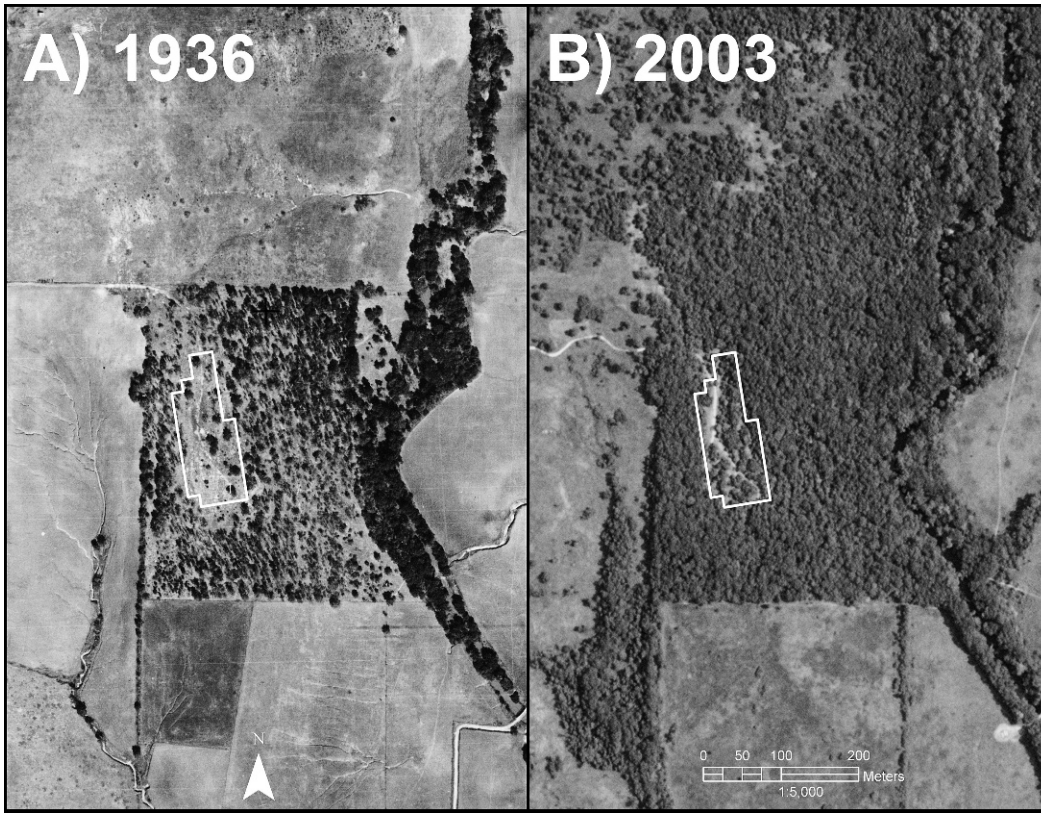

FIG. 1. Forest cover at Bloody Hill Glade, Wilson's Creek National Battlefield in (A) 1936 and (B) 2003. The study area boundary is shown in white.

outcrops in the Ozarks region. Shallow Gasconade series soils, classified as clayey-skeletal, mixed, superactive, mesic Lithic Hapludolls (NRCS 2008), with an interspersed limestone rock outcrop, characterize the site.

Using aerial photographs, an increase in forest cover at BHG between 1936 and 2003 was identified (Fig. 1). A 2000 color infrared satellite image showed that *Juniperus virginiana* accounted for a high portion of this increase. Accounts from the Battle of Wilson's Creek described site conditions at BHG in 1861 as "bare and imbedded with rock and gravel" and "covered with stunted or scrub oak trees" (John Millner Associates, unpublished data). This description contrasts with the well developed patches of *J. virginiana* and hardwood trees currently encountered on the site.

