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RESEARCH NOTE

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Plant Endemism on Mancos Shale Barrens

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ABSTRACT: During the past decade, three previously undescribed vascular plant species have been documented growing on Mancos Shale barrens in southwest Colorado. Soil chemistry has been correlated with the presence of some rare endemics elsewhere, such as species growing on serpentine soils. However, research on shale barrens suggests that structural components, rather than unique chemistry, more strongly influence endemism on this substrate. The effect of the structural characteristics of the barrens soil was examined in connection with the presence of cushion bladderpod (*Physaria pulvinata*), a rare barrens endemic. The results suggest that *P. pulvinata* may be uniquely suited to the shallow soil and low moisture characteristic of the shale barrens habitat. The need for long-term monitoring and management is discussed.

Index terms: drought, edaphic endemism, Mancos Shale barrens, *Physaria pulvinata*, shallow soils, southwest Colorado

INTRODUCTION

Rare, endemic plant species are often associated with unusual substrates, such as mine tailings, salt flats, and, more pervasively, geologic formations. These substrates, and the soils derived from the parent material, function to create discontinuity and diversity within the larger environments in which they occur (Kruckeberg 1986; Macnair 1987; Rajakaruna 2004). California, the Mediterranean, and the Cape Region of South Africa, areas known for exceptionally high degrees of plant species richness and endemism, are also known for their complex geologies (Stebbins and Major 1965; Médail and Verlaque 1997; Linder 2003). Similarly, the Colorado Plateau, in the southwestern United States, has long been recognized for an abundance of endemic plants, attributable in part to its aridity and geologic history (Welsh 1978). Seventy-one percent of imperiled and critically imperiled species growing within a 160-km (100-mi) radius of the Four Corners, the quadripoint where the boundaries of Utah, Arizona, New Mexico, and Colorado meet, have been identified as edaphic endemics, reported to occur exclusively in association with a particular geologic formation. Of these, 11% grow on fine-textured substrates, such as shale (NatureServe 2011).

During the past decade, three vascular plant species new to science have been described growing on the Mancos Shale formation in southwestern Colorado. These include one species from the mustard family, cushion bladderpod (*Physaria pulvinata* O'Kane and Reveal) (O'Kane and Reveal 2006), and two species from the aster family, Lone Mesa snakeweed (*Gutierrezia elegans* Schneider and P. Lyon) and Mancos Shale packera (*Packera mancosana* L. Yeatts, B. Schneid. and Al Schneid.) (Schneider et al. 2008; Yeatts et al. 2011). All three species have been identified on shale barrens habitat at Lone Mesa State Park, Dolores County, Colorado (Figures 1, 2). Of the three species, only *Physaria pulvinata* has been collected outside of the park and its environs. A population was identified at the Dan Noble State Wildlife Area, 22 air-kilometers northeast of Lone Mesa State Park. That population was not included in this study.

Barrens habitat is characterized by a low percentage of plant cover and a surface area of rock fragments. Some researchers have suggested that shale barrens soils are in some way distinguished by unusual soil chemistry. However, research on the Mid-Appalachian shale barrens has not supported this hypothesis. On the contrary, these barrens do not appear to vary significantly in this regard from adjacent nonbarrens areas (Braunschweig et al. 1999). This conclusion was echoed by a study of the chalk barrens of the Niobrara Formation in southeastern Colorado, a region noted for plant endemism. The authors found that the chalk barrens, a component of the Mancos Shale Formation, did not exhibit unusual chemistry, and they concluded that endemism was governed instead by structural components, such as shallow soil depth and particle-size composition (Kelso et al. 2003).

