Vegetation-Environment Relationships in a Rock Outcrop Community in Southern Oklahoma

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ABSTRACT.—Vegetation and environmental variables were sampled in 17 soil-filled depressions (islands) on a granite outcrop in southern Oklahoma. In addition, vegetation and soil depth were measured along a transect across the largest island. The number of species per island was significantly positively related to island size and maximum soil depth. Detrended correspondence analysis produced community gradients associated with island size, soil texture, soil pH, soil depth, organic matter and distance to the edge of outcrop. Factor analysis was used to derive associations among common taxa and environmental parameters. *Sedum nuttalianum* was associated with coarse textured soils, whereas other taxa such as *Talinum parviflorum, Rumex crispus, Croton lindheimerianus* and *Ludwigea glandulosa* were associated with habitats in larger islands with higher soil pH, finer textured soils and more soil organic matter. Although apparent vegetation zones were observed in the largest island, vegetation pattern changed gradually from one zone to the next in response to changes in soil depth. Therefore, island size and soil factors are the most important variables affecting species assemblages among soil islands on this outcrop, and soil depth is important in controlling species distribution within islands.

INTRODUCTION

The physical environment imposes various constraints on the composition and structure of plant communities. These constraints operate at many spatial scales. At a large spatial scale, for example, species composition may vary among soil-filled depressions on rock outcrops due to the vagaries of seed dispersal and differences in substrate (Burgman, 1987). Also, the harsh microclimate due to rapid desiccation and high soil and air temperatures limits productivity and species diversity in these depressions (Lugo and McCormick, 1981). At a smaller scale, factors such as soil depth, soil texture and organic matter produce complex environmental gradients within soil-filled depressions on rock surfaces (Whitehouse, 1933; Burbanck and Platt, 1964; Phillips, 1981; Uno and Collins, 1987). Despite these gradients within soil depressions, plants often form distinct zonal assemblages primarily due to competitive interactions (McCormick *et al.,* 1974; Baskin and Baskin, 1988).

Rock outcrops are abundant in the southeastern United States where they support a number of endemic species (Baskin and Baskin, 1988). Analyses of plant communities on the outcrops indicate that soil depth, soil organic matter, and species richness increase during succession in these depressions (Shure and Ragsdale, 1977). Compared to the Southeast, studies of outcrop communities are less common in the southwestern U.S. (Walters and Wyatt, 1982) and less is known about species–environment relationships in these communities (Uno and Collins, 1987). The purposes of this study of rock outcrop communities were to (1) describe vegetation gradients; (2) determine species–environment relationships; and (3) analyze vegetation patterns within an island along a soil depth gradient.

METHODS

Study area.—The study was conducted on Six-acre Rock, a 2.4-ha granite dome located approximately 1.2-km E of Troy in Johnston County, S-central Oklahoma. This region contains only a few areas of exposed granite. The outcrop we studied is surrounded by crosstimbers woodland dominated by *Quercus stellata, Q. marilandica* and *Carya texana* (plant nomenclature follows Waterfall, 1972). The area including the outcrop has been lightly grazed by cattle in the past, but no grazing occurred during the study period or during the previous year. Most of the average annual precipitation of 98.0 cm falls during April, May, and September. Average annual daily temperature is 17.2 C. The average daily minimum temperature ranges from −1.7 C in January to 20.7 C in August, while the average daily maximum ranges from 11.9 C in January to 35.1 in July and August.

Field methods.—Seventeen soil islands ranging in size from 1.0–50.8 m^2 were selected for sampling and environmental analysis. Within each island, species cover was visually estimated in 5% cover classes in randomly located 25 × 25-cm^2 quadrats. The number of quadrats per island ranged from four in the smallest island to 18 in the largest. Although fewer quadrats were used in the small islands, percent of area sampled was greatest in the smaller islands, 25% of the area, compared to 3–10% in the larger islands. In the larger islands, sampling was conducted until it was determined that additional quadrats would add few new species. Any species observed in an island but not occurring in any quadrats was listed as present. This added 1–2 species to the list only in the largest islands. All quantitative sampling of vegetation occurred during 15–21 May 1986. All islands were subsequently observed each month to add new species that appeared later in the growing season.