DENSITY CLASS ESTIMATES. BHG was divided into an orthogonal grid of 477, 5 × 5 m plots; this 1.1925 ha area included the great majority of *Lesquerella filiformis* plants at BHG. The 5 × 5 m plot corners were temporarily marked based on surveyed and permanently marked locations at 15 m intervals. In 2003, 2005, 2007, and 2008, six observers, usually working independently, estimated densities of *L. filiformis* plants in the 477 plots using a density class scale: 0 = no plants, 1 = 1–9 plants, 2 = 10–49 plants, 3 = 50–99 plants, 4 = 100–499 plants, 5 = 500–999 plants, 6 ≥ 1,000 plants (Young et al. 2008). Prior to the survey, observers calibrated their estimates against complete counts. Surveys were conducted in mid-April to early May during peak flowering.

JUNIPERUS VIRGINIANA BASAL AREA. During a restoration project in July 2004, slightly less than half (43.6%) of all *Juniperus virginiana* stems attaining breast height at BHG were cut to reduce canopy cover and removed from the site. This project intended to thin, by one-third to one-half, stems of all size classes across the entire site. In 2006, we measured the basal area of *J. virginiana* stems attaining breast height (1.37 m) in all 477 plots as a proxy for basal

area the year after cutting in 2005. In April 2008, we measured the stump basal area of all *J. virginiana* stems felled in 2004. Using these datasets, we reconstructed *J. virginiana* basal area in 2003, prior to cutting, and in 2005, following the cutting.

Cut and uncut plots were distributed haphazardly where *Juniperus virginiana* occurred across the study area. Of the total 477 plots, 183 contained no *J. virginiana*. In the remaining 294 plots, the number of cut and uncut plots was even with *J. virginiana* removed from exactly one-half ($n = 147$). Initial *J. virginiana* basal area differed among cut and uncut plots with an average basal area of 13.16 $cm^2\ m^{-2}$ and 5.53 $cm^2\ m^{-2}$, respectively. Because sites were not randomized before cutting, it is possible that tree removal could be correlated with confounding environmental variables. Given the relatively large number of cut and uncut plots, however, and their overall distribution across the study area, any potential environmental gradients across the glade were not likely an important source of bias.

The proportion of stems removed was relatively consistent across size classes. For stem dbh categories 0.1–5.0 cm, 5.1–10.0 cm, 10.1–15.0 cm, 15.1–20.0 cm, and 20.1–30.0 cm, 45.2% (n = 259), 43.7% (n = 180), 38.1% (n = 69), 48.6% (n = 17), and 30.1% (n = 4) of stems were cut, respectively. The basal area of *Juniperus virginiana* removed ranged from 0.11 to 60.00 $cm^2\ m^{-2}$ with an average of 9.69 $cm^2\ m^{-2}$. Following cutting, the average basal area of 3.48 $cm^2\ m^{-2}$ was relatively similar to uncut plots. As a percentage, basal area reduction tended to be high with removal of greater than 50% in 77.9% of plots, greater than 75% in 55.8% of plots, and 100% in 40% of plots.

HABITAT MAPPING. In April 2008, we mapped habitat cover types at BHG with a Trimble GeoXT GPS unit in the field using the following habitat categories: open, *Juniperus virginiana* cover, and hardwood forest cover (Fig. 2). Open habitat included several distinct physiognomic zones without a significant tree canopy. These zones included low-growing and often sparse vegetation near rock outcrops, annual grasses (e.g., *Panicum flexile* (Gattinger) Scribn. (wiry panic grass), *Sporobolus vaginiflorus*, native warm season grasses (e.g., *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), *Panicum virgatum* L. (switchgrass), *Schizachyrium scoparium*, *Sorghastrum nutans* (L.) Nash (indiangrass)), or, in fewer instances, low woody shrubs (e.g., *Celtis tenuifolia* Nutt. (dwarf hackberry), *Rhus aromatica* Aiton (fragrant sumac), *Symphoricarpos orbiculatus* Moensch (coralberry)). Our observations in the field indicated that within the open habitat, the highest *Lesquerella filiformis* densities were associated with the rocky sites, while lower densities were found in zones with taller vegetation. *Juniperus virginiana* cover and hardwood forest cover were defined by areas of continuous canopy. Visitor trails were excluded from the cover categories. After developing a habitat cover map in a GIS, we intersected a layer of each 5 × 5 m plot ($n = 477$) with the map to calculate the area of each habitat cover type per plot.

