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GEOBOTANY OF THE NIOBRARA CHALK BARRENS IN COLORADO: A STUDY OF EDAPHIC ENDEMISM

Sylvia Kelso 1, Nathan W. Bower 2, Kirsten E. Heckmann 1, Paul M. Beardsley 1, and Darren G. Greve 2

ABSTRACT.—The chalk barrens of the Niobrara Formation in the Arkansas River valley of Colorado exhibit a high degree of plant endemism and rarity. We examined their geochemistry and structure as well as the reproductive ecology of their signature species Mirabilis rotundifolius to assess factors influencing endemism. While no single component consistently identified the barrens soils, the natural locations that support Mirabilis can be identified using elemental profiles from a cluster analysis of soil extracts. Because seeds germinate and plants proliferate in transplant gardens with non-calcic soils, bedrock and soil chemistry do not appear to be determinant components of endemism. Mirabilis rotundifolius utilizes diverse pollinators but is capable of autogamy when insects are excluded; seed predation by harvester ants may be a limiting factor for population spread outside the barrens habitat. Mirabilis rotundifolius is a disturbance-tolerant species, part of a barrens cohort that shares traits of suffrutescence, woody caudices, or multibranched rhizomes penetrating the chalk strata. Its presence may be enhanced when disturbance inhibits the presence of other species that compete for limited water resources. We conclude that endemism is dictated not by unusual soil chemistry requirements but rather by structural components of the barrens. In a water-limited environment, shallow soils and thin chalk strata coupled with a functionally adaptive growth habit allow M. rotundifolius to survive when other species are excluded by disturbance or the physiochemical aspects of the barrens.

Key words: edaphic endemism, geobotany, rarity, chalk barrens, Mirabilis rotundifolius, Oxybaphus rotundifolius, soil extraction, Niobrara Formation.

The association of endemic, often rare, plant species with unusual or highly mineralized soils has long been recognized by botanists (see Mason 1946, Kruckeberg 1969, 1986, Willis et al. 1996). Some prominent forms of edaphic endemism include plant associations with ultramafic bedrock, such as serpentine, and with highly calcareous bedrock such as limestone, chalk, or dolomite, or evaporites such as gypsum (Meyer 1986). Edaphic endemic species frequently elicit conservation concern due to their restricted ranges and/or small population sizes. In Colorado, for example, of the 70 species rated G1 or G2 (globally imperiled with less than 20 known occurrences) by the Colorado Natural Heritage Program (1999), 42 species (60%) are apparent edaphic endemics (Spackman et al. 1997).

Assessment of soil- or bedrock-limited taxa often focuses on whether these taxa utilize unusual soil elements or compounds (Turner and Powell 1979, Kruckeberg and Reeves 1995), or whether unusual conditions exclude other taxa and thus provide low-competition environments (Anderson 1996). A third, non-equilibrium possibility examines whether endemics represent recent speciation or remnants of former distributions (Stebbins and Major 1965, Kruckeberg and Rabinowitz 1985, Nekola 1999). These factors often interact, making endemism difficult to interpret. However, multifaceted ecological and geochemical analyses of endemic species offer insights on critical habitat, ecological and phylogenetic relationships, and management of rare plant populations.

In southeastern Colorado the middle Arkansas River valley between Pueblo and Cañon City (Fig. 1) is well known for its unusual flora (Kelso et al. 1995, Spackman and Floyd 1996, Weber and Wittmann 1996). In particular, plants associated with chalk barrens of the Niobrara Formation, a mid-Cretaceous sedimentary bedrock complex forming shale, limestone, and chalk outcrops, exhibit a notable degree of endemism and, in some cases, rarity. Because this region currently faces strong development pressures, the nature of plant endemism here has evoked considerable conservation concern.
The term "barrens" denotes sparsely vegetated exposures of bedrock, typically on shales or shale-derived soils (Anderson et al. 1999). As used here, the term includes exposures of chalk, a soft limestone containing the remains of microorganisms in a calcite matrix (American Geological Institute 1976). These chalks occur in small pockets in this widespread formation that is the geological remnant of episodic deposition in the epicontinental inland seaway underlying the Western Interior Cretaceous Basin (Scott and Cobban 1964, Hattin 1982, Barlow and Kauffman 1985, Kauffman 1985). Extensively mapped outcrops in the region around Pueblo and Canon City consist of basal Fort Hayes Limestone overlain by the Smoky Hills Member (Fig. 2). High-resolution stratigraphy in Colorado has provided local details of the formation (Scott 1964, 1969a, 1969b, Scott and Cobban 1964, Barlow and Kauffman 1985, Kauffman 1985, Kauffman and Pratt 1985, Pollastro and Martinez 1985).