Because all islands were essentially elliptical, size of each island was calculated by measuring its length (L) and width (W) and using the formula for an ellipse (Area = $\pi LW/4$). Soil depth was measured in at least 15 randomly located positions in each island by inserting a wire probe through the soil until it struck bedrock. These measurements were used to calculate average soil depth and coefficient of variation of soil depth, which is a measure of habitat heterogeneity within an island. Additional variables measured for each island included distance from the island to its nearest neighbor island and distance to the nearest edge of the outcrop.

Five soil samples from the top 10 cm of soil were collected from each island. These samples were composited, mixed and two subsamples were analyzed for soil texture (hydrometer method), pH (1:1 soil : water suspension), organic matter (loss on ignition), and total Kjeldahl nitrogen. Soils were collected on 21 May 1986 for pH and N analyses, and on 15 October 1986 for measurement of soil texture and organic matter.

To determine vegetation patterns within the largest island, species cover was visually estimated (5% cover classes) in a belt transect of 62, 10 × 10 cm contiguous quadrats across the long axis of the island. Soil depth was measured with a wire probe in the center of each quadrat.

Data analyses.—Several ordination methods (principal components analysis, reciprocal averaging, detrended correspondence analysis, polar ordination and nonmetric multidimensional scaling) on matrices of species average cover values were used to analyze vegetation patterns among islands. All ordinations except principal components analysis (which was difficult to interpret) produced similar results. Thus, we present the detrended correspondence analysis (DCA) because of its wide applicability, reliability and ease of interpretation (Brown *et al.*, 1984; Peet *et al.*, 1988). The DCA ordination was based on a 30 species by 17 island data matrix. Species occurring in only one island were deleted prior to the ordination analysis. The remaining rare species (species occurring in <4 islands) were downweighted to reduce their influence on the ordination (Gauch, 1982). Relationships between environmental variables and ordination axes were determined by Spearman rank correlation.

Factor analysis (FA) was used to determine the relationship between cover of common

TABLE 1.—Species occurring in three or more islands (presence), life form (A = annual, P = perennial, G = grass, F = forb), average cover among islands in which the species occurred, maximum cover value, and smallest island (m^2) in which the species occurred

Species	Life form	Presence	Average % cover	Maximum % cover	Smallest island
Plantago wrightiana	AF	17	10.4	24.4	1.0
Sedum nuttalianum	AF	17	24.4	80.2	1.0
Foliose lichens	P	17	31.2	92.8	1.0
Moss	P	12	25.1	71.4	3.3
Croton lindheimerianus	AF	11	2.9	8.2	3.3
Talinum parviflorum	AF	11	4.1	10.1	1.0
Rumex crispus	PF	11	3.3	7.8	1.0
Ludwigia glandulosa	AF	11	4.6	15.7	1.0
Vulpia octoflora	AG	11	5.4	14.5	1.0
Chaetopappa asteroides	AF	9	14.5	35.4	3.8
Bouteloua gracilis	PG	7	2.0	5.3	3.4
Hedeoma hispidum	AF	6	1.8	4.8	6.5
Diodia teres	AF	5	3.0	5.0	6.5
Froelichia floridana	AF	5	2.2	5.0	6.5
Lepedium virginicum	AF	5	1.7	3.0	3.3
Triodanus perfoliata	AF	5	3.9	6.0	4.7
Krigia occidentalis	AF	4	1.5	2.0	6.5
Aira elegans	AG	3	3.1	5.0	12.6
Chaerophyllum tainturieri	AF	3	3.5	7.5	16.2
Camassia scilloides	PF	3	5.7	10.0	19.3
Eleocharis sp.	PG	3	1.4	2.3	6.5
Oxalis stricta	AF	3	1.1	1.2	6.5
Torilis arvensis	AF	3	5.3	10.0	37.2

Additional species: *Arenaria serpyllifolia, Bromus japonicus, Castalleja coccinea,* Unk. Compositae, *Daucus pusillus, Dicanthelium oligosanthes* var. *scribnerianum, Echinocereus baileyi, Euphorbia* sp., *Gaura parviflora, Linum sulcatum, Nothoscordum bivalve, Nostoc* sp., *Panicum* sp., *Polygala alba, Ptilimnium capillaceum,* Unk. Poaceae, *Selaginella peruviana,* Unk. forb

taxa (those present in >35% of the islands) and environmental variables (*cf.*, Schnell *et al.*, 1977). This analysis requires fewer variables than samples (islands). Thus, to reduce redundancy in the matrix, only one of a series of highly correlated environmental variables was retained for analysis. We then conducted FA (two axes) from a correlation matrix of the 10 most abundant species and five environmental variables.