ENVIRONMENTAL VARIABLES. In April 2008, we measured two additional environmental variables in the field: soil depth and photosynthetically active radiation (PAR). At four equidistant points in each 5 × 5 m plot, observers inserted pin flags vertically until bedrock was encountered to measure soil depth. Average soil depth was calculated for each plot. We measured PAR ($\mu mol\ sec^{-1}\ m^{-2}$ in the 400 to 700 nm wavelength) at each plot center, using LI-COR LI-250 light meters with LI-190 quantum sensors (LI-COR Biosciences, Lincoln, Nebraska). Observers used two-way radios to synchronize simultaneous measurement in an area with full sunlight. The fraction of full sunlight was calculated to characterize light conditions in each plot.

STATISTICAL ANALYSIS. Prior to analysis of *Lesquerella filiformis* density patterns and habitat relationships, we classified each plot according to dominant habitat cover type (i.e., the single cover type that constituted >50% of the plot area). A total of 248, 117, and 61 plots were classified as open, *Juniperus virginiana*, or hardwood forest habitats, respectively. Plots without a dominant cover type were eliminated from further analysis (n = 51). To evaluate the relationship between habitat type and *L. filiformis* density, Kruskal-Wallis tests were employed, using the midpoints of the density class categories. Data from 2007, a year of moderate *L. filiformis* density, and 2008, a year of relatively low density, were analyzed because of their proximity to the date of habitat mapping. To evaluate the relationship between habitat type and soil depth, a one-

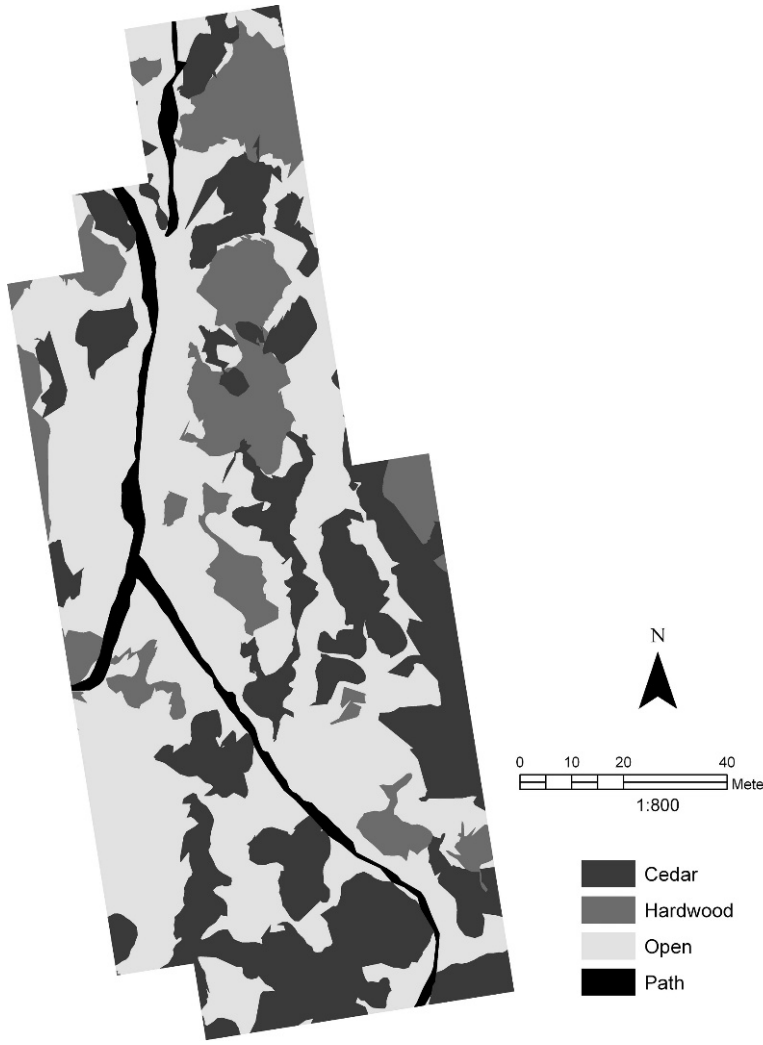

FIG. 2. Habitat cover types in the study area at Bloody Hill Glade, Wilson's Creek National Battlefield. Habitat cover types include treeless areas characterized as "open", *Juniperus virginiana* canopy, and hardwood forest canopy. Footpaths are shown, but were not included in the analyses.

way ANOVA was used. Because PAR data did not appear to come from a normal distribution—and transformations were unsuccessful in normalizing the data—the relationship between habitat type and PAR was analyzed with a Kruskal-Wallis test.