The Mancos Shale Formation was laid down during the Upper Cretaceous period. At that time, the Western Interior Seaway divided North America, depositing dark organic-rich mud over the west-central

Figure 1. Cushion bladderpod (*Physaria pulvinata*), Lone Mesa State Park, Dolores County, Colorado, 2011.

portion of the continent, from the Gulf of Mexico in the south to the Arctic in the north (Fillmore 2011). The soft sedimentary rock comprises primarily fine-textured shale and mudstone, and it weathers to produce soils of high clay content. Clay soils of the Mancos Shale Formation are noted for being particularly inhibitive to plant growth (Welsh 1978; Potter et al. 1985). In arid ecosystems, fine-textured soils are noted for absorbing and storing water less efficiently than coarse-textured soils (Rosenthal et al. 2005). Due to the large surface area to volume ratio and flake-like structure, clay particles may absorb a great deal of water; however, due in part to the layered orientation of the particles, much of the water is unavailable for plant growth. Clay soils have very small pore spaces and retain water against the power of roots to extract it (Rajakaruna and Boyd 2008). Exacerbating the difficulties for plants, shale soils are easily compacted. Root tips are particularly sensitive to the lack of oxygen because they undergo cell division at a high rate (Potter et al. 1985; Brady and Weil 2008). In addition, the barrens soil does not contain an organic ("O") horizon but is instead covered by a layer of thin, flat, broken rock (here referred to as "chiprock"). This chiprock cover, in turn, suggests a soil of shallow depth, with a limited capacity to support plant growth, because the rocky surface is unfavorable to plant establishment and also because shallow soils cannot provide mechanical support required by larger plants (Rajakaruna and Boyd 2008).

The largest expanse of barrens habitat at Lone Mesa State Park, located at the southern entrance, has a gently rolling topography, outcropping across an area no greater than 5 km^2. The barrens outcrops are situated within a large expanse of shrubland dominated by sagebrush (*Artemisia* L.) and golden-hardhack (*Dasiphora fruticosa* (L.) Rydb.). Shifts of only a meter or so may result in different plant assemblages. The barrens supports species of herbaceous perennials and nonrhizomatous perennial grasses; no annuals have been observed and very seldom do shrubs occur. Some species, such as Missouri milk-vetch (*Astragalus missouriensis* Nutt.), are limited to barrens habitat, while other species, such as spear-leaf wild buckwheat (*Eriogonum lonchophyllum* Torr. and Gray) and small-head dwarf-sunflower (*Helianthella microcephala* (Gray) Gray), are abundant on barrens habitat and on adjacent nonbarrens habitat, but do not grow in other areas of the park. Of the three recently described rare endemic species, *Physaria pulvinata* appears to have the greatest fidelity to the harshest barrens habitat—one of the very few species observed to grow where chiprock is most pervasive (>80% cover).

The purpose of this study was to delineate structural components most closely associated with *Physaria pulvinata*. It was hypothesized that soil depth of the *P. pulvinata* habitat differed from the soil depth of adjacent habitat where *P. pulvinata* was less frequently observed. Specifically, shallower soil was predicted to be correlated with the presence of *P. pulvinata*. It also was hypothesized that soil moisture, chiprock cover, and soil texture varied with *P. pulvinata* habitat.

Study Species

The genus *Physaria* was redefined in 2002 to include most species previously assigned to *Lesquerella* (Al-Shehbaz and O'Kane 2002). This genus now contains more than 100 species, most of which are found in the interior western United States. *Physaria* is hypothesized to be of relatively recent origin. The evolution of this genus appears to have been driven by Quaternary climatic changes that have resulted in migration, isolation, and rapid speciation (Holmgren et al. 2005). Approximately 10% of *Physaria* species are classified as critically imperiled and imperiled (NatureServe Global Conservation Status Ranks G1 and G2). Most of these occur on fine-textured soils or in rocky habitats (NatureServe 2014).

Physaria pulvinata is a long-lived, caespitose perennial with a deep taproot that terminates in a buried caudex (Figure 1). It forms compact dense mats of up to several hundred stems with persistent and pubescent gray-green leaves. Individuals produce inflorescences of a few to many small, yellow flowers shortly after the last snow has melted, during late May–June. Infructescences composed of ellipsoid siliques form shortly thereafter. Other details of its life history, such as pollination ecology, are not known.