Community pattern within the largest island was determined using the pattern analysis technique of Whittaker *et al.* (1979). The first axis score of a DCA ordination of species cover values in the 62 quadrats was plotted against quadrat sequence to produce a trace of vegetation pattern across the island. Vegetation pattern was then related to soil depth along the transect using correlation analysis.

RESULTS

A total of 41 species occurred among the 17 soil islands on the outcrop. Most of the species in these islands were annuals or short-lived perennials (Table 1). Three taxa (*Plantago wrightiana, Sedum nuttallianum* and foliose lichens) occurred in every island (Table

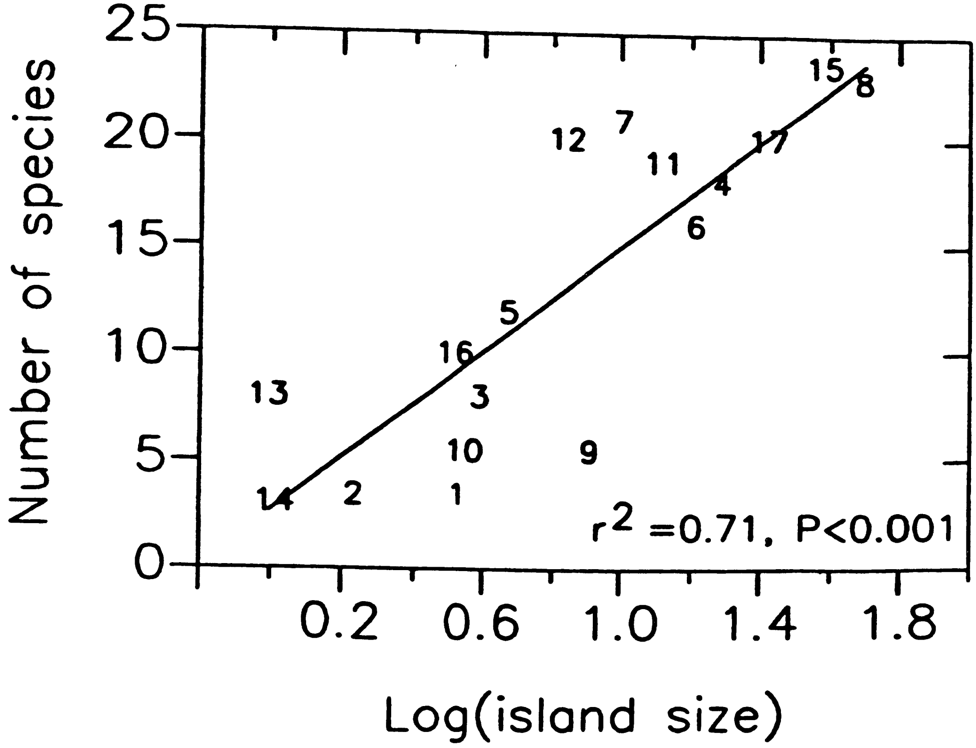

FIG. 1.—Number of species vs. log island size. S = 2.69 + 12.34 log AREA, where S = number of species and log AREA = log of island size (m^2)

1), whereas 18 species occurred in only one or two islands. *Sedum nuttallianum* had the highest average cover value among the species, and its greatest cover occurred in the smallest island. For most other species, cover generally increased with island size.

The number of species per island was significantly positively related to log island size ($r^2 = 0.71$, $P < 0.001$, Fig. 1). Using partial correlation to hold size constant, there was no relationship between species richness and average soil depth ($r^2 = 0.06$, $P > 0.05$). Species richness, however, was correlated with maximum soil depth ($r^2 = 0.40$, $P = 0.006$).

The first axis of the DCA ordination (Fig. 2) was a gradient of 2.54 SD units. An axis length of ca 4.0 SD units represents a complete turnover of species along a DCA axis (Gauch, 1982). Compositional differences along the first axis reflected an environmental gradient from large, deep islands with high organic matter and pH (Table 2) containing weedy taxa such as *Lepidium virginicum, Euphorbia* spp., *Camassia scilloides* and *Ptilimnium nuttallii* to smaller islands dominated by lichens, *Plantago wrightiana* and *Sedum nuttallianum*. The second axis (1.20 SD units) reflects a soil texture gradient from islands with fine textured soils (Table 2) containing species such as *Oxalis stricta, Arenaria serpyllifolia* and *Chaerophyllum tainturieri* to islands with sandy soils with taxa such as *Eleocharis* spp. and *Aira elegans*.

