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VEGETATION ZONES AND SOIL CHARACTERISTICS IN VERNAL POOLS IN THE CHANNELED SCABLAND OF EASTERN WASHINGTON

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ABSTRACT.—Vernal pools are seasonal pools occurring in Mediterranean-type climates within which grow concentric zones of vegetation. We studied two vernal pools that lie within an *Artemisia tridentata/Festuca idahoensis* shrub-steppe landscape in the Channeled Scabland of eastern Washington to determine the relationship between vegetation zonation and soil characteristics. Abundant plant species in the pools include *Elymus cinereus, Poa scabrella, Lomatium grayi, Allium geyeri, Eleocharis palustris, Epilobium minutum, Myosurus aristatis, Deschampsia danthonioides,* and *Psilocarphus oregonus.* We surveyed topography, measured plant species frequency and cover to describe the vegetation zones, and used Sorenson's index of percent similarity to verify our designation of plant zones as communities. In one pool we described soil profiles and sampled soils throughout the growing season according to plant communities. We analyzed soils for pH; electrical conductivity; sodium, calcium, and magnesium ions; sodium adsorption ratio; particle size; organic carbon; and water matric potential. ANOVA tests of soil characteristics and topography among plant communities showed that only differences in topography are statistically significant. There are, however, trends in particle size, some soil chemical parameters, and soil moisture potential among plant communities along the topographic gradient. Electrical conductivity decreased with increasing dryness of the soil through the spring and summer. Seasonal changes in soil moisture potential showed that shallower soils in the centers of pools are wetter during the wet season and drier during the dry season than are deeper soils. These changes in moisture may be the most important influence on vegetation distribution within the vernal pools.

Key words: vernal pool, vegetation zones, soil characteristics, eastern Washington.

Vernal pools occur in grasslands, parklands, and forests where Mediterranean-type rainfall patterns prevail. These biotic systems are geographically widespread and are among the casualties of the widespread modification of natural landscapes. Vernal pools are typically formed in shallow depressions where soils have impermeable hardpans or are underlain by impermeable bedrock. Vernal pools fill with water from winter rains (and snowmelt in colder climates) and gradually dry during late spring and early summer through evapotranspiration. Vegetation within the pools is different from that of the surrounding landscape and often forms a pattern of more or less concentric zones of different species groupings. These unique natural sites are excellent for studying ecological processes in relatively self-contained ecosystems.

Zonal vegetation patterns of vernal pools have attracted many researchers in California, where vernal pools are numerous. Scientists have approached the study of pools by examining aspects of seasonal hydrology and soil physical and chemical characteristics. One theory is that seasonal duration of standing water directly affects distribution of plant species according to their ability to germinate and/or grow either under water or within the shortened growing season after evaporation of the pool (Purer 1939, Lin 1970, Zedler 1987). Other researchers have found trends in soil particle size, available nitrogen and phosphorus, exchangeable magnesium and sodium, electrical conductivity, pH, and unsaturated soil moisture potential that correlate to position along the gradient from outside to inside the pool (Lathrop 1976, Bauder 1987). Thus, a second theory is that soil chemical and physical factors influence plant distribution.

Researchers have taken different views as to whether there are spatially discrete zones of species groupings (plant communities) or whether the distribution of species is continuously variable, with overlapping growth ranges. Some argue the latter case and maintain that

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only temporal groupings of species occur (Purer 1939, Zedler 1987). The alternate view has been supported by several studies whose authors typically have delineated three to five zones, one of which is the surrounding grassland vegetation (Lin 1970, Kopecko and Lathrop 1975, Macdonald 1976).

Pools of the Pacific Northwest, specifically those in central and eastern Oregon and Washington, have been little studied. We chose two vernal pools in eastern Washington to examine the validity of vegetation zonation and to determine a possible relationship between vegetation zones and soil properties.

STUDY AREA

We chose to study vernal pools in the Marcellus Shrub Steppe Natural Area Preserve (47°14′N, 118°24′E, Sec. 15, T20N, R35E, WBM, in Adams County, Washington) because the site has not been seriously degraded by past grazing (Schuller 1984) and because it has been fenced as a preserve since 1986. The preserve covers approximately 290 ha (Fig. 1) and is at the northeast end of a larger tract of uncultivated scabland, surrounded by wheat fields, that extends west-southwest for approximately 6.5 km along Rocky Coulee, part of the Channeled Scabland, an enormous landscape in eastern Washington formed by repeated cataclysmic glacial outburst floods during the Pleistocene (Fig. 1; Baker 1978).

Surrounding the Channeled Scabland and in some areas within it are deposits of Pleistocene-age loess (windblown silt) many meters thick (Busacca 1991) that overlie the Miocene Columbia River Basalt. The last glacial floods about 15,000 years ago removed most of the older loess from the Telford–Crab Creek Scabland tract, including the project site, so that the thin cover of loess presently on the site has accumulated, and soils have developed, only since the last floods. Deeper soils of the site, approximately 40–150 cm deep, are on the loess mounds. Soils within the vernal pool basins are only approximately 10–30 cm deep. Most vernal pools are part of an interrupted channel system running through the study site (Fig. 1). Solitary pools and those in the intermittent channel system may have been formed by a combination of cataclysmic flood scour, variable loess deposition, and local slope erosion.

Rainfall distribution of the Columbia Plateau is a Mediterranean type. Forty years of average temperatures, precipitation, and evapotranspiration were used to produce a climate diagram (Thornthwaite 1948, NOAA 1988–89), which indicated that November through March are the months of greatest precipitation (approximately 60% of the yearly total) and soil water storage, whereas April through October bring little precipitation and high evapotranspiration.

METHODS

Average monthly precipitation and temperature values recorded at the Ritzville 1SE weather station (NOAA 1988–89) were used to compute average monthly evapotranspiration for the months of pool filling and plant growth in the study year (Palmer and Havens 1958). Precipitation values for November 1988 through March 1989, the months typically receiving the majority of precipitation, and April through June of 1989, the months during which most vernal pool species grow vegetatively and flower, were compared with average values for these time periods.

We chose two vernal pools for this study and called them South Pool and North Pool. South Pool is 109 m long and 70 m wide, and North Pool (Fig. 2) is 57 m long and 34 m wide. A 25-m-wide swath through South Pool (Fig. 3) and all of North Pool were surveyed using a Leitz Set2 Total Station Electronic Distance Meter and SDR22 data collector to produce topographic maps. Within the two pools, groups of plant species formed concentric zones from the outsides to the centers of the pools. Although zones were uneven in width and some were even absent in some places, the sequence in which they appeared was consistent. Six vegetation zones were identified in each pool. Boundaries of the vegetation zones were marked along transect lines across each pool. We marked four sites for plant and soil sampling within each vegetation zone, two on either side of each pool center (Fig. 3).