To evaluate the relationship between *Lesquerella filiformis* density class in 2003, prior to cutting, and *Juniperus virginiana* basal area, we used a one-way ANOVA following a $\log_{10}$ transformation of basal area to normalize the distribution. A chi-square test was applied to determine whether plots in which *J. virginiana* was removed in 2004 experienced relatively greater increases in *L. filiformis* abundance from 2003 to 2005. To elucidate the relationship between the amount of *J. virginiana* removed and the change in *L. filiformis* density class, a one-way ANOVA was employed following a square root transformation of the removed *J. virginiana* basal area to normalize the data. Dunnett's T3 multiple comparison procedure, which does not assume equal variances, was applied following the ANOVA to test for differences among the factor level means. SPSS 16.0.1 for Mac OSX (SPSS 2007) was used for all analyses.

Results. *LESQUERELLA FILIFORMIS* DENSITY. *Lesquerella filiformis* density varied signifi-

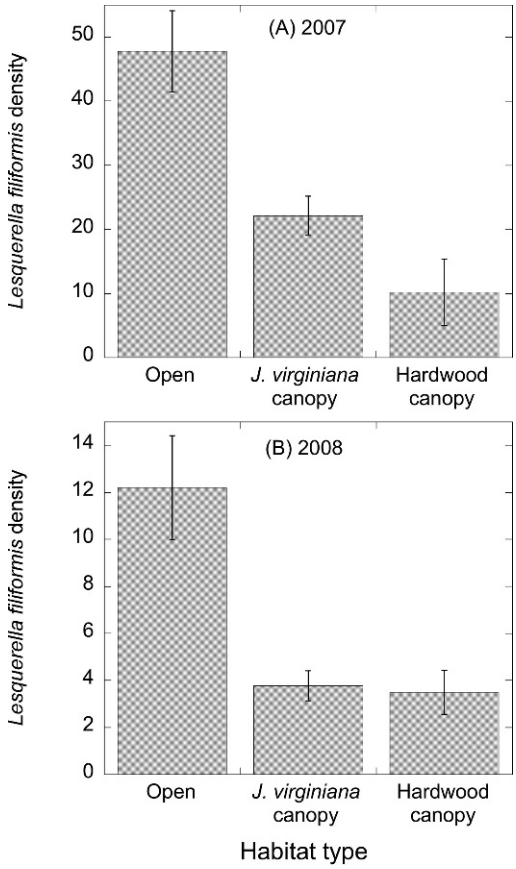

FIG. 3. *Lesquerella filiformis* density (plants per 5 × 5 m plot) as a function of habitat type for (A) 2007 and (B) 2008. Note differences in *y*-axes. Error bars indicate ±1 SE.