The most botanically important barrens on the Niobrara Formation occur on the Middle Chalk and Upper Chalk units of the Smoky Hills Member (Fig. 2). They erode easily and form moderate slopes with a surface layer of small, thin rock fragments above a shallow layer of fine mineral soil that covers fissile layers of chalk. In comparison, the harder layers of shale and limestone are much more resistant to erosion and typically form nearly vertical ledges, or in flat areas they are often covered by granitic Quaternary gravels (Scott 1969b). Throughout eastern Colorado the Niobrara Formation supports arid grassland or shrub-grassland communities dominated by *Pinus edulis* (piñon pine), *Juniperus monosperma* (singleseed juniper), and bunchgrasses such as *Stipa neomexicana* (New Mexico needlegrass), *Aristida purpurea* (three awn), *Hilaria jamesii* (galleta grass), and *Oryzopsis* (Indian ricegrass; Shaw et al. 1989, Clark 1996, Polzin 1999; taxonomy follows Hartman and Nelson 2001).

Although the Niobrara Formation underlies much of eastern Colorado and extends to parts of Kansas, Wyoming, and New Mexico, chalk barrens are relatively infrequent due to the shallow vertical extent of the 2 chalk layers which form approximately 11 m of the almost 500 m total in the formation (Fig. 2). They appear as geological islands of exposed bedrock on mesas and bluffs where rivers or geological uplift have provided the opportunity for erosion-prone slopes to develop. Barrens are typically small in size, ranging from a few kilometers to less than 10 m in length, with short, vertical slopes 3–10 m from base to summit. They occur in Colorado most abundantly in Pueblo and Fremont Counties where the Arkansas River and its tributaries have cut through the sedimentary layers, but they also appear sporadically in Las Animas and Otero Counties where regional uplift has formed topographic breaks.

For the past 7 years, we studied the Niobrara chalk barrens and their distinctive flora. We wished to examine whether plant endemism on the barrens was caused by unusual geochemical conditions, or whether ecological or anthropogenic factors might be dominant in restricting these plant distributions. One of the signature endemics, *Mirabilis rotundifolius*...
Fig. 2. The Niobrara Formation and regional geology in southeastern Colorado. Details of the Niobrara Formation adapted from Scott and Cobban (1964).

(Nyctaginaceae, roundleaf four o’clock; also treated as Oxybaphus rotundifolius, cf. Nau mann 1990, Weber and Wittmann 1996), has been a focal point of our analysis. This species is of high conservation concern due to its narrow range, small populations, and accelerating loss of critical habitat (Spackman et al. 1997, Colorado Natural Heritage Program 1999). Our investigation included the following goals:

1. To provide a soil analysis that would elucidate any selective or restrictive geochemical constituents or composition including the presence or absence of gypsum (CaSO₄·2H₂O), unusual soil pH levels, or atypical element distributions associated with common soil components. Gypsum, often associated with edaphic endemism in the arid Southwest (Turner and Powell 1979), has been suggested as a requisite soil component for several Arkansas River valley species
This compound can affect soil chemistry in its immediate vicinity, changing the part of the soil (fraction) on which a given element may concentrate, and thus its availability or toxicity. However, the geological literature notes only sporadic local occurrence of gypsum in the Niobrara as a whole and in the chalk layers in particular. Therefore, a soil fractionation analysis that looks for a similar pattern of element distribution should be useful for investigating the origins of any such plant-gypsum associations. Element profiles based on the 5 soil fractions (ion-exchangeable clays, carbonates, iron hydrous oxides, organics, and basal minerals; Tessier et al. 1979) also provide a "fingerprint" that can be used to discern the similarity of soil composition from different sites when they are coupled with statistical methods such as cluster analysis.

2. To provide an assessment of the physical structure of the chalk barrens, including particle size composition, soil depth, slope angles, and slope aspects. Studies on other barrens habitats in the eastern United States have suggested that unusual structural characteristics are important factors in distinguishing shale barrens from surrounding environments (Braunschweig et al. 1999).

3. To provide an assessment of the reproductive ecology of the barrens signature species, Mirabilis rotundifolius, including its potential for self-fertilization, possible dependence on limited pollinators, seed dispersal mechanisms, and capacity to grow in transplant gardens with soils very different from those in which it occurs in the wild.

4. To examine how different disturbance regimes affect the floristic composition of the barrens, in particular whether anthropogenic disturbance influences the abundance or distribution of Mirabilis rotundifolius.

**STUDY SITES**

Our field and laboratory investigations for this study encompassed 3 dry years (1996, 1998, 2000) and 3 relatively wet years (1995, 1997, 1999; Doesken and McKee 2000). Prior fieldwork (Naumann 1990) and the comprehensive geological analysis available for the region enabled us to identify chalk barrens locations very precisely.