The first axis of factor analysis (Fig. 3) separated the association of *Sedum nuttallianum* and percent sand, from the association of most other species with soil pH, island size, percent clay and organic matter. Essentially, this indicates that *S. nuttallianum* occurs in areas with

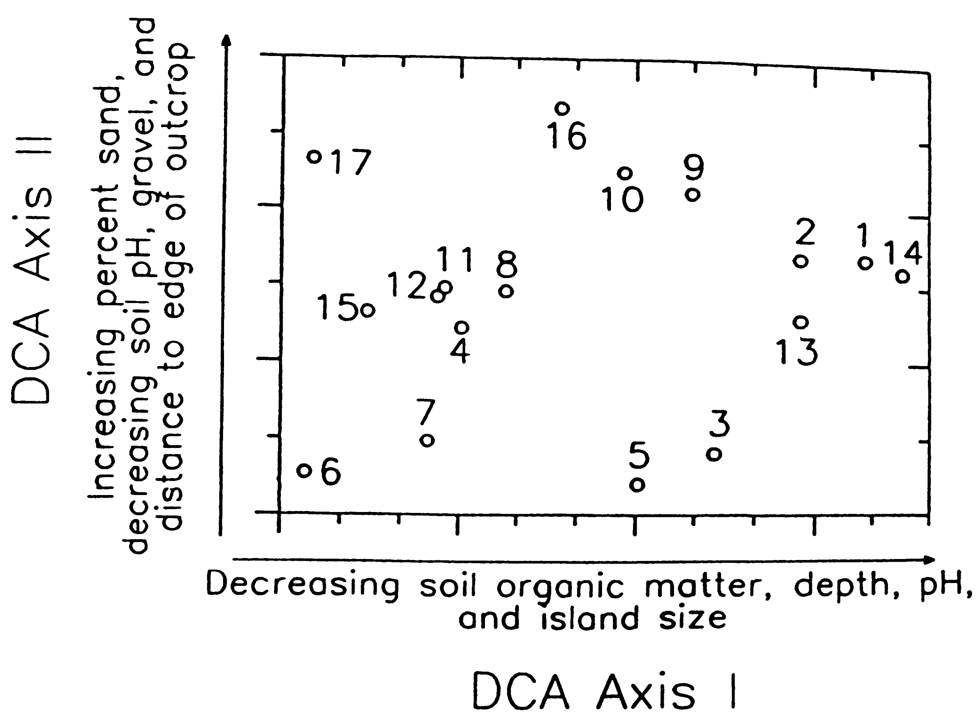

FIG. 2.—Detrended correspondence analysis (DCA) of vegetation in 17 soil-filled depressions on Six-acre Rock. Axis I is a gradient of decreasing island area and soil organic matter, depth and pH. Axis II reflects a gradient of increasing sand, decreasing gravel and soil pH, and decreasing distance from the edge of the outcrop

coarse textured soils, whereas other species occupied habitats with finer textured soils, higher soil pH and more organic matter. These latter habitats typically occurred in larger islands. The second FA axis related lichens to percent sand, clay and organic matter. Lichens tended to occupy areas with little other vegetation either in areas of organic matter and fine textured soils or in areas with sandy soils.

The trace of community pattern in the largest island suggests that there are two apparent zones of vegetation in the largest island (Fig. 4A). The zone of vegetation near the edge of the island is dominated by *Sedum nuttallianum* and *Plantago wrightiana.* A second zone of species-rich vegetation occupies the center of the island. However, the trace does indicate that a gradual transition between these zones occurs over ca. 2.0 m of the transect (quadrats 20–40, Fig. 4A). This vegetation pattern is highly significantly correlated with soil depth along the transect (Fig. 4B). Towards the end of the transect (quadrats 53–62) soil depth decreases rapidly and the vegetation changes rapidly. It appears, therefore, that zonation in these islands only occurs if soil depth remains constant; otherwise vegetation changes gradually in response to changes in soil depth.