Vegetation (in both pools) and soils (in South Pool only) were sampled on 23 April, 10 May, 24 May, 11 June, 29 June, and 13 July 1989. Repeated sampling was done to monitor maturation of vegetation. When plants within each zone reached their seasonal maturity, we measured frequency and coverage for each

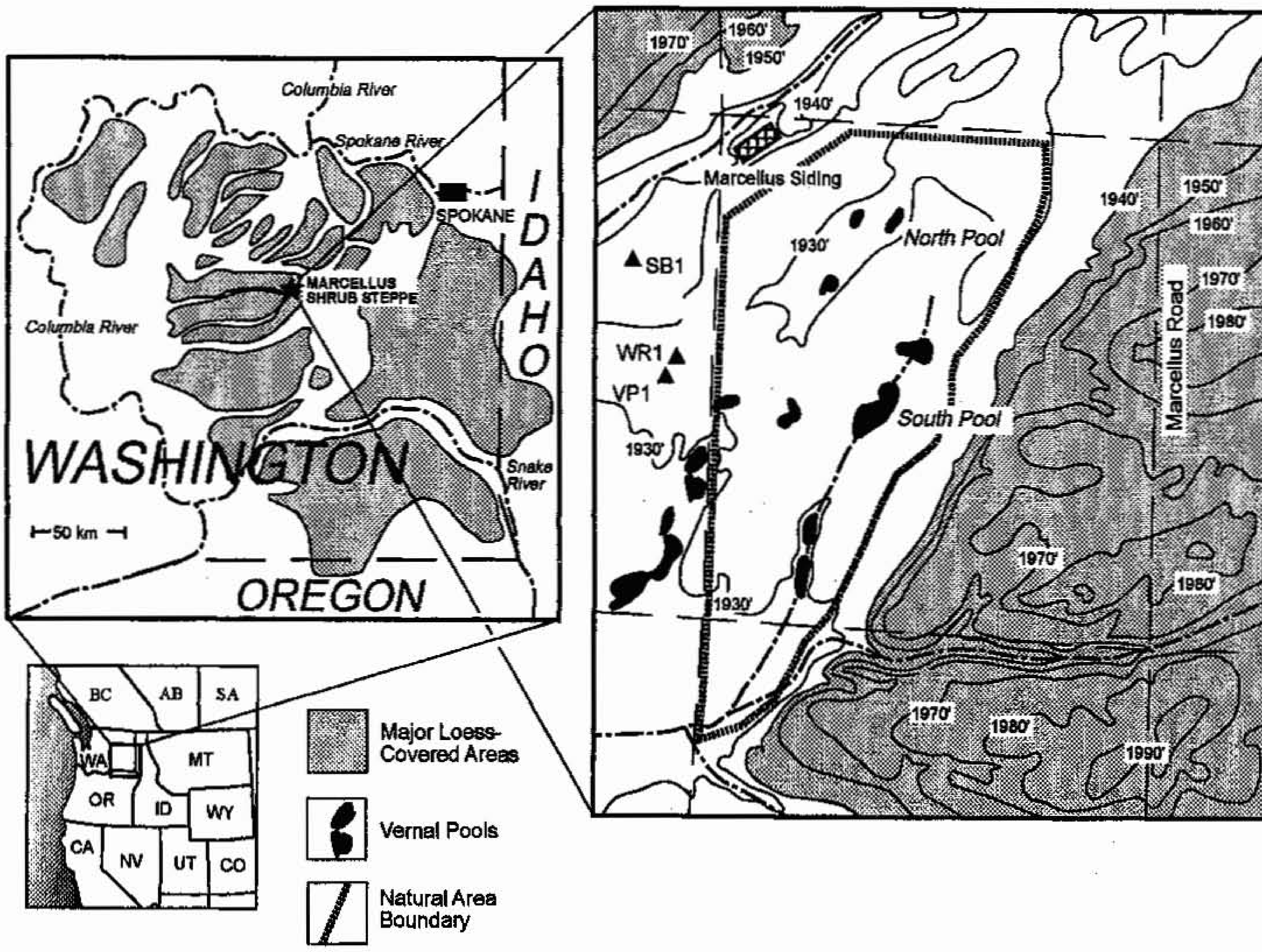

Fig. 1. Map of the Marcellus Shrub Steppe Natural Area in eastern Washington state with inset map showing generalized topography, natural area boundary, and principal vernal pools. Triangles are locations of the sagebrush (SB1), wildrye (WR1), and vernal pool (VP1) soil profile sampling sites; North Pool and South Pool are labeled.

species in forty 20 × 50-cm plots along contours. We used nested frequency plot sizes of 5 × 5 cm, 12.5 × 20 cm, 20 × 25 cm, 20 × 37.5 cm, and 20 × 50 cm and cover classes of 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100% (Daubenmire 1970). Frequency and cover values were averaged over the forty plots for analysis.

Soil samples were collected in South Pool with a 2-cm-diameter probe. The first sets of soil samples were collected at site stakes. On each successive date, samples were taken approximately 10 cm from the previous sample at the same elevation as the site stake. Sampling depth increments were 2–10 cm, 10–30 cm, 30–60 cm, 60–90 cm, etc., until we reached basalt bedrock (0–2 cm consisted of ash from the 1980 eruption of Mount St. Helens).

We measured the matric potential of soil moisture in soil samples collected on all dates using the filter paper equilibration method (Campbell and Gee 1986, Campbell 1988). We produced a moisture characteristic curve specifically for the filter paper (Whatman #42) used for determination of water potential from water content. Organic carbon and particle-size distribution were measured using wet combustion (Nelson and Sommers 1975) and the hydrometer method (Gee and Bauder 1986), respectively. The only pretreatment used in the particle-size analysis was sodium hexametaphosphate. We analyzed the 2–10-cm samples collected on 24 May from sites S1–S12.

Saturation extracts (using distilled H_2O) were collected from all samples from the 23 April and 28 June sampling dates (early and late in the growing season in the pools) and from all morphological description site samples. Electrical conductivity (EC) and pH were measured on the extracts, as well as soluble Na^+, Ca^{+2}, and Mg^{+2} to determine the sodium adsorption ratio (SAR). All ion concentrations were measured on an atomic absorption spectrophotometer.

To observe morphological properties of the soils (e.g., thickness of horizons and presence