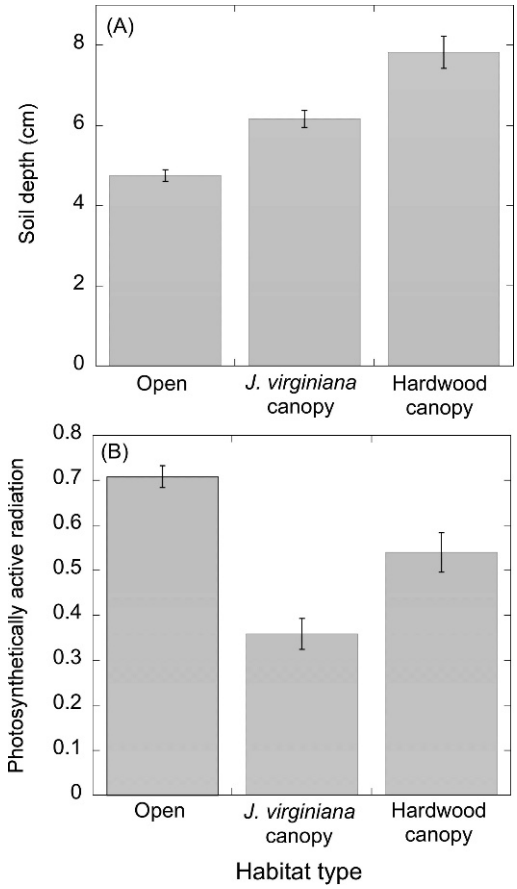

FIG. 4. Soil depth (A) and photosynthetically active radiation (B) as a function of habitat type. Error bars indicate ±1 SE.

cantly with habitat cover type (2007: $\chi^2 = 43$, $P < 0.001$, df = 2; 2008: $\chi^2 = 21$, $P < 0.001$, df = 2; Kruskal-Wallis tests) and was highest in open areas in 2007 and 2008 (Fig. 3). *Lesquerella filiformis* densities were higher in *Juniperus virginiana* habitat compared to hardwood forest habitat in 2007, but were similar in 2008.

HABITAT RELATIONSHIPS. Soil depth ($F = 45$, $P < 0.001$, df = 2, 423; one-way ANOVA) and photosynthetically active radiation (PAR) ($\chi^2 = 66$, $P < 0.001$, df = 2; Kruskal-Wallis test) varied significantly among the three habitat types (Fig. 4). Average soil depth was most shallow in the open habitat, intermediate in *Juniperus virginiana* habitat, and deepest in hardwood forest habitat. Average PAR was highest in the open habitat, intermediate in hardwood forest habitat, and lowest in *J. virginiana* habitat.

JUNIPERUS VIRGINIANA REMOVAL EFFECTS. In *Juniperus virginiana* plots, *Lesquerella filiformis* density class, prior to cutting, was negatively associated with *J. virginiana* basal area (Fig. 5). A one-way ANOVA revealed a significant difference among the means of the density classes ($F = 6.6$; df = 4, 289; $P < 0.0001$).

The *Lesquerella filiformis* population size at BHG was higher in 2005 than in 2003 (Morrison et al. 2008), with 201 plots increasing, 84 plots stable, and 9 plots decreasing in density class. The distribution of plots as a function of change in plant density differed significantly, however, depending upon whether or not *Juniperus virginiana* was removed (Table 1). Plots in which no change occurred or in which density class changed by one (increasing or decreasing) were more often those where no *J. virginiana* stems had been

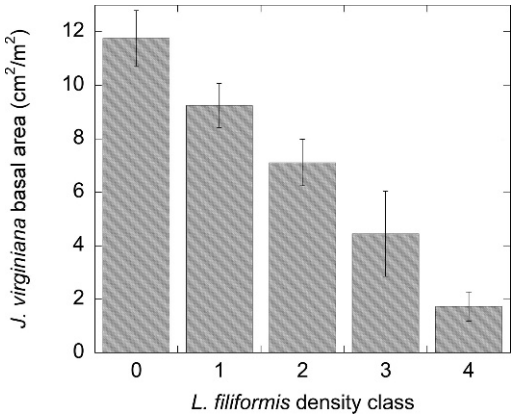

FIG. 5. *Lesquerella filiformis* density class as a function of *Juniperus virginiana* basal area ($cm^2\ m^{-2}$) in 2003. Error bars represent ±1 SE. Only plots with *J. virginiana* present ($n = 294$) are included.