We used 9 primary areas (Appendix A) representing the major barrens spread across Las Animas, Otero, Pueblo, and Fremont Counties in Colorado, a geographic transect of approximately 240 km, to determine physical attributes of the barrens and to assess the effects of disturbance on M. rotundifolius (Fig. 1). Elevation (1500–1900 m) and climate across the sites are comparable, with relatively warm and dry summers and winters (July temperature and precipitation means are 22.5–24°C and 4.5–6.7 cm, respectively; Colorado Climate Data Center, statistics from 1995 through 1998).

These 9 primary areas were each divided into several 10-m-diameter plots for sampling purposes, providing 29 sites for disturbance regime study (Appendix A) and 30 sites for geochemical study (Appendix B). Selection criteria included documented geological context from geological maps and literature, accessibility, sufficient size, availability of both sloped and flat surfaces, and either an identifiable disturbance factor (e.g., grazing, camping, road proximity, motorcycle racing, or army tank maneuvers) or a demonstrable isolation from ongoing disturbance. Thirteen plots were classified as low disturbance and 16 as high disturbance. We included several sites under study for conservation purposes by the Colorado Natural Areas Program and/or the Nature Conservancy. Other sites included land owned by the Colorado Division of Wildlife and the U.S. Army. Site-specific species lists were composed for each plot; this enabled us to compare floristic differences between disturbance regimes and to assess the response of M. rotundifolius to different levels and types of disturbance.

Geochemical analyses were performed on sites used for ecological analysis with some additional representative sites used in the early phases of this study. Our access to military and private land was sporadic, and some of our initial geological plots were destroyed by development or became restricted before we used them for ecological analysis. For these reasons, the sites for geochemical and ecological analysis are not parallel. However, all sites were
matched as closely as possible on the basis of proximity and available geological information.

**Materials and Methods**

**Geochemical Analyses**

In each primary study plot, we assessed slope angle and exposure with a clinometer and compass and measured soil depth to bedrock at the top, middle, and bottom of the slope. In each flat plot we averaged 3-10 readings to obtain soil depth. We visually made qualitative estimates of percent cover following the Ocular Plant Composition method of the U.S. Forest Service (USDA Forest Service 1996) and compiled a plot-specific species list. Voucher specimens are deposited at the Colorado College Herbarium (COCO).

We obtained soil pH measurements from 18 of the study sites (Appendix B) to confirm that our sites conformed to the regional pH range documented by the USDA Soil Conservation Service (1979), using unfrozen soil samples prepared according to Hendershot et al. (1993). We measured each sample twice and averaged the readings.

To examine whether barrens soils supporting *Mirabilis rotundifolius* populations consistently contained gypsum, we used a powder diffractometer XRD (Phillips Instruments 1700). Lack of continuous access to some sites and the time-consuming nature of the analysis made it necessary to use a subset of soil samples for XRD analysis. We took samples from 10 sites (Appendix B) and split these into subsets, which were sieved through 200 mesh to remove larger bedrock fragments and analyzed using random-orientation powder mounts. Spectral peaks of the samples were compared with known gypsum standards to determine if gypsum was present.

We measured particle-size distribution using a particle-size analyzer (Beckman-Coulter LS-230). Samples were obtained from 3 study sites in Pueblo and Fremont Counties at the top, middle, and bottom of slopes. Given the availability of detailed regional soil information from previous geological surveys (Scott and Cobban 1964, USDA Soil Conservation Service 1979, Pollastro and Martinez 1985), these 3 sites were chosen to represent the barrens. The samples were air-dried, then split into 3 subsets for triplicate analysis of sand, silt, and clay components with USDA particle-size categories of <2 μm for clay, 2-50 μm for silt, and >50 μm for sand. Organic materials were removed by treatment with 6% hydrogen peroxide.

For chemical analysis we collected 3 samples of soil from different locations in 4 study areas (Appendix B: sites 5-7, 8-11, 12-14, 15-17) where *M. rotundifolius* grew abundantly. Four samples were collected from different locations in 2 areas (Appendix B: sites 23-26, 27-30) where viability was more variable and both Fort Hayes Limestone and the Smoky Hills Member were represented. We also collected single soil samples from 2 areas where *M. rotundifolius* grew weakly (Appendix B: sites 2, 20). An additional 8 samples were collected from surrounding sites, primarily on Fort Hayes Limestone, where the test species did not grow at all. These locations were similar to the test sites in exposure, climate, and elevation. Samples were chosen near the centers of plant populations and the top 2 cm of substrate removed from the ground surrounding the plants. Soils are very shallow on the barrens and this depth allowed us to sample consistently. We also collected samples at 1- and 4-cm depths from a few sites (Appendix B: sites 5, 8, 10, 23, 24, and nearby controls) to verify that the 2-cm samples were representative. All samples were placed in separate plastic bags and homogenized, then stored at -30°C until analysis.