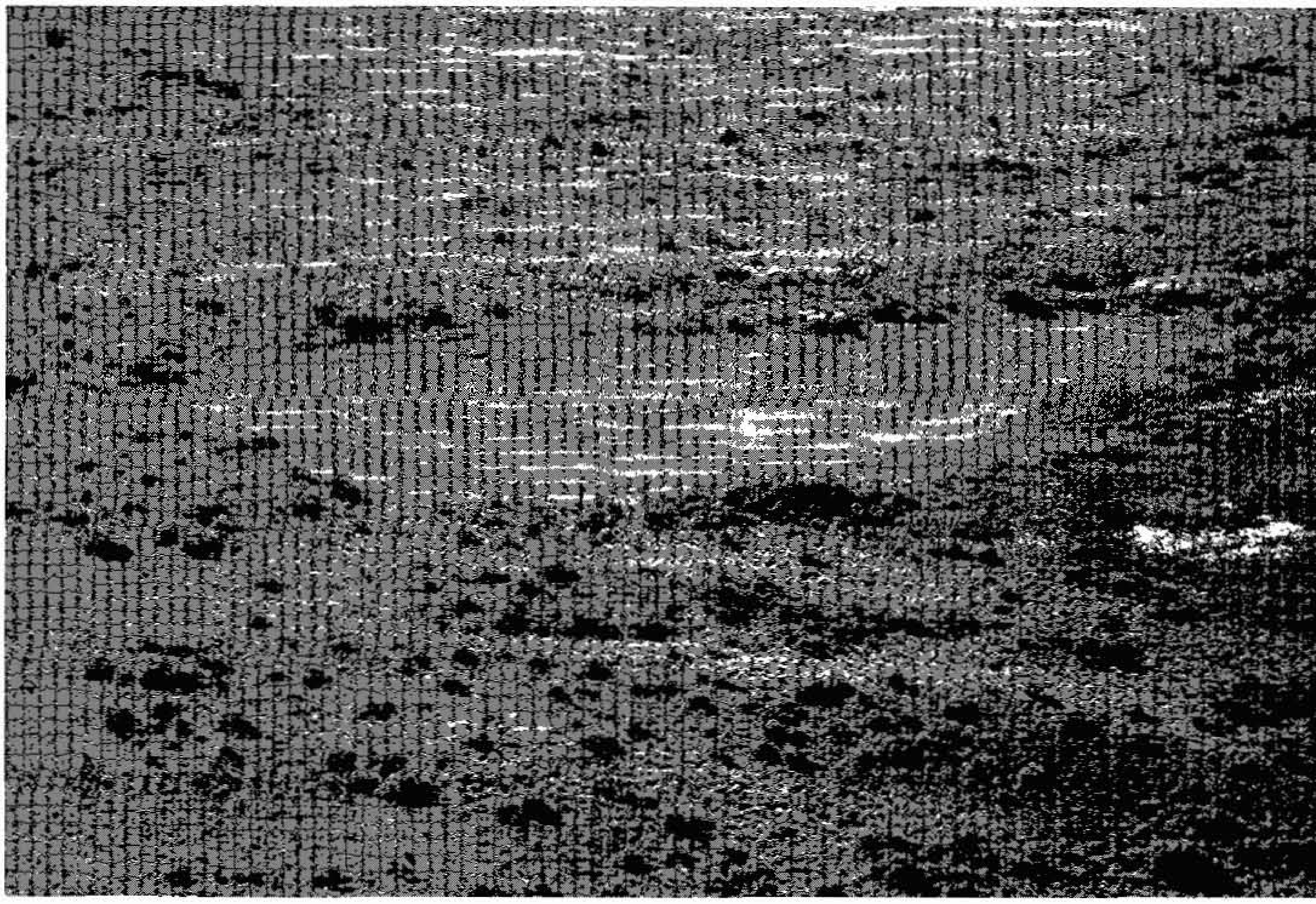

Fig. 2. Low-angle oblique aerial photograph of North Pool taken in May 1990. View is to the west; the pool is 57 m in length. *A. tridentata* is the dominant shrub in the plant zone 1 area surrounding the pool.

of structure that would indicate certain pedological processes), we excavated three soil pits: one in an upland position surrounding the pools (SB1), one in a pool rim (WR1), and one in a pool basin (VP1). To avoid damaging pools of the preserve, we located pits in the adjacent scabland tract (Sec. 16, T20N, R35E; Fig. 1), where soils were similar to those of the study site. Morphological features were described, block descriptions written, and horizons sampled for the three profiles. Block descriptions are in Crowe (1990). The three profiles were classified according to Keys to Soil Taxonomy (Soil Survey Staff 1990). We also analyzed horizons for particle size and SAR according to methods discussed above.

Vegetation, soil, and topographic data were analyzed using descriptive and inferential statistics. From the vegetation tallies we compared different vegetation zones (e.g., zone 1 vs. zone 2, zone 1 vs. zone 3, etc.) using Sorensen's similarity index for frequency (combining all frequency plot sizes) and for frequency weighted by cover (Barbour et al. 1980). Zonal elevations, particle-size classes, and organic matter were statistically compared among zones using a one-way analysis of variance (ANOVA). A repeated-measures ANOVA was used to analyze differences in soil matric potential among the vegetation zones over all five sample dates. The repeated-measures ANOVA was also used to analyze EC, pH, and SAR among all plant zones and between the 23 April and 28 June sampling dates.

RESULTS

Precipitation

Comparison of the long-term average monthly precipitation with monthly totals for November 1988 through March 1989 revealed that total precipitation for that period was almost identical to the long-term average (169 mm during 1988–89 vs. 168 mm on average). April through June precipitation totals (58 mm) were also quite similar to the long-term average (63 mm); however, only 1.52 mm of rain fell in June compared to an average of 23 mm, and temperature and evapotranspiration were slightly higher than average. Matric potential values measured during April and May thus were probably indicative of the moisture normally available to vernal pool species at that time of year, and those measured in June were