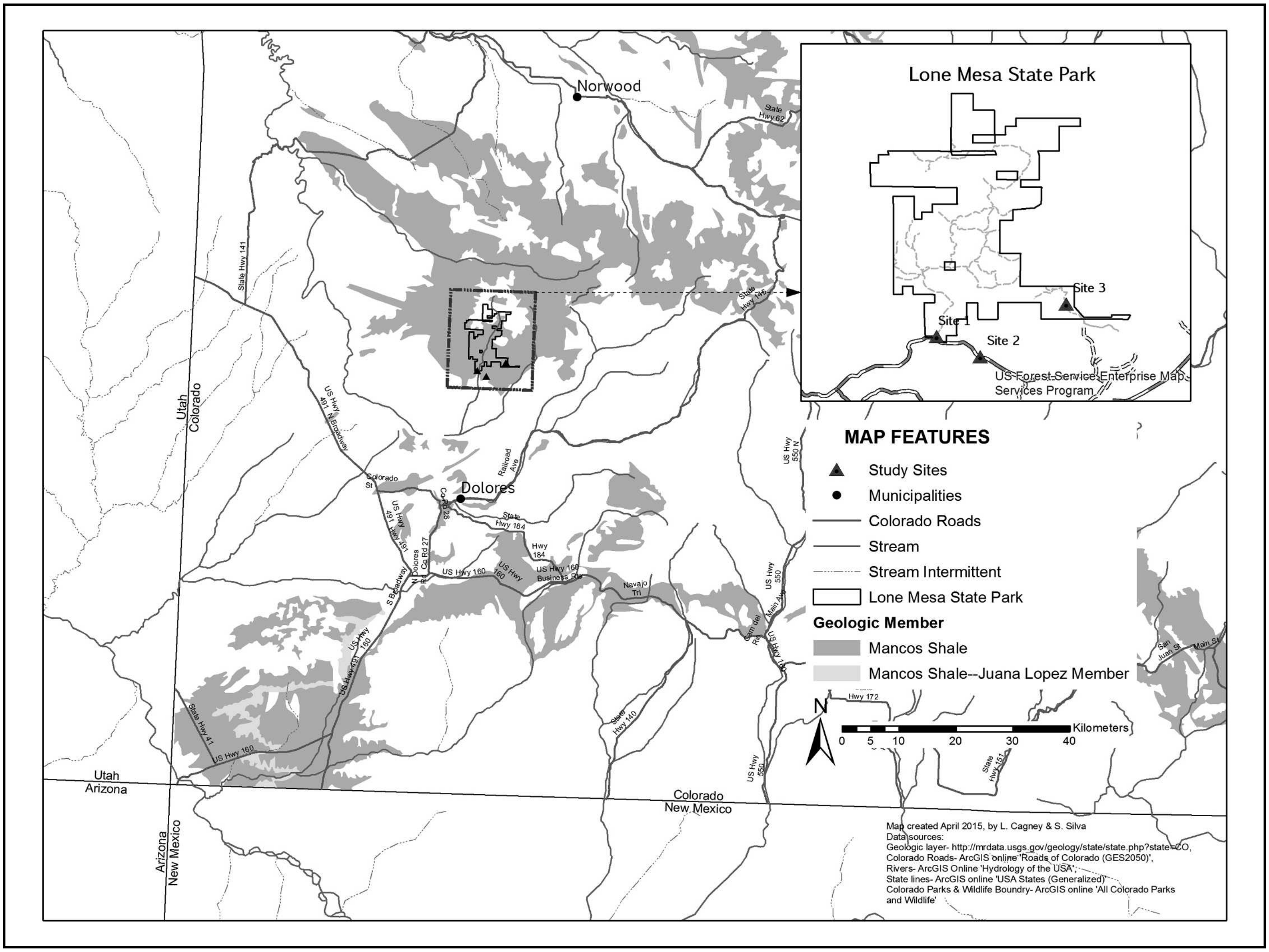

Figure 2. Lone Mesa State Park, Dolores County, Colorado, with the location of the three study sites in the study area.

Plants were identified following Weber and Wittman (2012), and nomenclature follows Kartesz (2015).