Soil extracts of the 30 soils were analyzed for 30 elements in each of 5 soil fractions with an argon plasma ICP-OES (Thermo Elemental Atomscan 16) in multi-quant mode. All samples were also prepared for elemental profiling by adding 20 mL of 0.5 M HCl to 1 g of soil. This reagent extracts the majority of labile metals for low organic matter soils (Church et al. 1994). The soil samples collected at 1- and 4-cm depths were also prepared for soil fractionation. We used a modification of Tessier’s (1979) method of soil fractionation analysis in which the time for extractions was significantly reduced by assuming the rate doubled for each 10°C increase and the extractants were heated to 85°C (Bower et al. 1997). Tessier’s method uses 5 reagents sequentially to obtain the distribution of elements bound to the ion-exchangeable clay, carbonate, hydrous iron and manganese oxides, organics, and mineral-bound fractions of the soil. The single-step 0.5 M HCl extraction provides a profile similar to
the total of these fractions, except the mineral-bound fraction, which is only slowly available to plants.

Only 10 metals proved to have levels that were routinely detectable, and the simpler HCl extract data were used in the statistical data reduction (Minitab 2000) presented here. Cluster analysis was used with a Z-score normalized correlation matrix of the data using Ward’s (1963) method, which minimizes the variance within clusters in the hierarchy. Although Ward’s method is not well known for ecological classification, it has mathematical properties useful for metric data such as those generated in this study, and it is 1 of the 4 most common clustering techniques (Aldenderfer and Blashfield 1984). A discriminant function analysis with cross validation (Minitab, Inc. 2000) was conducted to determine which elements best predicted the locations where *Mirabilis rotundifolius* was or was not viable.

**Field and Ex-situ Garden Studies**

Transplant gardens at the Denver Botanical Garden and in Colorado Springs allowed us to assess whether *Mirabilis* seeds would germinate and the plants tolerate soil conditions dissimilar to those found in the wild. Both beds were composed of local granitic loam topsoil covered with gravel or limestone fragments. Seeds collected from wild populations of *Mirabilis rotundifolius* were stratified at 4°C for approximately 30 days, then germinated at room temperature. We transplanted seedlings to test gardens where they received full sun and exposure to local rainfall supplemented by additional water at several-week intervals.

We used 5 primary populations of *M. rotundifolius* (Appendix A: 8.1, 9.1, 9.2; B: 12, 13) to examine its reproductive ecology. These sites were selected because their relatively large size and abundance of plants would avoid negative impacts of isolation or fragmentation on insect visitation. For pollen reference, we collected unopened *Mirabilis* buds and placed them in preservative (BioNeat, Carolina Biological Supply). Pollen was later extracted, mounted on permanent slides or stubs, and photographed using electron and optical microscopy. These sites were used to capture insects visiting open pollinated plants between sunrise and sundown. The insects were captured, killed with ethyl acetate, then identified according to Slater and Baranowski (1978), McAlpine et al. (1987), Michener et al. (1994), and the entomology collection at Colorado College. We also washed the insects with glycerin jelly using techniques adapted from Kearns and Inouye (1993) to remove pollen that was then compared under microscopy to the reference pollen taken from unopened buds. This enabled us to determine if any particular insect was carrying *Mirabilis* pollen.

Four insect enclosures, each with a single plant containing only young, unopened buds, were placed at each of 3 study sites (Appendix A) used for insect collection. Three of the 12 enclosures were destroyed by nocturnal animals; the surviving enclosures were used for our seed set analysis along with an additional 20 experimental plants growing in test plots at the Denver Botanical Garden. In the wild, enclosures were placed over entire plants and covered in fine white mesh to avoid heat buildup, and the bases were buried to prevent insects from crawling under the mesh. At the Denver Botanical Garden, where larger size and rapid growth made it difficult to work with entire plants, we placed similar mesh enclosures over branches with 5 unopened involucres on each of the 20 test plants. Inflorescence structure in this species consists of an open involucre where 3 to 4 individual flowers develop with easily visible fruits, so we were able to assess whether seed set was successful or not. However, because the anthocarps drop readily when ripe and are often taken by seed predators, it is not possible to quantify seed production accurately enough for comparison between open pollinated plants and those within enclosures.