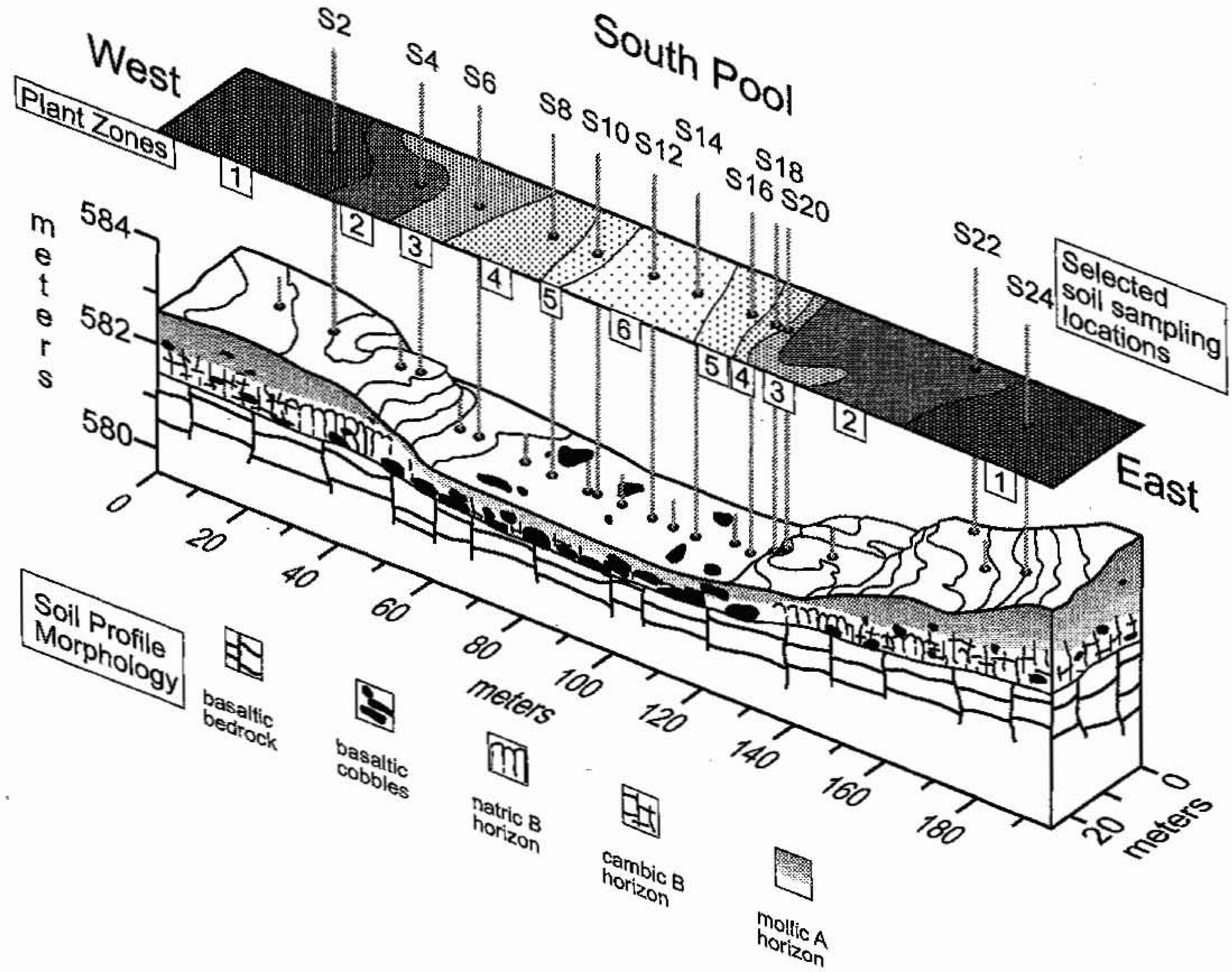

Fig. 3. Topographic cross section through South Pool showing selected soil sampling locations, plant zones, and soil profile morphology. Note ca 10X vertical exaggeration. Shaded areas indicate plant zones. Zones are numbered and correspond to text. S2–S24 are selected soil sampling locations.

probably lower than normal. The pools probably dried faster than they do in some years, which would shorten life cycles of annuals that normally flower during June or early July.

Vegetation

We identified six vegetation zones (zones 1 through 6) in South Pool (Fig. 3), five similar zones (zones 1, 3, 4, 5, and 6) in North Pool, and an additional zone (zone 7) of rush (*E. palustris*) that occurs only in North Pool. Total species cover and frequency in the 25% cover class for all zones in the South and North pools are shown in Table 1. Zone 1 was an example of a shrub-steppe community as described by Daubenmire (1970). It was dominated by *F. idahoensis* with a scattered shrub overstory of *A. tridentata.* More abundant forbs included *Plectricus macrocera, Plantago patagonica,* and *Draba verna.* Shrub height was about 70 cm and herb height about 40 cm. Zone 2 was dominated by *E. cinereus,* with a shrub overstory of *Chysothamnus nauseosus* and *C. vicidiflorus.* The more abundant forbs included *Senecio interrigemus, P. macrocera, D. verna,* and *Achillea millefolium.* Average height of vegetation in this community was about the same as in zone 1.

Zones 3–7 had no shrub overstory. In zone 3 *Poa scabrella* (40 cm in height) dominated, with *Lomatium grayi, A. geyeri,* and *Montia linearis* scattered throughout. *Deschampsia danthonioides* had very high cover in zones 4, 5, and 7. Other forbs and graminoids in zones 4 and 5 were *E. palustris, Agrostis diegoensis,* and *Agoseris heterophylla.* Forbs that distinguished zone 4 were *A. geyeri* and *E. minutum;* those that distinguished zone 5 were *Navarettia intertexta, Grindelia nana,* and *Myosuris aristatis.* Zone 7 had an abundance of *E. palustris* and well-distributed *M. aristatus, Alopechurus geniculatus,* and *E. minutum.* Vegetation height in these zones averaged 30 cm. Zone 6 was dominated by the low-growing annual forbs *N. intertexta* and *Plagiobothrys scouleri* (5–10 cm). Other forbs included *Psilocarphus oregonus* and *G. nana*.

We calculated similarity indices from our comparisons of plant communities of different zones within each of the two pools (Table 2). Results from comparisons using absolute frequency of species alone resulted in higher similarity indices between zones, whereas the addition of total canopy cover of species reduced most indices substantially. In the latter comparison only the comparison of zones 4 and 5 in South Pool and zones 5 and 7 in North Pool produced similarity indices greater than 50%.

Species that were fairly well established (i.e., they have high cover and/or frequency percentages) in two or more zones were mostly annual forbs and graminoids: *D. verna*, *A. heterophylla*, *E. minutum*, *D. danthonioides*, *A. diegoensis*, *N. intertexta*, and *M. aristatus*. In addition, three perennial herbs, *E. palustris*, *G. nana*, and *A. geyeri*, had a strong presence in more than one zone. Species that were noticeably unique to one zone were *F. idahoensis* and *A. tridentata* (zone 1), *E. cinereus* and *Chrysothamnus* spp. (zone 2), *P. scabrella* (zone 3), and *Boisduvalia stricta* (zone 6).

Soils

Microtopography, soil sampling points, and soil morphology are depicted for South Pool in Figure 3. An ANOVA of zonal elevation means demonstrated strongly significant differences among zones in each pool ($P < .0001$).

Soil profiles examined in the soil profile pits off the Marcellus site confirmed morphological characteristics of the soils surrounding (SB1), on the margins of (WR1), and within (VP1) vernal pools of the area, including those of North and South Pool (full soil profile descriptions in Crowe 1990). We produced a cross section showing the soil morphology of South Pool (Fig. 3) based on features seen in the offsite soil profile pits combined with soil properties and depths to bedrock measured during the repeated soil sampling of South Pool. SB1 was typical of the deeper soils in the shrub-steppe zone surrounding the pools. It is classified as a Xerollic Camborthid. VP1 was typical of the shallow, stony soils within the pools and is classified as a Lithic Camborthid. The two soils differed primarily in that VP1 was shallower to bedrock (33 cm in VP1, 116 cm in SB1). Neither of these soils had strongly developed soil profile features. They consisted principally of a dark, organic matter–rich mollic epipedon or topsoil horizon typical of steppe soils, and a blocky brown cambic subsoil horizon.

WR1 was typical of the pool rim or margin landscape position that supported the wildrye zone (zone 2) . It is classified as a Lithic Natrixeroll and is distinguished by its natric horizon (a clay-enriched or argillic horizon caused by a high exchangeable sodium percentage), shallow depth to bedrock, and mollic epipedon. The SAR (a measure of the dominance of sodium on the exchange complex of clay colloids) of the natric horizon of WR1 was 9.7, which is less than the value of 13, i.e., the lower limit set for the definition of the natric horizon (Soil Survey Staff 1990); however, other features typical of the influence of high exchangeable sodium were present, including columnar structure in the natric horizon, dark organic colloid stains on these columns, and an overlying eluvial horizon. Clay content of the natric horizon of WR1 was 17.0% compared to 11.0% in the overlying eluvial horizon.

ANOVAs performed on soil physical and chemical properties among zones were not statistically significant, but there are recognizable trends in some properties that may have ecological significance. Sand, silt, and clay contents differed with respect to South Pool topographic positions (Fig. 4). Sand percentage was greater and silt percentage was less in zone 3 than in other zones. In zone 3, at the bottom of the pool "rim," erosion and deposition may have caused a winnowing of fines from and an accumulation of sand in the soils. Clay content increased modestly from the outer zone to the center of South Pool. Organic carbon values were higher in the plant zones dominated by *A. tridentata*, *E. cinereus*, and *P. scabrella* (zones 1, 2, and 3) than in the remaining zones of South Pool (Fig. 4).