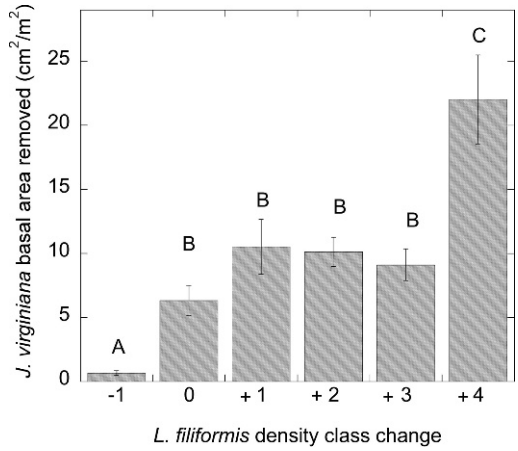

FIG. 6. *Lesquerella filiformis* density class change from 2003 to 2005, as a function of *Juniperus virginiana* basal area ($cm^2\ m^{-2}$) removed in 2004. Error bars represent ±1 SE. Only plots in which *J. virginiana* was removed ($n = 147$) are included. Letters represent significantly different means according to a Dunnett's T3 multiple comparison procedure (which does not assume equal variances) following a one-way ANOVA.

removed ($\chi^2 = 35$, $P < 0.0001$, df = 5, $N = 294$) (Table 1). In contrast, plots in which density class increased by two or more were more often those where *J. virginiana* had been removed. In the 32 plots in which density class increased by three or four, *J. virginiana* had been removed in 29 (91%).

Furthermore, greater *Juniperus virginiana* basal area removal corresponded positively with the magnitude of increase in density class (Fig. 6). A one-way ANOVA revealed a significant difference among the means of the density class changes ($F = 5.4$; $df = 5, 141$; $P < 0.0001$). Decreases in *Lesquerella filiformis* abundance were associated with very small amounts of *J. virginiana* removal, whereas moderate amounts of removal were associated with changes of 0 to +3 density classes. Removal of larger amounts of *J. virginiana* was associated with an increase of four density classes.

Table 1. Change in density class of *Lesquerella filiformis* from 2003 to 2005, as a function of removal or not of *Juniperus virginiana* in 2004. Observed values are number of 5 × 5 m plots; expected values are in parenthesis. Density class scale: 0 = no plants, 1 = 1–9 plants, 2 = 10–49 plants, 3 = 50–99 plants, 4 = 100–499 plants, 5 = 500–999 plants, 6 ≥ 1,000 plants.

Density class change from 2003 to 2005	*J. virginiana* not removed	*J. virginiana* removed
−1	6 (4.5)	3 (4.5)
0	52 (42.0)	32 (42.0)
+1	52 (42.0)	32 (42.0)
+2	34 (42.5)	51 (42.5)
+3	3 (12.0)	21 (12.0)
+4	0 (4.0)	8 (4.0)
Total number of plots	147	147

Discussion. In 2007 and 2008, moderate- and low-abundance years, respectively, *Lesquerella filiformis* density was highest in open habitat, which included characteristic rocky microhabitats in XLPs. Furthermore, open habitats, which accounted for over half of the XLP area at BHG, were associated with the shallowest soil depth and highest PAR measurements. *L. filiformis* abundance decreased on an increasing soil depth-vegetation gradient along which photosynthetically active radiation (PAR) varied. *L. filiformis* densities were higher below *Juniperus virginiana* canopy than below hardwood forest canopy in 2007, but were similar in 2008. Soil depth was greater in hardwood forest habitat than in *J. virginiana* habitat, while PAR during *L. filiformis* flowering in April and prior to leaf-out was greater below hardwood canopy than below evergreen *J. virginiana* canopy. While differences in average soil depth among habitats were statistically different, the average depths reflected generalized depths at a 25 m^2-scale. The actual rooting depths required to support trees are likely deeper and found in cracks, fissures, and depressions in the bedrock (Ware 2002, Nelson 2005).

In this study, *Lesquerella filiformis* abundance was positively associated with *Juniperus virginiana* removal. Additionally, increases in abundance following treatment were proportional to the basal area removed. These findings support the observation that increased competition in deeper soil microhabitats at least partially accounts for edaphic endemism in *L. filiformis*. Because land managers removed *J. virginiana* following flowering and senescence of *L. filiformis*, its increased abundance was not related to increased fecundity of adult plants. Rather, cutting increased rates of germination, seedling establishment, or overwintering rosette survival. In *J. virginiana* forest, which accounted for only 30.4% of the study area at BHG, mechanical clearing appeared to be an effective option for increasing habitat suitability for winter annuals, such as *L. filiformis*, in XLPs experiencing *J. virginiana* encroachment. We note that this study focused primarily on *J. virginiana* and hardwood forest habitat inclusions within an XLP. Future studies could focus on the effectiveness of mechanical clearing in extending habitat suitability on the periphery of XLPs.