**RESULTS AND DISCUSSION**

**Profile of a Typical Chalk Barren**

Table 1 summarizes the physical profile of typical chalk barrens. They commonly develop on moderately steep slopes, but can also occur on flat mesa tops. Slope communities can face all directions but usually face south or southeast. Vegetative cover is low, typically ranging from 10% to 20%. Surface characteristics are uniform, with a highly weathered bedrock facies consisting of small (<4 cm long), platy pieces forming a thin surface layer underlain by very shallow mineral soil. These soils are fine-grained, with approximately 60% of the
particles composed of silts and clays. Soil pH ranges from moderately alkaline with a pH of 7.4–7.9 (15 of 18 samples) to strongly alkaline with a pH of >8 (3 samples). This pH range and high percentage of fine particles are typical for soils based on the Niobrara Formation in Pueblo County (USDA Soil Conservation Service 1979).

**Geochemistry of the Barrens Soils**

Of the 10 chalk barrens soil samples analyzed by X-ray diffraction, only 3 had a gypsum spectrum. This result is consistent with the geological reports of regionally sporadic gypsum lenses in the Niobrara Formation (Scott 1969a). It strongly suggests that gypsum is not a determinant of the occurrence of *Mirabilis rotundifolius* and that chalk barrens species should not uniformly be considered gypsumophiles.

The elemental analysis, using 1-way ANOVA (Minitab 2000) and summarized in Table 2, shows that sites where *M. rotundifolius* thrives are lower in manganese and iron and higher in calcium, strontium, and cadmium than those where its presence is weak or nonexistent. As might be expected for these elements, the manganese and cadmium differences are most significant in the carbonate and iron hydrous oxide fractions conducted using our higher temperature modification of Tessier’s procedure (1979). Calcium and strontium differences were greatest in the carbonate-bound fraction using this procedure, also as expected. These trends were essentially the same at both the 1-cm and 4-cm depths in the soils measured (data not shown).

Linear discriminant function analysis with cross-validation (Minitab, Inc. 2000) suggests that manganese alone can be used to predict with 86% accuracy which sites will be viable (data not shown). A scatterplot (Fig. 3) of manganese and strontium from the simple HCl extract illustrates that population locations may be identified by just these 2 elements; the poor or weak sites are divided about equally between locations with thriving populations and those with none. Despite the differences between locations, levels of these and other elements are well within normal ranges for calcareous soils (McBride 1994), suggesting they are simply correlated with plant distribution and not the source of endemism.

Although levels of elements bound to the ion-exchangeable (mostly clay) fraction were relatively low compared to the carbonate and hydrous iron fractions for barrens soils, none of the time- and labor-intensive soil fractionation results produced unusual geochemical signatures that might have been indicative of a hidden toxicity or unusual opportunity due to element mobility. Cluster analysis (Fig. 4) shows that chalk barrens have a recognizable “fingerprint” that is not immediately obvious from individual elements alone. When coupled with the knowledge that *M. rotundifolius* thrives in standard potting soil with normal levels of nutrients, these results suggest that total element concentrations are not a definitive factor in plant endemism in this case. They also suggest that endemism is more likely due to limitations of water and nutrient availability for other plants than any enhancement for *Mirabilis*.

Six distinct groups are found with unsupervised cluster analysis using the threshold where the similarity coefficient becomes negative as a demarcation. The large branch on the left (Fig. 4) contains mostly Fort Hayes samples with no viable plants and a few sites with weaker populations. The branch on the right contains 3 groups with 16 samples, only 1 of which (taken from the shale layer at the top of the chalk) does not support *M. rotundifolius*. These groupings imply there is little distinction between soils that support the plant even kilometers apart, but that a shift of a meter from chalk to shale (with only minor chemical variation) can change the soil enough to exclude the species. This indicates that the barrens provide a fairly
TABLE 2. Comparison of element composition of soil extracts (0.5 M HCl) between sites with strong (n = 16) and weak or nonexistent (n = 14) populations of *Mirabilis rotundifolius*. Elements are listed with their analytical wavelengths. All values are in ppm in the soil. One, 2, and 3 asterisks indicate significant differences at 95%, 99%, and 99.9% confidence levels, respectively, using a 1-way ANOVA (Minitab 2000).