Study Area

The study area is located in Dolores County, Colorado (Figure 2), at sites that range from 2300 to 2500 m in elevation. Southwest Colorado has an arid continental climate (Comstock and Ehleringer 1992) with a bimodal moisture pattern, characterized by snow in winter and monsoon rain from mid-July to September (Colorado Climate Center 2013). The Western Regional Climate Center (WRCC) weather station closest to Lone Mesa State Park that provides long-term temperature and precipitation data, is located in Norwood, Colorado, approximately 48 air-kilometers northeast of the park. The average maximum annual temperature recorded at Norwood is 15.4 °C and the average minimum is -1.1 °C (WRCC 2013). July is the hottest month, with a mean maximum temperature of 28.7 °C, and January is the coldest, with a mean maximum temperature of 3.1 °C. Based on data recorded from 1948 to 2006, Norwood received on average 40 cm of precipitation annually.

MATERIALS AND METHODS

Sampling was initiated in late July of 2012, following flowering and fruiting of *Physaria pulvinata*, and concluded in late September. Seven 100-m transects were sampled at Lone Mesa State Park and in adjacent San Juan National Forest. The transects were located in areas where *P. pulvinata* was known to occur. One set of three parallel 100-m transects was located at the southern park entrance; an additional set of three parallel 100-m transects was located in adjacent San Juan National Forest; and one 100-m transect was located near the eastern park boundary, where a small population of *P. pulvinata* was identified growing above a ravine. The beginning of each transect was selected randomly, but oriented such that each transect crossed shale barrens to include nonbarrens habitat. The latitude and longitude of the start point of each transect was marked with a Garmin GPSmap 60 CS. Fossils were collected at the southern park entrance in order to establish the identity of the geologic formation.

Ten 1-m^2 plots were sampled at 10-m intervals along each transect. Each plot was evaluated for percentage of chiprock cover to the nearest 5%, defined as rock fragments >10 mm. Additionally, each plot was evaluated for average chiprock thickness, soil depth to bedrock, vascular plant species, percentage of plant cover to nearest 5%, and percentage of *Physaria pulvinata* cover to nearest 5%. Finally, a soil sample was collected from a corner of each plot and stored in double, zippered plastic bags for soil moisture and texture analysis.

Laboratory Analysis

Soil moisture was determined in the laboratory by the gravimetric method. A soil sample of 10 g was placed in a tin and then dried at 105 °C for 24 hrs. The moisture content (M) in g dry weight was determined by the following method:

M = (wt of wet soil + tare) – (wt of dry soil + tare) / (wt of dry soil + tare) – (tare)

Soil texture was determined in the laboratory using the hydrometer method (Gee and Bauder 1986). A soil sample from each plot was sieved down to 2 mm, and then a 20-g sample of the soil was mixed with 50 ml of the deflocculate sodium hexametaphosphate (50 g/liter deionized water). This solution was mixed with deionized water in a blender for five minutes and then transferred to a 500-ml sedimentation cylinder, where it was measured with a hydrometer at intervals of 30 sec, 60 sec, 90 min, and 24 hrs. A simplified modification of the Day method was used to determine the clay fraction. This calculation uses a weighted average of the 90 min and 24 hr readings (Gee and Bauder 1979). Thereafter, percentages of sand, silt, and clay were calculated using the following formulas (Gee and Bauder 1986):

Percent silt and clay: corrected silt and clay average reading (g/l) * 100 / original sample wt

Percent sand: 100% – (silt and clay percent)

Percent clay: corrected clay reading (g/l) * 100 / original sample wt

Percent silt: 100% – (sand percent + clay percent)

Data Analysis

The plots were organized into three classes based on soil depth: ≤5 cm, >5 to ≤10 cm, and >10 to ≤15 cm. One-way ANOVA was performed to assess the relationship between soil depth and other characteristics: species richness, percentage of plant cover, soil moisture, and chiprock cover. In addition, ordinal logistic regression was used to examine the effects of soil depth, percent chiprock cover, and percent soil moisture on the presence of *Physaria pulvinata*. The predictor variables were used to determine the odds ratio of the response variable, *P. pulvinata*. This analysis allowed for an overall assessment of the relationship between predictor variables and the presence of *P. pulvinata*.