DISCUSSION

The vegetation patterns among soil-filled depressions on this rock outcrop are similar to those described for outcrop communities in the southeastern United States (Keever *et al.*, 1951; Burbanck and Platt, 1964; Wyatt and Fowler, 1977) and elsewhere (Rundel, 1975;

TABLE 2.—Spearman rank correlation coefficients between the first two axes from the detrended correspondence analysis (DCA) and environmental variables. Correlations > |0.43| are significant at $P = 0.05$. AREA = island area (m^2), N = total nitrogen, pH = soil pH, DPTH = average soil depth (cm), CVD = coefficient of variation of soil depth, OM = soil organic matter, G = percent gravel, S = percent sand, C = percent clay, NBR = distance (m) to nearest island, EDGE = distance (m) to the edge of the outcrop

	DCAI	DCAII	AREA	N	pH	DPTH	CVD	OM	G	S	C	NBR
DCAII	0.19											
AREA	−0.78	−0.22										
N	−0.34	−0.19	0.09									
pH	−0.70	−0.58	0.73	0.10								
DPTH	−0.71	−0.38	0.78	0.19	0.80							
CVD	0.43	0.23	−0.31	−0.53	−0.39	−0.29						
OM	−0.52	0.13	0.25	0.56	0.30	0.20	−0.30					
G	−0.19	−0.83	0.21	0.07	0.55	0.42	−0.12	−0.22				
S	0.24	0.84	−0.23	−0.05	−0.62	−0.42	0.19	0.09	−0.96			
C	−0.29	0.35	0.20	−0.08	0.15	0.08	−0.11	0.50	−0.36	0.11		
NBR	0.24	−0.03	−0.15	0.17	−0.20	−0.24	−0.03	0.24	−0.11	−0.02	0.31	
EDGE	−0.32	−0.53	0.07	0.31	0.32	0.19	−0.50	0.20	0.40	−0.39	−0.30	−0.24

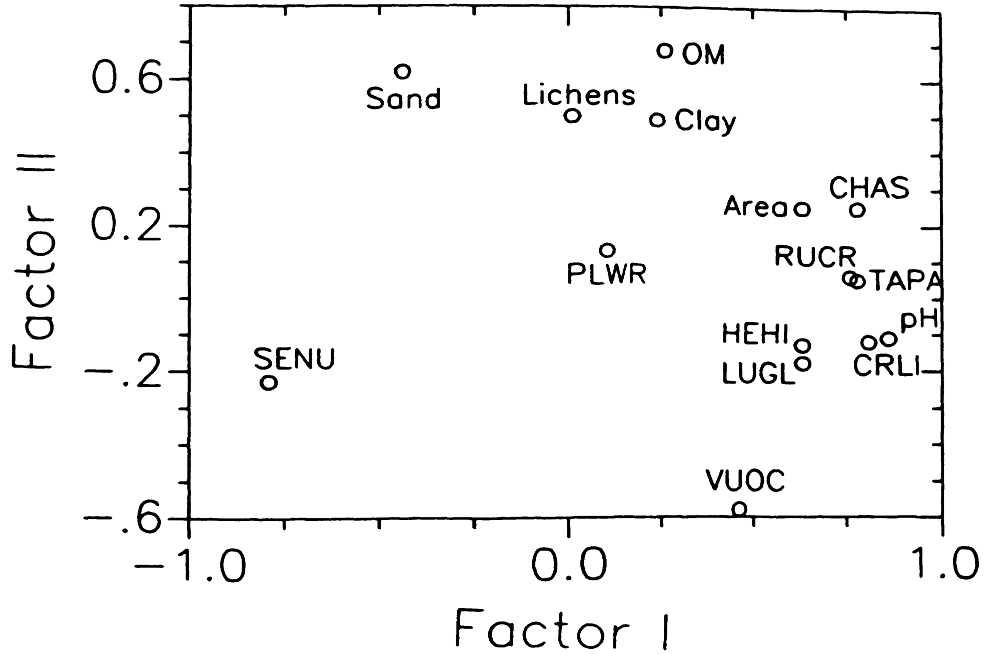

FIG. 3.—Factor analysis (FA) of common taxa and five environmental variables. FA axis I associates *Sedum nuttallianum* with percent sand, all other species are associated with increasing island area, soil pH, percent clay and organic matter (OM). CHAS = *Chaetopappa asteroides,* CRLI = *Croton lindheimerianus,* HEHI = *Hedeoma hispidum,* LUGL = *Ludwigia glandulosa,* PLWR = *Plantago wrightiana,* RUCR = *Rumex crispus,* SENU = *Sedum nuttallianum,* TAPA = *Talinum parviflorum,* VUOC = *Vulpia octoflora*