The rapid plant response following *Juniperus virginiana* removal suggests that light may be the limiting resource affecting *Lesquerella filiformis* density. A high photosynthetic photon flux density requirement is a common characteristic of outcrop endemic plants (Baskin and Baskin 1988). Light, however, may not be the only limiting factor that changes following *J. virginiana* removal. Soil temperature and evaporative demand may increase, although changes in transpiration rates may result in a net increase in soil moisture as was observed in an old field (Meiners and Gorchov 1998). The direction of change in litter depth, decomposition, and nutrient availability may depend on response in the herbaceous stratum and the resulting change in litter quality (Norris et al. 2001). Our observations provided a case-in-point that factors other than light may also be limiting. Although light availability was higher below hardwood forest canopy than below *J. virginiana* canopy, *L. filiformis* density was equal or lower in one of two years. In hardwood forests, factors such as leaf litter, soil depths at fine scales, or competition in lower forest strata may also limit *L. filiformis* abundance.

Our observations in this study generally support Ware's (2002) hypothesis regarding plant distribution in XLPs: drought tolerance or avoidance likely explains high *Lesquerella filiformis* abundance in open, shallow-soil microhabitats, while competition limits its abundance in deeper soils. While not delineated in this study, the open microhabitats may be further differentiated, following Thomas (1996) and Ware (2002), as consisting of sparsely vegetated microhabitats near exposed bedrock, microhabitats supporting increasing forb cover, and microhabitats with dominant C_4 perennial grass cover. As with other winter annuals in rocky microhabitats, reproduction prior to summer droughts or dormancy in a persistent seed bank may allow *L. filiformis* to avoid or tolerate stress, respectively (Baskin and Baskin 1985). The functional traits that facilitate life-cycle completion may vary, however, within these finer-scale open microhabitats. For example, by completing reproduction in April and May prior to seasonal growth in open, perennial, C_4 grass-dominated sites, *L. filiformis* may avoid competition rather than environmental stress per se. Below a forest canopy, particularly following disturbances, a persistent seed bank or dispersal traits may allow *L. filiformis* to exploit microsites with sufficient light to meet photosynthetic requirements.

Given that occupancy of multiple microhabitats may contribute to the long-term viability of *Lesquerella filiformis* populations in isolated XLPs, management actions should be microhabitat-specific. For example, trampling, which reduced *L. filiformis* survival at BHG (Thomas and Willson 1992), may be more severe in shallow soils near outcrops on XLPs. On the other hand, fire is likely unimportant in maintaining plant species in such microhabitats, but may be important in grass-dominated and forested microhabitats. Fire dramatically reduced woody stem densities, including those of *Juniperus virginiana*, in a savanna-glade complex in Arkansas (Jenkins and Jenkins 2006) and in the Ketona dolomite glades of Bibb County, Alabama (Duncan et al. 2008). In this study, *J. virginiana* removal increased habitat suitability in habitats that are marginal compared to open microhabitats. Land managers must nevertheless cautiously manage XLPs. Reintroduction of fire at Ketona Glades resulted in immediate post-fire declines in three of 14 species of concern, although populations recovered during the second year. In a study at BHG, shaded

microhabitats supported higher rates of *L. filiformis* survivorship during one year, while survival rates were higher in rocky microhabitats during another year (Thomas 1996). With this in mind, managers must carefully consider microhabitat-specific responses to management, as well as XLP size, microhabitat abundance and distribution, and current and historical population sizes of edaphically-restricted plant species in relation to land-use history. In addition to immediate and long-term monitoring of XLP plant population responses (including lag effects) to management actions, controlled demographic studies on multiple XLP sites are needed to experimentally evaluate management effectiveness and to further evaluate the findings of this study across a broader range of sites.

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