Soil-water matric potentials were similar, zone by zone, in the 2–10-cm and 10–30-cm depth increments on the first sampling date, 24 May (Fig. 5). On successive dates the 2–10-cm increment dried more than did the 10–30-cm increment as plants extracted soil moisture from the near-surface zone and soil moisture evaporated from the soil surface. On 11 June in

TABLE 1. All-species rélève showing total canopy cover and percent frequency in the 25% cover class by vegetation zone.

Species	Zone 1 South	Zone 1 North	Zone 2 South only	Zone 3 South	Zone 3 North	Zone 4 South	Zone 4 North	Zone 5 South	Zone 5 North	Zone 6 South	Zone 6 North	Zone 7 North only
	% total cover / % frequency in 25% cover class											
SHRUBS												
Artemesia tridentata	4.9/2.5	0.9/2.5										
Artemesia tripartita		3.3/2.5										
Chrysothamnus vicidiflorus	0.4/0.0		0.4/0.0									
Chrysothamnus nauseosus			4.7/10.0									
Tetradymia canescens			2.6/7.5					0.4/0.0				
PERENNIAL FORBS												
Dodecatheon conjugens	0.5/0.0											
Delphinium nuttalium	2.6/5.0	0.4/7.5										
Lomatium triternatum	0.1/2.5	0.1/2.5										
Frasera albicaulis	0.4/0.0	2.5/2.5										
Senecio interrigemus	3.1/10.0	0.1/0.0	6.0/0.0	0.1/0.0								
Achillea millefolium	0.6/7.5	0.3/5.0	3.5/10.0	0.5/2.5	0.7/10.0							
Lomatium grayi	1.7/10.0	2.1/17.5	2.7/0.0	11.8/35.0	13.4/32.5		15.1/22.5	0.4/2.5				
Erigeron sp.		0.4/0.0										
Chondrilla juncifolia			0.1/2.5									
Allium geyeri				5.9/37.5	0.2/0.0	18.6/45.0	22.6/55.0	0.8/2.5				
Grindelia nana				1.1/17.5		2.8/17.5	3.3/5.0	8.3/90.0		0.8/15.0	6.6/90.0	
PERENNIAL GRASSES/GRASSLIKES												
Elymus cinereus			37.4/52.5									
Festuca idahoensis	39.4/42.5	27.8/52.5			0.4/0.0							
Poa sandbergii	3.1/10.0	11.9/47.5	4.1/17.5									
Poa scabrella		0.1/2.5		38.1/92.5	30.1/85.0							
Agropyron spicatum			1.9/2.5									
Eleocharis palustris				3.1/20.0		10.5/42.5	4.3/10.0	14.1/50.0	15.8/35.0	31.7/0.0	5.3/17.5	63.6/95.0
Alopechurus geniculatus				0.1/2.5		0.1/0.0		0.4/2.5	0.7/15.0			5.1/80.0
Sitanion hystrix					2.8/10.0							

TABLE 1. Continued.

Species	% total cover / % frequency in 25% cover class											
	Zone 1 South	Zone 1 North	Zone 2 South only	Zone 3 South	Zone 3 North	Zone 4 South	Zone 4 North	Zone 5 South	Zone 5 North	Zone 6 South	Zone 6 North	Zone 7 North only
ANNUAL/BIENNIAL FORBS												
Plantago patagonica	4.9/50.0	0.9/5.0										
Plectricus macrocera	10.3/47.5	12.2/47.5	5.8/47.5		1.5/32.5							
Agoseris heterophylla	1.1/17.5	0.4/5.0	0.1/0.0	1.3/30.0	2.6/42.5	6.1/65.0	24.6/87.5	4.3/42.5	6.9/0.0			0.1/5.0
Draba verna	4.6/10.0	4.1/48.0	4.9/37.5	4.3/40.0	4.6/60.0	8.3/42.5		0.1/5.0	0.3/0.0			
Epilobium minutum	0.9/15.0	1.1/10.0	1.3/0.0	3.3/55.0	8.5/70.0	15.5/65.0	37.4/97.5	1.4/15.0	31.2/87.5			6.9/95.0
Montia linearis	2.2/12.5		0.2/0.0	3.9/60.0	1.5/25.0	0.8/0.0	0.1/0.0					
Holosteum umbellatum		1.0/2.5	1.3/7.5			0.1/2.5	3.3/5.0					
Veronica peregrina		0.1/2.5		0.8/12.5	2.0/17.5							
Lepidium perfoliatum			2.6/5.0			0.4/2.5						
Myosurus aristatus				0.1/2.5	0.1/2.5	2.3/0.0		5.3/60.0		2.1/17.5	0.9/7.5	15.5/75.0
Navarettia intertexta				0.2/0.0		1.0/2.5		18.3/100		23.5/97.5	20.3/100	1.6/12.5
Plagiobothrys scouleri				0.4/5.0	0.2/7.5	1.2/2.5		1.7/17.5		31.7/95.0	24.1/100	0.4/5.0
Lactuca serriola						0.6/15.0		0.1/0.0	0.3/2.5			0.4/7.5
Polygonum sp.						0.8/0.0	0.2/2.5	0.6/0.0		29.6/85.0	3.1/30.0	1.6/27.5
Psilocarphus oregonus						0.1/0.0		0.7/12.5		2.2/77.5	8.4/97.5	0.1/2.5
Downingia elegans								0.1/2.5	0.1/0.0	0.1/0.0	0.9/20.0	0.1/2.5
Boisduvalia stricta										2.3/32.5	1.6/42.5	
ANNUAL GRASSES/GRASSLIKES												
Bromus tectorum	1.1/15.0	1.2/18.0	4.3/22.5	0.6/5.0	1.1/7.5	2.8/12.5	0.2/0.0					
Deschampsia danthonioides	0.2/2.5	0.4/2.5		0.1/2.5		57.9/100	15.6/77.5	56.4/92.5	63.0/95.0	5.1/17.5	0.4/2.5	79.9/97.5
Festuca bromoides	1.9/27.5	0.7/17.5	0.3/7.5									
Agrostis diegoensis		0.1/5.0				17.6/75.0	3.3/55.0	9.1/65.0	0.1/2.5	0.1/2.5		0.1/0.0
Carex filifolia		0.1/0.0										
Bromus japonicus						0.4/25.0			0.2/2.5			

TABLE 2. Similarity index comparison of plant zones.

SOUTH POOL		Similarity index (frequency only)					
		Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
Similarity index (weighted by cover)	Zone 1	***	57.9	42.1	25.0	26.3	7.0
	Zone 2	26.6	***	42.1	35.0	21.1	0.0
	Zone 3	11.9	12.2	***	65.0	68.4	41.4
	Zone 4	6.9	8.4	19.5	***	80.0	51.6
	Zone 5	2.7	2.3	9.8	66.4	***	62.1
	Zone 6	0.3	0.0	6.9	11.3	35.5	***

NORTH POOL		Similarity index (frequency only)					
		Zone 1	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7
Similarity index (weighted by cover)	Zone 1	***	50.0	34.3	28.6	11.1	21.6
	Zone 3	15.6	***	51.9	47.1	21.4	27.6
	Zone 4	4.4	36.4	***	62.1	43.5	50.0
	Zone 5	2.6	11.5	46.2	***	66.7	83.9
	Zone 6	0.6	0.4	9.1	23.2	***	72.0
	Zone 7	1.4	5.9	17.9	60.7	31.1	***

zone 2, for example, the average matric potential was −56 MPa in the 2–10-cm increment, −27 MPa in the 10–30-cm increment, and −2 MPa in the 30–60-cm increment.