Burgman, 1987). Essentially, the general distribution of species among islands was a function of island size and correlated edaphic variables such as soil depth, pH and organic matter. Uno and Collins (1987) reported that *Sedum nuttallianum* and *Plantago wrightiana* occurred in soils that were significantly shallower than soils occupied by species such as *Bouteloua hirsuta.* Thus, the ubiquitous distribution of lichens, *S. nuttallianum* and *P. wrightiana* observed in this study indicated the occurrence of shallow, coarse-textured soils in all islands regardless of size. *Bouteloua hirsuta* was uncommon on Six-acre Rock. Compositional differences among islands reflected variation in habitat quality as well as stochastic variation associated with seed dispersal and establishment. Dispersal, in particular, appears to be stochastic because there was no relationship between species composition in an island and the distance to its nearest neighbor. There was a relationship between DCA axis II and distance of the island from the edge of the rock. This is somewhat a function of island size because large islands were found in the middle of the rock where it was nearly level, whereas smaller islands occurred closer to the edge of the rock surface.

Few species in these islands are restricted to outcrop communities. Most species are weedy annuals that occur in disturbed habitats. Nevertheless, the shallow, droughty soils in these depressions create an environment that produces an assemblage of species that is distinct from the adjacent crosstimbers vegetation. This phenomenon also occurs in southwestern Oklahoma where the outcrops are surrounded by mixed-grass prairie (Uno and Collins,