<table>
<thead>
<tr>
<th>Element</th>
<th>Strong population</th>
<th>Standard error</th>
<th>Weak population</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Al</td>
<td>309.271</td>
<td>52.4</td>
<td>9.7</td>
<td>48.3</td>
</tr>
<tr>
<td>Ba</td>
<td>233.52</td>
<td>42.3</td>
<td>5.6</td>
<td>34.9</td>
</tr>
<tr>
<td>Ca</td>
<td>317.933**</td>
<td>2300</td>
<td>144,900</td>
<td>2900</td>
</tr>
<tr>
<td>Cd</td>
<td>228.802***</td>
<td>1.8</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>Fe</td>
<td>259.940*</td>
<td>48.6</td>
<td>6.4</td>
<td>80.5</td>
</tr>
<tr>
<td>K</td>
<td>766.490</td>
<td>48.8</td>
<td>9.9</td>
<td>97.6</td>
</tr>
<tr>
<td>Mg</td>
<td>279.553</td>
<td>496</td>
<td>31</td>
<td>702</td>
</tr>
<tr>
<td>Mn</td>
<td>260.569***</td>
<td>28.5</td>
<td>3.4</td>
<td>108</td>
</tr>
<tr>
<td>Sr</td>
<td>346.446**</td>
<td>452</td>
<td>20</td>
<td>367</td>
</tr>
<tr>
<td>Zn</td>
<td>213.856</td>
<td>9.7</td>
<td>1.3</td>
<td>6.5</td>
</tr>
</tbody>
</table>

Higher levels of manganese and iron found in unpopulated locations (primarily the Fort Hayes Limestone samples) suggest that iron nodules may also be a factor in negatively influencing the spread of these plants, even though these elements are usually considered nutrients. The viability of populations under both low and high concentrations of the calcium analog toxins (barium and cadmium) in the right branch of the dendrogram (Fig. 4) indicates these elements do not limit *M. rotundifolius*, although they may hinder other plant species to some extent.

The overall abiotic profile of the barrens, therefore, indicates an environment that may be stressful enough to exclude certain species, but not an environment with truly anomalous chemical conditions that require unusual tolerances or physiological adaptations. Although *M. rotundifolius* is entirely restricted to chalk soils in the wild, it thrives in gardens composed of granitic loam at the Denver Botanical Garden and in Colorado Springs. Seeds germinate easily in potting soil and the resulting garden transplants grow robustly, producing flower, fruit, and seedlings even after 7 years. Young seedlings are easily distinguished from mature plants by their glabrous rather than hirsute stems and their growth approximately 3 m from the parent plants. Although qualitative, these observations are replicated with other barrens species growing in the transplant gardens (e.g., in the genera *Penstemon* and *Lesquerella*), and they support our conclusion that the narrow distribution of these species in the wild is not related to any requirement for unique soils on the chalk barrens.

Reproductive Ecology of *Mirabilis rotundifolius*

To test whether *Mirabilis rotundifolius* might be limited in distribution because of dependence on a restricted pollinator fauna, we observed insect visitation at several study sites in the wild (Appendix A). Observations taken in June 1995 (a wet year with abundant flowering) indicated that flowers are routinely visited by a diverse array of insect taxa (Table 3), the most frequent of which are syrphid flies and halictid bees. Six of the insect taxa we collected carried *Mirabilis* pollen and are presumably capable of facilitating pollen transfer...
between plants. The other species may also act in this capacity, but we did not document them as pollen carriers.

Although insect visitation in the wild (and presumably also pollen transfer) appears to be sufficient for pollination, *M. rotundifolius* also readily produces seeds without insect facilitation. All plants under exclosures produced fruits abundantly in the wild and in transplant gardens. Typically, 3 or 4 flowers in each involucre produce an anthocarp, both in open-pollinated plants and in those where insects are excluded. Throughout the period of anthesis, annual flowering and seed set appear to be limited more by temperature and moisture than by insect visitation. In the wild, *M. rotundifolius* usually ceases flowering by mid-July, but in the transplant gardens, plants with supplemental water flower and produce fruits continuously until frost in September.

These observations suggest that *M. rotundifolius* is an opportunistic species, not dependent on a limited pollinator fauna for successful reproduction. It appears to have a mixed mating system employing several common insect taxa while also being capable of facultative selfing. In this respect it resembles its widespread weedy congener *M. nyctagineus* more closely than its regional relative *M. multiflora*, which is self-incompatible and exclusively pollinated by the hawkmoth *Hyles lineata* (Cruden 1973, Hodges 1995). No evidence of wind pollination has yet been found in the Nyctaginaceae, so it is unlikely that this is a factor affecting reproduction; however, wind may act as an agent in seed dispersal at least over short distances.

We found that *Mirabilis* plants are also visited by 2 species of mound ant (*Formica* spp.) that appear to be only nectar thieves, and by western harvester ants (*Pogonomyrmex occidentalis*) that commonly provide a dual role of seed predation and dispersal in the Southwest (MacMahon et al. 2000). Seed predation from harvester ants may be a prevalent factor during years when flowering and seed set is otherwise abundant in *Mirabilis*; we observed numerous instances of these ants carrying anthocarps away from the plants and nocturnal disappearance of anthocarps from involucres.