All statistical analysis was conducted with JMP 11.1.1 (SAS 2013).

RESULTS

The study area was confirmed as Mancos Shale Formation due to the presence of the Cretaceous era fossils *Ptychodus* Agassiz, a shark genus; *Inoceramus* Sowerby, a clam genus; and *Pycnodonte newberryi* Stanton, an oyster species (P. Leschak, Fluids Geologist, BLM, pers. comm.). Because a stratigraphic analysis has not been conducted at the study area, it was not possible to identify which member of the Mancos Shale Formation is represented.

Twenty-eight vascular plant species were identified growing in 70 plots at the study area (Table 1). Forty-six (46%) of the species in study plots belong to the Asteraceae family. This percentage is higher than Lone Mesa State Park as a whole, which contains 20% Asteraceae species (Silva 2014). Herbaceous perennials made up 79% of the species, with shrub species making up the remainder. With one exception, shrubs were observed growing only in plots with a soil depth of at least 15 cm.

Physaria pulvinata occurred in 14 (20%) of the plots at the study area. Five of the ten plots (50%) with a soil depth of ≤5 cm contained *P. pulvinata*. Eight of the 31 plots (26%) with a soil depth of >5 to ≤10 cm contained *P. pulvinata*. One of the 29 plots (3%) with a soil depth of >10 to ≤15 cm contained *P. pulvinata*. No seedlings were observed.

Although plant assemblages differed, species richness varied little among soil depth classes, averaging three species per plot. Thirteen species were identified growing in plots with a soil depth of ≤5 cm, 15 species were identified growing in plots with a soil depth of >5 to ≤10 cm, and 25 species were identified growing in plots with a soil depth of >10 to ≤15 cm (Table 1).

The percentage of plant cover was higher on plots with greater soil depth, as expected ($F_{2,69}$ = 7.73, P < 0.001; Figure 3). Plant cover on plots with soil depth of ≤5 cm averaged 17%, plant cover on plots with soil depth of >5 to ≤10 cm averaged 15%, and plant cover on plots with soil depth of >10 to ≤15 cm averaged 32%.

The percentage of soil moisture was greater on plots with greater soil depth ($F_{2,69}$ = 5.40, P < 0.0067; Figure 4). Soil moisture on plots with soil depth of ≤5 cm averaged 5.3%, soil moisture on plots with soil depth of >5 to ≤10 cm averaged 6.5%, and soil moisture on plots with soil depth >10 to ≤15 cm averaged 9.0%.

Chiprock cover was greatest on plots of shallower soil depth ($F_{2,69}$ = 12.0, P < .0001; Figure 5). Plots with soil depth of ≤5 cm averaged 61%, plots with soil depth of >5 to ≤10 cm averaged 40% chiprock cover, and plots with soil depth of >5 to ≤10 cm averaged 16% chiprock cover.

The percentages of fine-textured soil (silt and clay combined) were greatest on plots with soil depth of >10 to ≤15 cm, averaging 82% (Figure 6). Plots with soil depth of >5 to ≤10 cm contained an average of 75% fines, and plots with soil depth of ≤5 cm

Table 1. Plant species found within 1-m^2 plots at the study area in Lone Mesa State Park and San Juan National Forest, Dolores County, Colorado, July–September 2012.