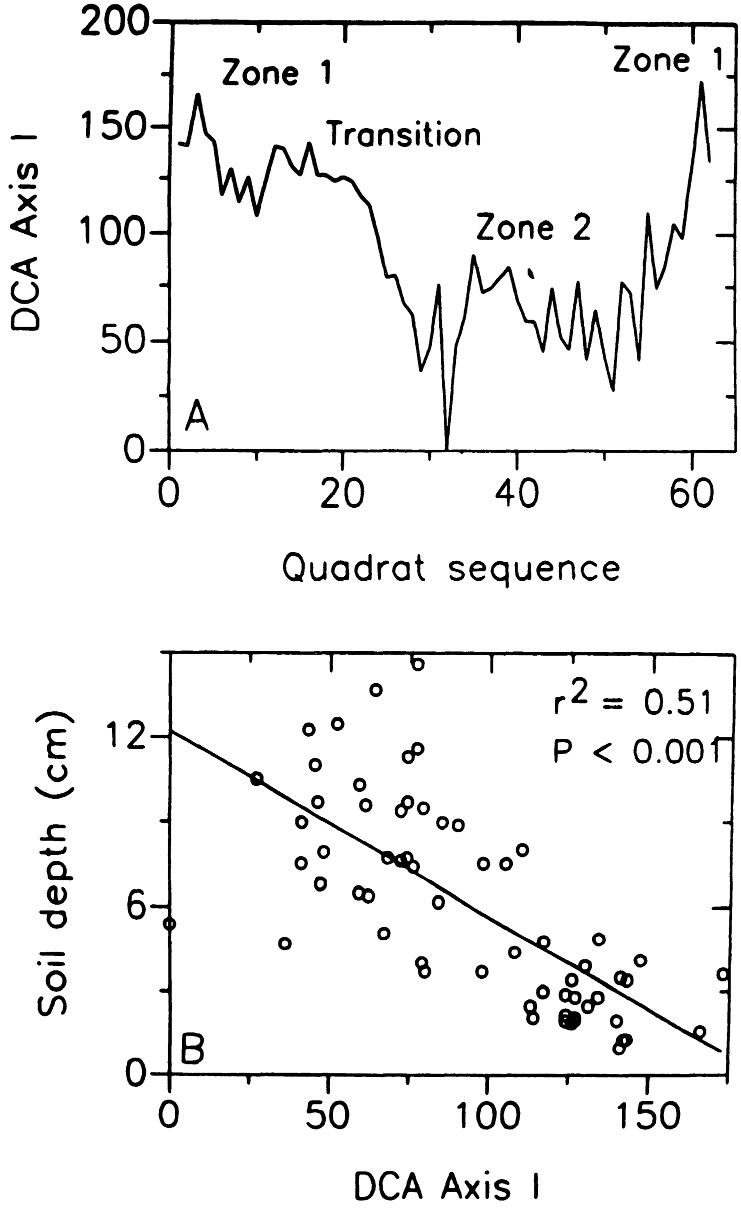

FIG. 4.—(A) Trace of community pattern across the largest soil-filled depression on Six-acre Rock. The x-axis is the quadrat sequence along a belt transect across the island. The y-axis is the first axis of a detrended correspondence analysis (DCA) ordination of the quadrat data. (B) Relationship between DCA axis I and soil depth in each quadrat along the belt transect. DPTH = 12.2 − 0.66DCA1, where DPTH = soil depth and DCA1 = Axis I score from the ordination of the belt transect quadrat data

1987). Two genera, *Sedum* and *Talinum,* are commonly represented in granite outcrop communities in the southwestern and southeastern U.S. (Wyatt and Fowler, 1977; Uno and Collins, 1987). The occurrence of these taxa on rock outcrops is a function of their high light requirement and poor competitive ability (Baskin and Baskin, 1988). This does not completely explain their presence in outcrop vegetation, however, because these species must also be highly drought-tolerant. Thus, those species found on outcrops in Oklahoma probably have life histories preadapted to tolerating (*e.g., Bouteloua gracilis*) or avoiding (*e.g., Sedum nuttallianum*) drought. Because most species are annuals that grow during the spring rainy season, drought avoidance would appear to be the most effective life-history strategy in these soil depressions.

Island size, soil depth and pH are positively correlated, as are organic matter and total nitrogen (Table 2). Changes in these edaphic conditions are often associated with plant succession (Shure and Ragsdale, 1977; Phillips, 1981; Burbanck and Phillips, 1983). In southeastern outcrops, Keever *et al.* (1951) and Burbanck and Platt (1964) described successional changes involving general stages of (1) mosses and lichens; (2) lichens and annuals; (3) annuals and perennials; and (4) woody vegetation. Shure and Ragsdale (1977) and Burbanck and Phillips (1983) reported an increase in soil depth and soil nitrogen along this successional sequence. Succession, however, in many soil depressions is simply a general correlate of island size. This relationship can be inferred for the vegetation on Six-acre Rock. Bare rock is occupied by scattered patches of crustose and foliose lichens and mosses (pers. observ.). Shallow depressions on the outcrop contain few species other than lichens, *Sedum nuttallianum* and *Plantago wrightiana.* As soil depth increases, the islands are colonized by many other weedy species such as *Ptilimnium nuttallii, Torilis arvensis* and *Camassia scilloides.* In areas on the rock where fissures occur, deeply rooted species, including the bunchgrass *Andropogon scoparius* and trees such as *Quercus stellata,* become established (pers. observ.). The soil in the depressions rarely gets much deeper than 30–40 cm, however, so successional development in these habitats is limited as a result of environmental constraints imposed by a limited capacity for soil development.

Traditionally, vegetation in soil-filled depressions has been described in association with distinct zonation of communities resulting from distinct environmental changes from the edge to the interior of the soil depression plus competitive interactions among species (McCormick *et al.,* 1974). The trace of community pattern across the largest soil depression on Six-acre Rock (Fig. 4) indicates that species composition does reflect zonation. There is, however, a gradual change in community pattern from one zone to the next and the overall pattern is highly correlated with changes in soil depth, a factor positively correlated with increasing soil pH (Table 2). Visually, the distinct physiognomy of the *Sedum*-dominated areas along the edge of the depression lends the appearance of zonation in these soil islands, but the subtle environmental gradients within an island actually produce gradual changes in vegetation composition.

Overall, the physical environment induces severe environmental constraints on the vegetation among and within soil-filled depressions on this granite outcrop. Although differences in the physical environment among and within islands are often subtle, considerable variation exists among the vegetation within these islands of soil. Differences in community composition reflect differences in the degree of soil development. Soil development, however, is also constrained by very slow erosional processes that may only gradually increase island size and depth. This combination of environmental limitations on rock outcrops results in an assemblage of species that is characterized by their ability to tolerate or avoid low water and nutrient availability within soil-filled depressions on the rock surface.

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