On 23 April, when soils were moist, ECs were consistently higher in all plant zones and in both depth increments than they were on 28 June when soils had dried considerably (Fig. 6). Zone 2, the pool rim, had the highest ECs of any plant zone in the 10–30-cm increment on both the 23 April and 28 June sampling dates (Fig. 6). All mean ECs of saturation extracts, however, were below 2 dS/m, the minimum value for designation of a saline soil (Bohn et al. 1985). In the 2–18-cm soil increment of profile pit VP1 and the 30–48-cm increment of profile pit WR1, EC values were 2.20 and 2.62, respectively, indicating the potential for at least modest salinity in soils of the vernal pools.

The range of mean pH values of the 2–10-cm samples for each zone increased from 23 April (6.2 to 7.5) to 28 June (7.7 to 8.1; Fig. 6). pH values of the 10–30-cm, 30–60-cm, and 60–90-cm depth increments in zone 2 averaged 8.4, 9.1, and 9.3 over both dates, respectively. pH values of the WR1 soil profile pit, which has natric features, ranged from 7.3 to 7.9 among its horizons.

Sodium adsorption ratios (SAR) in soils of zone 2 of South Pool met the definition of sodic soil. Average SARs were 15.5 and 14.0 in the 10–30-cm depth increment on 23 April and 28 June, respectively (Fig. 6); 11.8 and 27.2 in the 30–60-cm increments on the earlier and later dates; and 27.4 in the 60–90-cm increment on 28 June. High SAR values in zone 2 of South Pool were in concert with moderately high SAR values of 9.7 in the 26–30-cm increment and 9.5 in the 30–48-cm increment of WR1. The SAR in the 2–10-cm increment of zone 3 was slightly higher than in other zones on 28 June.

DISCUSSION

Our study examined vegetation patterns and soil characteristics of vernal pools on the Marcellus site. Zedler (1987) suggested that the cycle of regional weather patterns is reflected in patterns of species germination and distribution in vernal pools. Monthly averages of precipitation, temperature, and evapotranspiration during our study season were fairly typical of the approximately 100-year climatic record in the Ritzville area; therefore, although we do not have data for many seasons, our data represent the vegetation structure and composition as expressed during a typical annual climatic pattern.

Cover-weighted similarity indices with two exceptions support the vegetation zone divisions we made at the outset of the study. It is not surprising that similarity indices based on frequency alone are inconclusive in that there were many species present in several zones. Cover values are a much better indicator of the strength of that presence. For example, although *D. danthonioides* had a high cover value in three different zones, each zone had a unique combination of co-occurring species:

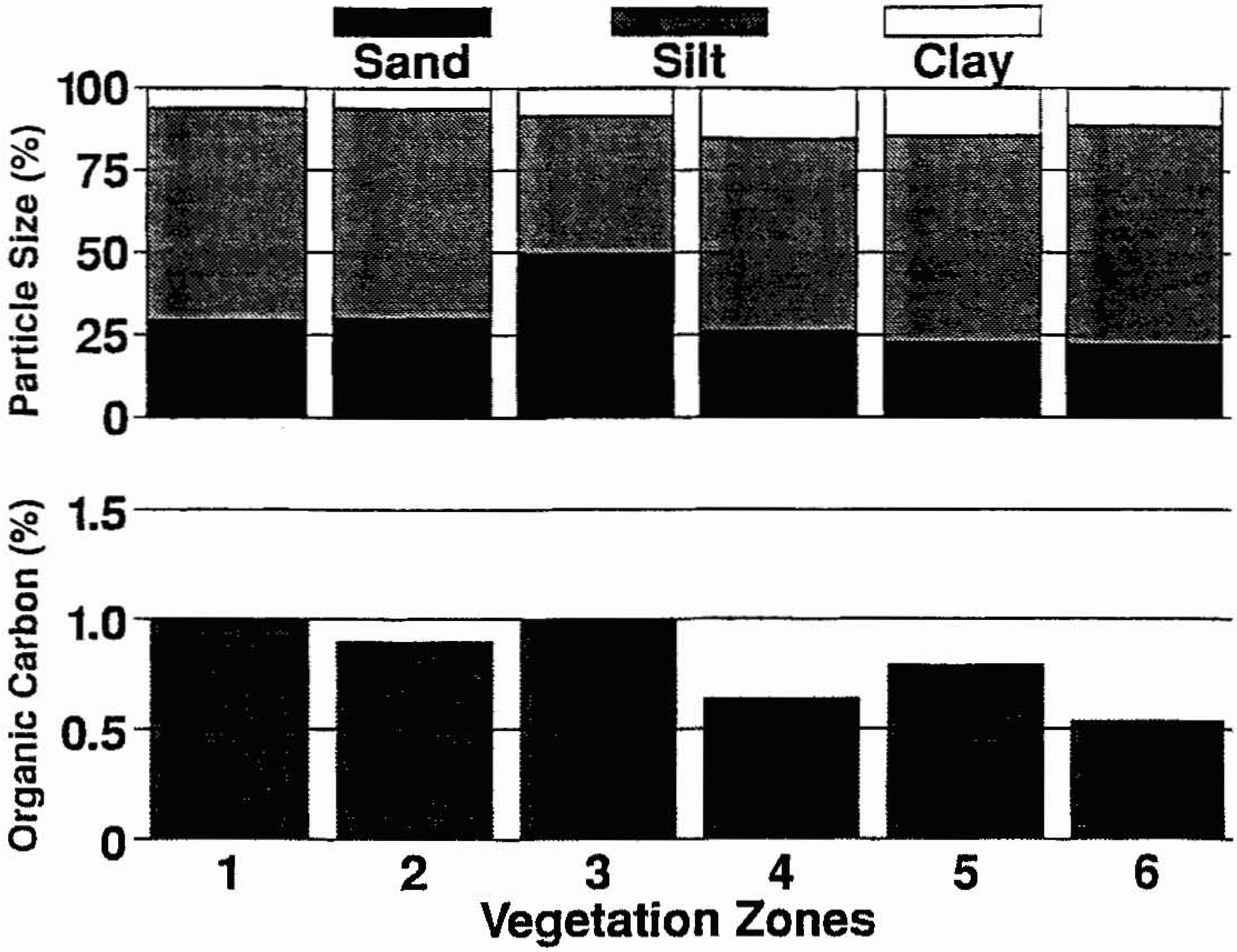

Fig. 4. Particle size and organic carbon content of the 2–10-cm depth of soils by vegetation zone in South Pool.

In zone 4, *A. geyeri, A diegoensis,* and *E. minutum* had highest cover values after *D. danthonioides.* In zone 5 those niches were filled by *N. intertexta* and *E. palustris,* and in zone 7 by *E. palustris* and *M. aristatus.*

Higher similarity indices between zone 4 and zone 5 (Table 2) reflect their position in the transition between drier upland-type communities and the pool basin area that contains standing water and/or has saturated soils more consistently and for a longer time period. We feel that species unique to each of these zones are ubiquitous and abundant enough to classify them as separate communities.