	Soil Depth (cm)		
	≤5	>5 to ≤10	>10 to ≤15
Perennials			
Small-head dwarf-sunflower, *Helianthella microcephala* (Gray) Gray	X	X	X
Grassy rock-goldenrod, *Petradoria pumila* (Nutt.) Greene	X	X	X
Stemless four-nerve daisy, *Tetraneuris acaulis* (Pursh) Greene	X	X	X
Lone Mesa snakeweed, *Gutierrezia elegans* Schneider & P. Lyon	X	X	X
Common Townsend daisy, *Townsendia leptotes* (Gray) Osterhout	X	X	X
Hairy false golden-aster, *Heterotheca villosa* (Pursh) Shinners		X	X
Thistle, *Cirsium* sp. P. Mill			X
Nevada showy false goldeneye, *Heliomeris multiflora* Nutt.	X	X	
White sagebrush, *Artemisia ludoviciana* Nutt.			X
Common yarrow, *Achillea millefolium* L.			X
Hoar false tansy-aster, *Dieteria canescens* (Pursh) Nutt.		X	
Cushion bladderpod, *Physaria pulvinata* O'Kane & Reveal	X	X	X
Sharp-leaf bladderpod, *Physaria acutifolia* Rydb.			X
Field bindweed, *Convolvulus arvensis* L.			X
Missouri milk-vetch, *Astragalus missouriensis* Nutt.	X	X	X
Boreal sweet-vetch, *Hedysarum boreale* Nutt			X
Prairie flax, *Linum lewisii* Pursh			X
Lavender-leaf sundrops, *Oenothera lavandulifolia* Torr. & Gray		X	
Purple-white owl-clover, *Orthocarpus purpureoalbus* Gray ex S. Wats.	X	X	X
Tufted beardtongue, *Penstemon caespitosus* Nutt. ex Gray	X	X	X
Indian ricegrass, *Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkwort	X	X	X
Spear-leaf wild buckwheat, *Eriogonum lonchophyllum* Torr. & Gray	X	X	X
Shrubs			
Big sagebrush, *Artemisia tridentata* Nutt.			X
Black sagebrush, *Artemisia nova* A. Nels.			X
Creeping Oregon-grape, *Mahonia repens* (Lindl.) G. Don			X
Gambel's oak, *Quercus gambelii* Nutt.	X		X
Woods' rose, *Rosa woodsii* Lindl.			X
Golden-hardhack, *Dasiphora fruticosa* (L.) Rydb.			X

contained an average of 68% fines.

Logistic regression indicated that shallow soil depth rather than moisture, texture, or chiprock cover was the characteristic most closely associated with the presence of *Physaria pulvinata.* The two-way interaction of soil depth and *P. pulvinata* was statistically significant (likelihood ratio chi-square = 14.89, $P = 0.0001$, df = 1).

DISCUSSION

Two models have been developed to explain the presence of edaphic endemics (Palacio et al. 2007). According to the refuge model, edaphic endemic species possess no special adaptations but are able to tolerate conditions too harsh for more widespread species. These species cannot compete with dominant species and take refuge in marginal habitats. Alternatively, the specialist model conceives of edaphic endemics as having qualities that make them specially suited to harsh habitats and, therefore, more competitive in these habitats than nonspecialists.

Although the specialist model has commonly been invoked to explain the presence of species in habitats with harsh chem-

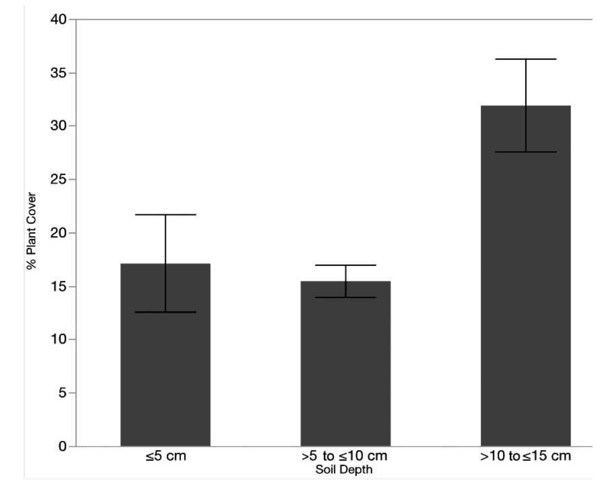

Figure 3. Mean percentage of plant cover with respect to soil depth at study area, Dolores County, Colorado, July–September 2012.

istry (Meyer 1986; Palacio et al. 2007), the physical characteristics imposed by certain habitats may require specialized adaptations as well. Soil texture has been shown to influence species distribution in a variety of environments (Kinraide 1984; Polley and Wallace 1986; Itoh et al. 2003). However, at the study area, all soil classes occur on Mancos Shale substrate, which is characterized by a high percentage of fine-textured soil. *Physaria pulvinata* was found predominantly on habitat with the shallowest soil, suggesting that in this case texture is not driving endemism.