Thus, the greatest constraints on reproduction may come from granivory and from moisture-limited flower production and seedling recruitment in dry years. Having observed several wild populations of *M. rotundifolius* over multiple years, we became aware that plant size, number of flowers, and number of visible stems vary dramatically from year to year in response to rainfall. In extreme drought years, plants may be virtually dormant or show...
very restricted growth and flowering, and consequently little seed production. When moisture levels are high, flowering and seed production are high, but seed predation may diminish recruitment and limit the potential for population expansion.

Effects of Disturbance on the Chalk Barrens Flora

Floristic comparisons of plots with low and high levels of disturbance showed that disturbance does not significantly decrease the presence of *Mirabilis rotundifolius*, which occurs in 9 of 13 low-disturbance plots and 12 of 16 high-disturbance plots. To the contrary, *Mirabilis* stems were typically abundant on the disturbed plots. We note this effect only anecdotally as the growth habit and opportunistic responses to precipitation make it difficult to assess population sizes because *M. rotundifolius* produces widely spaced genets off multi-branched rhizomes, and aboveground stems vary in abundance with precipitation, both intra- and interannually. Late summer monsoonal rains can stimulate a sprouting effect of new growth, even toward the end of the usual growing season. Thus, demographic profiles for this species are inconsistent from year to year and reliable population numbers difficult to achieve.

Our floristic inventories reveal that highly disturbed sites are inhabited by a suite of species with striking similarities in growth habit that may help explain their apparently positive response to disturbance. The disturbance-tolerant species typically are suffrutescent with woody caudices and/or thick, multibranched roots or rhizomes that invade the interstices of the bedrock strata. In addition to *M. rotundifolius*, other examples include *Parthenium tetraneuris* (Arkansas River feverfew), *Artemisia bigelovii* (Bigelow sage), *Tetraneuris acaulis* (actinea), *Gutierrezia sarothrae* (snakeaia), *Melampodium leucanthum* (blackfoot daisy), *Eriogonum lachnogynum*, and *E. fendlerianum* (wild buckwheat). These species match the profile for plants able to inhabit a “persistence niche” (Bond and Midgley 2001), buffered from disturbance regimes by the ability to sprout and regenerate from permanent tissues when aboveground parts are damaged. In contrast, disturbance-intolerant species such as *Arenaria hookeri* (sandwort), *Paronychia sessiliflora* (nailwort), *Lesquerella spp.*, *Hoffmannseggia drepanocarpa*, and most grasses show a very different growth habit. They are typically herbaceous cushion or rosette plants with shallow fibrous or taproots and limited underground biomass, and little regenerative capacity to escape or recover from damage. Moderate disturbance on the barrens therefore results in plant communities dominated by species with a similar growth habit; the removal or inhibition of the sensitive species may decrease competition for water or nutrients and enhance the presence of others, including *M. rotundifolius*.

**CONCLUSIONS**

Our results indicate that plant endemism on the Niobrara chalk barrens is not caused by a requirement for unique geochemical conditions. The most limited representative of the barrens cohort, *Mirabilis rotundifolius*, is not restricted by narrow reproductive partnerships, but appears to be successful in the wild only where anomalous substrate prevents extensive cover by grasses or shrubs. The barrens provide restrictive conditions with their hot, dry slopes and extremely shallow, mineralized soils. Many of the barrens species have woody rhizomes or roots penetrating the thin, moisture-retentive chalk strata, and can exploit a habitat that excludes other locally abundant species intolerant of the physical conditions. This growth habit also provides inherent protection from disturbance such as slope instability, grazing, or moderate vehicular traffic. Disturbance also
inhibits the presence of species that might otherwise compete for limited water resources.

Plant endemicism on the Niobrara chalk barrens is not due to a simple cause and effect, but rather to a complex of factors. In this the chalk barrens are very similar to the Appalachian shale barrens (Braunschweig et al. 1999) where edaphic restrictions are primarily structural and competitive rather than geochemical as they may be in serpentine barrens (Meyer 1986, Kruckeberg 1999, Tyndall and Hull 1999). The sedimentary habitat is shaped by geological history and the ancient ecosystem that provided the strata of today, and ecological limitations stem from our arid contemporary climate and the regional dominance of species adapted for water competition. Granivory, which lessens seedling establishment, coupled with adverse, low-moisture soil conditions, may also preclude population spread outside the barrens. Growth habit of the barrens species appears to be a critical factor enabling them to successfully utilize a habitat where other species are restricted.