We found a greater ratio of annual to perennial species in wetter zones (zones 4–7) of the pools than in drier ones (zones 1–3). This tendency was also found in vernal pools in California (Holland and Jain 1977) and in a study of a seasonally flooded river marsh in Zimbabwe in which vegetation zonation was also reported (Cole 1973). It is difficult for perennials to withstand large changes in microenvironmental factors throughout the year, whereas the short life cycles of annual species may be completed within only one set of edaphic conditions. Annuals also produce abundant seeds, thus ensuring some survival due to variation in adaptability and the opportunity to delay germination until conditions are favorable.

Morphology and chemistry of the soils allow us to reconstruct the genesis of the pool system soils. Natric horizons have been documented as occurring in several situations in loessial soils across parts of the Columbia Plateau region where the mean annual precipitation is low to moderate (Peterson 1961). One specific situation is on the flanks of low mounds in areas of mound-and-swale microrelief where shallow soils are underlain by an impervious hardpan or bedrock. Calcium ion is presumed to become tied up as precipitated $CaCO_3$ in the calcic horizons of these soils over time. Apparently, water has moved laterally down the slope gradient within the mound soil during its genesis, transporting sodium ions and gradually concentrating them

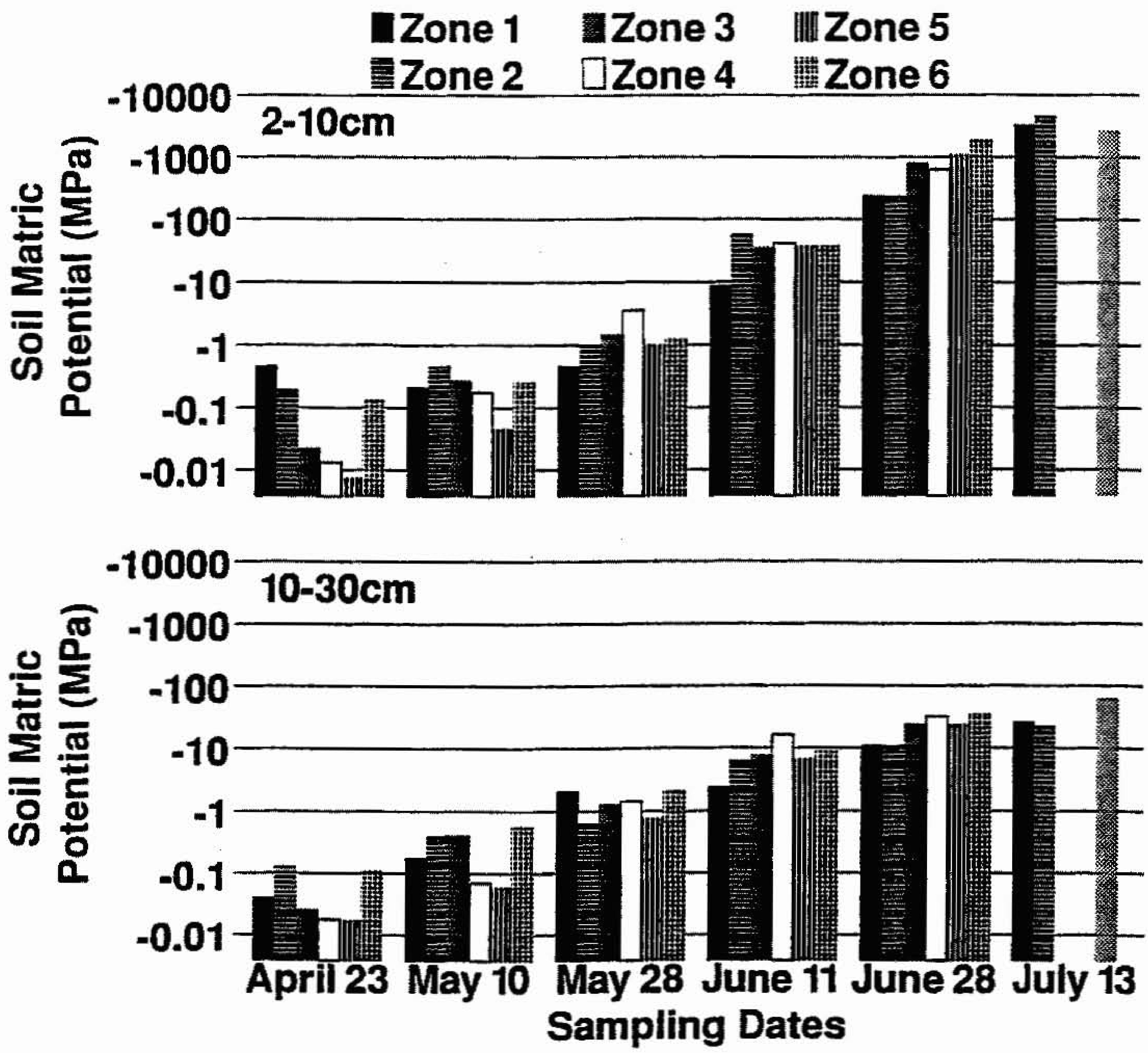

Fig. 5. Soil matric potential at 2–10-cm and 10–30-cm depth intervals by vegetation zone and sampling date in South Pool.

on the exchange complex of soil clays where the slope levels. Exchangeable sodium must accumulate to a critical level to effect the dispersion of clay colloids and organic matter, which in turn leads to the development of the typical natric soil morphology with a pale eluvial horizon overlying the clay-enriched, columnar-structured natric horizon. We observed a large variation in degree of expression of this morphology in pool-rim soils across the Marcellus site.

A natric horizon can have several adverse effects on the growth of plants. (1) When saturated, sodic soil horizons become dispersed and disaggregated, thereby clogging pores and preventing the flow of oxygen to plant roots. (2) When they dry, natric soils can form dense surface crusts that can prevent seedling emergence. (3) The availability of calcium, magnesium, and potassium can decrease in the soil due to preferential replacement of these ions by sodium on the exchange sites of clays and organic matter. (4) Sodium salts can create osmotic stress or be toxic to plants by interfering with their physiological processes (Black 1968).