Soil moisture varied with soil depth. However, it was not a good predictor of *P. pulvinata* presence in study plots. Instead, the strongest predictor was soil depth, with the shallowest soils associated with the rare endemic species. *Physaria pulvinata* produces a long taproot, like the rare endemic Lone Mesa snakeweed and other barrens species. It is not uncommon to find various barrens species growing in roughly parallel rows, which appear to be congruent with cracks that have formed in the underlying bedrock; presumably these cracks create reservoirs, providing water unavailable in the otherwise low-moisture soil. *Physaria pulvinata* has been observed growing in this manner, and perhaps more significant, it is one of the very few species found growing between these rows in areas of pervasive chiprock cover (>80%) and shallow soil to bedrock (2.5 cm).

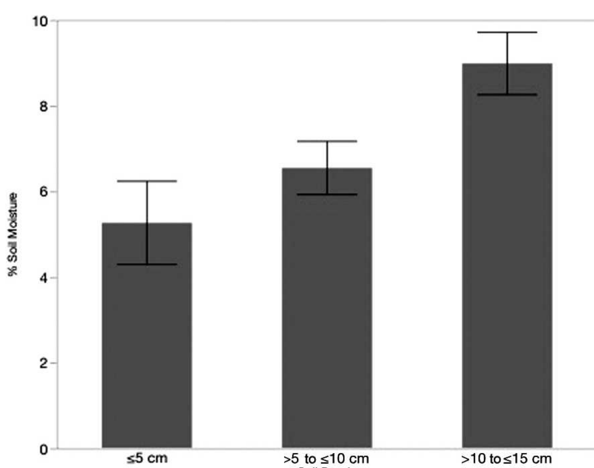

Figure 4. Mean percentage of soil moisture (dry weight basis) with respect to soil depth at study area, Dolores County, Colorado, July–September 2012.

Research on endemic species that occur in shallow, seasonally dry ironstone soils and granite outcrops suggests that these species may have rooting systems that make them specially adapted for their habitats (Poot and Lambers 2008; Poot et al. 2012). The species appear to invest more of their biomass in roots than do their nonendemic congeners and, therefore, may be able to access fissures in the underlying bedrock, where water has collected. Their specialized root systems may come at a cost of being less efficient and more expensive to produce, making these shallow-soil endemics less competitive in habitats with deeper soil.

Without analyzing soil chemistry, it is not possible to examine the hypothesis that plant communities in the shallowest soil are determined by plant-inhibiting compounds, or are lacking in important nutrients. However, the contiguity of the barrens with nonbarrens habitat of the same geologic formation, yet different plant assemblages, suggests that chemistry may not be the primary factor driving endemism. On the barrens habitat, shallow soil and low moisture content may together create an environment unfavorable to the recruitment of plants that are not specialized to the unique conditions. In a harsh dry environment, drought tolerance may precipitate isolation and lack of gene flow, thereby promoting speciation in genera such as *Physaria*, which may be more competitive for the available water than other species. In order to test this, it would be necessary to grow *Physaria pulvinata* in controlled conditions to assess whether this species does in fact have a competitive advantage over other species, and whether its rooting system is maladaptive in deeper soil.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The results suggest that *Physaria pulvinata*