Beyond the proximate multiple interactions that we can see and assess, there is an element of change over ecological time that we cannot measure directly. Few environments in North America have undergone such dramatic climatic and biological shifts since the last glacial episode as the American Southwest (Spaulding et al. 1983). These shifts have undoubtedly exerted profound selective pressures on the flora and perhaps provide some ultimate causes of regional endemicism. Because we can only speculate as to historical distributions of individual barrens species, the question of whether the habitat currently acts as a refugium remains unanswered. However, the prominence of warm-climate southwestern species here (those with their primary distribution in the region from New Mexico to Arizona) suggests that they may represent the remnants of flora more widespread during early Holocene times when the climate was warmer and drier (Van Devender 1990, Dick-Peddie 1993). Since presettlement ecology also included a natural disturbance regime in the form of extensive bison herds, these conditions may well have provided more extensive suitable habitat than exists today for the barrens species.

Chalk barrens are signature environments for landscapes of the middle Arkansas River valley and contain a regionally unique biogeographic profile (Kelso et al. 2001). Although our investigations have revealed encouraging examples of opportunistic responses in rare species, the Niobrara barrens and their biota remain of considerable conservation concern. These sites are rapidly diminishing in extent and much yet remains to be learned about the ecology of their inhabitants, their interactions with each other, and their long-term responses to climate and to anthropogenic pressures. Although regenerative species in a persistence niche may be buffered from some conservation concerns such as loss of pollinators or low recruitment years, they may also be vulnerable to habitat alteration and changing climatic or ecological conditions (Bond and Midgley 2001). Chalk barrens present a model opportunity to see the interactive effects of past and current geological history and how this history shapes our current biotic patterns. For multiple reasons, these deceptively simple ecological communities should receive attention as conservation targets.

ACKNOWLEDGMENTS

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LITERATURE CITED


COLORADO CLIMATE DATA CENTER. http://ccere.atmos.colorado.edu.


MICHENER, C.D., R.J. McGINLEY, AND B.N. DANFORTH. 1994. The bee genera of North and Central America
(Hymenoptera: Apoidae). Smithsonian Institution Press, Washington, DC.


NAUMANN, T. 1990. Status report for Oxybaphus rotundifolius. Colorado Natural Areas Program, Department of Natural Resources, Denver, CO.


USDA FOREST SERVICE. 1996. Rangeland analysis and training guide. Rocky Mountain Region, Denver, CO.

USDA SOIL CONSERVATION SERVICE. 1979. Soil survey of Pueblo County area, Colorado.


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**APPENDIX A.**—Reference information for ecological studies and disturbance classification. LD-S = Low disturbance/Slope; HD-S = High disturbance/Slope; LD-F = Low disturbance/Flat; HD-F = High disturbance/Flat. An asterisk (*) indicates sites used for observations on insect visitation and with insect enclosures. Slopes given as a range rather than a single percentage changed substantially across the plot diameter.

An additional area for insect collection is located at Portland (Appendix B: 12, 13). This site is on the property of a commercial cement plant and became profoundly degraded during the later phases of the study; it is therefore not included here as a primary study plot.

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<table>
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<th>Site Name</th>
<th>Type</th>
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<td>2 Comanche National Grasslands: Timps</td>
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<td>HD-S</td>
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<td>18% S</td>
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<tr>
<td>5 Motocross</td>
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<td>7 Fort Carson</td>
<td>HD-F</td>
<td>tank maneuvers</td>
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<tr>
<td>8 Juniper Breaks</td>
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<tr>
<td>9 Wildlife Area</td>
<td>HD-S</td>
<td>camp ground</td>
<td>flat</td>
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**Notes:**
- LD-S = Low disturbance/Slope; HD-S = High disturbance/Slope; LD-F = Low disturbance/Flat; HD-F = High disturbance/Flat.
- Slopes given as a range rather than a single percentage changed substantially across the plot diameter.
- An asterisk (*) indicates sites used for observations on insect visitation and with insect enclosures.
- GPS coordinates are given for each site.
- County and location information are provided for each site.
APPENDIX B.—Reference locations for ICP geochemical sampling (Fig. 4, Table 2). Superscript numbers indicate sites sampled for the following: 2 = pH, 3 = X-ray diffraction (gypsum), 4 = particle size, and 5 = soil profiles at 2 depths. Numbers in parentheses indicate the related disturbance study site listed in Appendix A. Those marked “vic.” are either adjacent to or within 2 km of the plot noted. Plots 12–14 were destroyed from development during the course of the study and were not available for ecological analysis; plots 15–17 were low-disturbance sites with *Mirabilis rotundifolia* populations not used for intensive study due to access restrictions on private land.

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<td>Beaver Creek/COSO Pueblo/Fremont line (vic. 7)</td>
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