Soil in zone 2 on the rim of the pools was not saturated during the part of the year when plants are physiologically most active, and the concentration of exchangeable calcium and magnesium was actually higher in zone 2 than in zone 1 (perhaps due to a higher cation exchange capacity in zone 2 soil). Osmotic stress and sodium salt toxicity appear to be the most likely conditions excluding zone 1 plants from zone 2, especially *A. tridentata,* whose roots

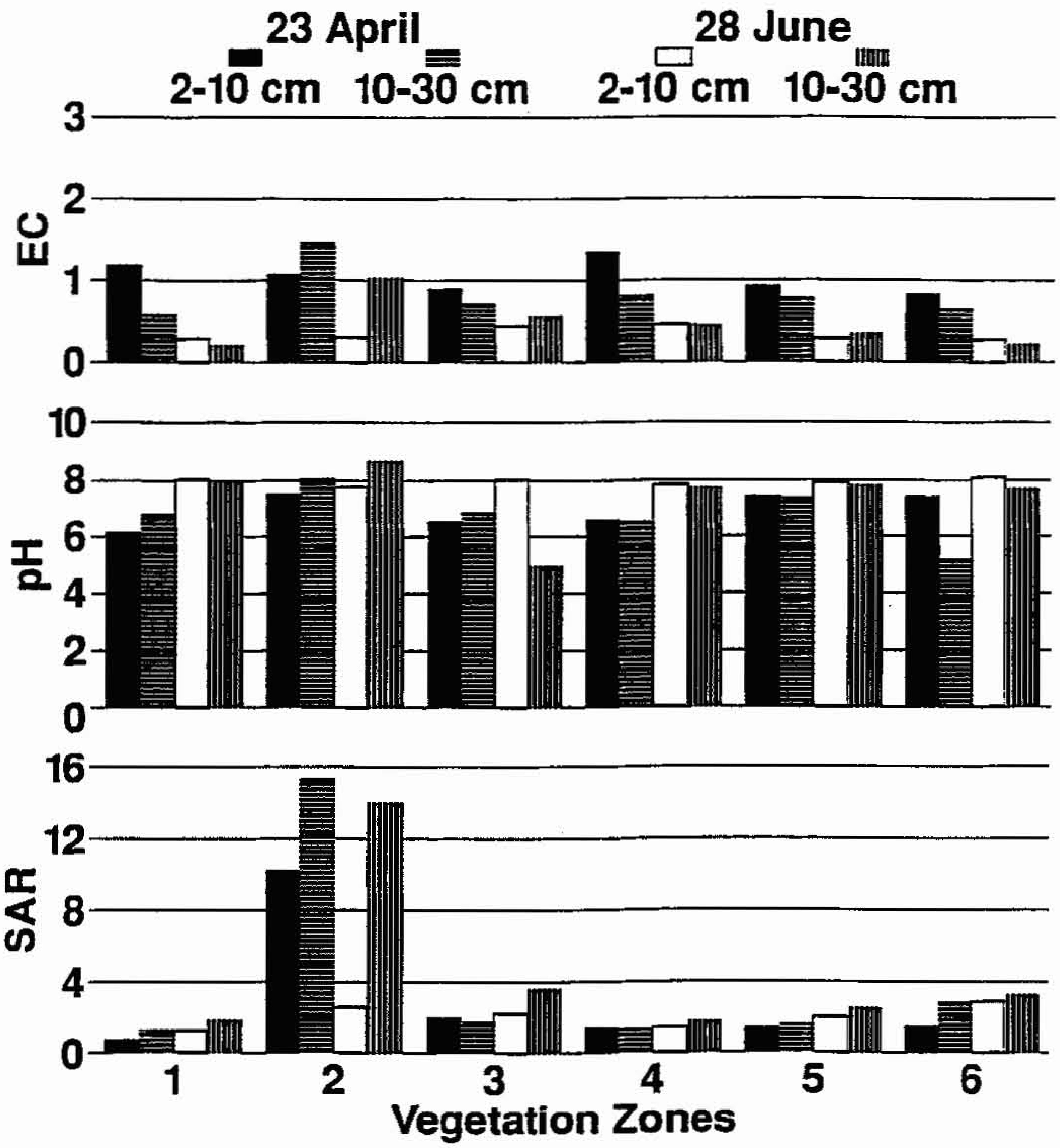

Fig. 6. Electrical conductivity (EC), pH, and sodium adsorption ratio (SAR) at 2–10-cm and 10–30-cm depth intervals by vegetation zone and sampling date in South Pool.

would penetrate to the most saline and sodic soil horizons. These conditions favor zone 2 plants such as *E. cinereus*. Choudhuri (1968) tested effects of soil salinity on *E. cinereus* and *A. tridentata* and found that *E. cinereus* was very tolerant of sodium salts and that *A. tridentata* was not. Surface crusts, high bulk density, and potassium deficiencies may also adversely affect zone 1 plants.

Although none of the ECs in South Pool were greater than 2 dS/m, soil salinity may have subtler influences on plant distribution. The 2 dS/m salinity limit is based on studies of crop plants, which generally are not native to the area in which they are grown. Limits of tolerance of native plants, such as *E. cinereus* as mentioned above, can be higher than in crop plants. Unfortunately, no specific studies exist of salinity tolerance of the species or genera found in vernal pool basins, either in California or Washington. Choudhuri (1968) found that all species he tested had a certain degree of self-adaptive capacity to increase their tolerance to salinity if the increase was gradual. Because plant tolerances to salinity can vary with environment (Levitt 1980), the interaction of slightly different salinity levels with changing moisture conditions may produce varying responses among the pool species. Some species will take up soluble ions through the cell walls of their roots, but the ions either will not pass through the cell membranes or will be stored inside cell vacuoles and thus not interfere with physiological processes in the plant (Levitt 1980). The decrease in soil ECs from the 23 April sampling date to the 28 June sampling date may be the result of plants preferentially taking up soluble ions to decrease their water potentials as soil water potential decreased.

Increased pH values from the first to the last sampling dates may indicate precipitation of alkaline salts. Again, specific responses of plants to this phenomenon can vary, and controlled studies of individual species would be necessary to make any further conclusions.

Our particle-size results coincide with those of California researchers (Lathrop 1976, Bauder 1987), who also found that finer particle sizes increased and sand fractions decreased from outside to the interior of the pool basins. Slightly more clay occurred in zone 4 soils than in zones 5 and 6 (the center of South Pool; Fig. 4), which is similar to the pattern in vernal pools on Kearny Mesa in California (Zedler 1987). A higher percentage of silt-sized particles can give a soil greater water-holding capacity under unsaturated conditions. The lack of a statistically significant difference in soil moisture potentials from the first to the last sample dates is difficult to understand. Given the generally large spatial variability in properties such as soil moisture potential, analysis of a greater number of samples would perhaps result in the finding of significant differences between dates and might also show significant differences among zones on particular sampling dates. It is interesting to note that some species were still surviving and in some cases photosynthesizing in soil matric potentials far less than −15MPa, commonly considered the permanent wilting point for plants. This seems to indicate an adaptability of vernal pool species to seemingly unfavorable moisture conditions.

Zedler (1987) stated that duration of standing water is the crucial factor in structuring plant distribution of vernal pools. The highly significant statistical difference we found between topographic elevation of the vegetation zones should be most closely related to the location and extent of above- and below-ground free water. We believe that soil moisture potential under unsaturated conditions probably also has a large effect on plant growth in the various vegetation zones. For example, different vernal pool species may have different types of root systems to take advantage of moisture in different parts of the soil profile, as was found in a study of several eastern Washington grasses (Harris and Wilson 1970). Also, maximum physiological activity can occur at different water potentials for different species (Wieland and Bazazz 1975). The duration of free-standing water and changes in unsaturated soil water potential through the season are probably both important to plant distribution in the pools.

Vernal pools can help us understand the physiological ecology of self-contained, water-controlled terrestrial ecosystems. We need to learn more about specific ecological processes in the vernal pool system to understand larger functions described so far. Future studies might include (1) examination of rooting systems and their relationship to water use and availability, (2) determination of the minimum physiologically detrimental salinity (especially of various sodium salts) and optimal pH levels for individual species, and (3) tolerance of individual species to varying durations of standing water and levels of unsaturated soil moisture potentials.

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