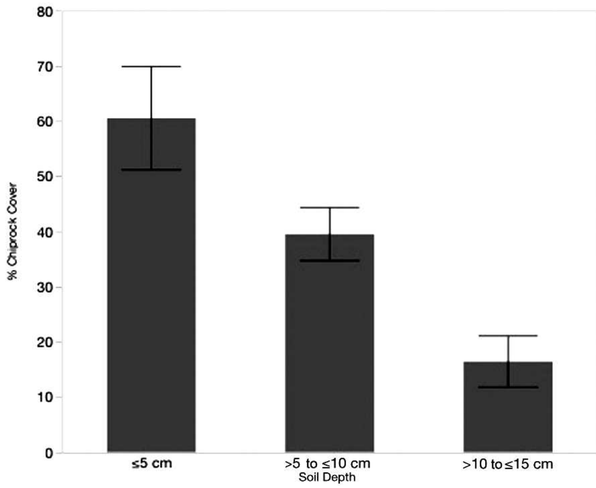

Figure 5. Mean percentage of chiprock cover (rock fragments >10 mm) with respect to soil depth at study area, Dolores County, Colorado, July–September 2012.

survives in the harsh environment of the Mancos Shale barrens due to its adaptation to shallow soil and low moisture availability. The same may be true for the other two new species found on the Mancos Shale barrens, Lone Mesa snakeweed and Mancos Shale packera. Yet, little is known about the general biology and life history characteristics of these species, such as their breeding systems, seed production, germination requirements, or longevity of seed in the soil.

Furthermore, 400 cow/calf pairs are rotated through pastures within Lone Mesa State Park boundaries each year, potentially making plant species vulnerable to trampling. Currently, the park is not open to the public, except for hunting by special-use permit. However, the state of Colorado is considering developing it for recreational use (S. Elder, Park Manager, Lone Mesa and Mancos State Parks, CO, pers. comm.). *Physaria pulvinata* and other rare endemic species should be protected from livestock and human disturbance.

In addition, population biology studies of all three species are recommended. Of further concern is the ability of these species, which grow on virtual islands, to adapt to climate change. Recent analyses have shown Colorado Plateau edaphic endemics to be threatened (Krause and Pennington 2012). Information from the above studies should guide the design of long-term monitoring plans. These data should aid in providing the information needed to prepare federal threatened and endangered species listing packages, if so indicated.

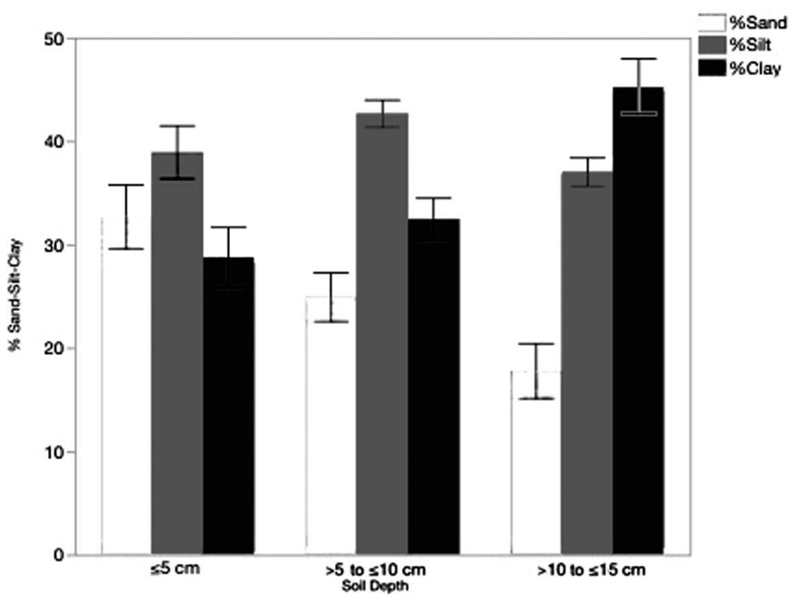

Figure 6. Mean percentages of soil fractions (sand, silt, clay) with respect to soil depth at study area, Dolores County, Colorado, July–September 2012.

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Shelley Silva conducted this research as part of the requirements for her Master of Science of Biology degree at Northern Arizona University. Since completing her degree, she has continued teaching introductory biology lab courses at NAU.

Tina Ayers is an Associate Professor in the Department of Biology at Northern Arizona University, where she is also curator of the Deaver Herbarium. She is currently completing a monograph of Lysipomia *(Campanulaceae), a genus of about 40 species endemic to the Andean alpine tundra. Her research interests include plant systematics, biogeography, and floristics.*

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