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PHYTOSOCIOLOGY OF PAVEMENT PLAINS IN THE SAN BERNARDINO MOUNTAINS

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Introduction

Pavement plains in the San Bernardino Mountains are floristically and physiognomically unique (Derby and Wilson 1978). Quantitative sampling now allows the phytosociologic similarities among pavements to be examined (Derby 1979) and correlated with physical site characteristics. Conditions which apparently act to maintain pavements as discrete vegetative units are examined here, thus preparing the way for ecological studies of the interactions between pavement-plain associations and adjacent forest communities through time.

Study Area

The three pavement plains selected for study: 1) Sawmill, 2) Van Duesen and 3) Arrastre Flat represent the triangular center of the geographic range for pavement plains (Derby and Wilson 1978). Distinctive physical features of pavement plains are vegetation physiognomy, soil color and texture, and a surface pavement of Saragosa Quartzite. Forest vegetation surrounding pavement plains includes *Pinus monophylla* Torr. & Frem., *Juniperus occidentalis* Hook ssp. *australis* Vasek, and *Pinus jeffreyi* Grev. & Balf. in A. Murr (Fig. 1). Nomenclature follows Munz (1973, 1974). Climate in the Big Bear Basin is influenced by the Mojave Desert. Pavement plains receive less than 38 cm of precipitation per year with most of that occurring as snowfall. A nighttime temperature inversion in the Big Bear Basin (Minnich 1971) creates a colder, more continental environment than would be expected at 2100 m elevation.

Pavement plains exist on the north block of the San Bernardino Mountains, geologically a part of the Mojave crustal block uplifted during Quaternary time. The San Bernardino Mountain Saragosa Quartzite Formation of Precambrian age is lithologically correlated with eastern Mojave Desert and Great Basin units, thus providing evidence for extension of the Cordilleran Miogeosynclinal Belt to the San Andreas Fault (Stewart and Poole 1975). Detailed descriptions of soils, geology, and climate for the study area are reported in the study of Derby (1979).

Materials and Methods

Prospective study sites were subjected to rigorous selection criteria, including: 1) a minimum of past disturbance; 2) no natural disturbance such

Fig. 1. Sawmill pavement plain, San Bernardino Mountains, with Jeffrey pine and pinyon pine silhouetted in the background and distinctive pavement rock surface with characteristic caespitose, perennial vegetation in the foreground.

as fire within 50 years; 3) uniformity in elevation, slope, exposure, soils, and geology; 4) no introduced vegetation present. Each of the three study sites was sampled quantitatively using three random 30-meter line-intercepts. Five one-meter^2 quadrats were placed at 5-meter intervals along each 30-meter line. Presence of vegetation, rock pavement, bare ground or litter were recorded from 150 points taken per line (one every 20 cm on the 30-m lines). In addition, total cover in centimeters was recorded by species for all plants intercepting the 30-m line. Overlapping individuals were measured separately. Overlap was very infrequent. From these data, relative percent cover for each plant species, frequency of rock pavement, bare ground, and litter relative to total vegetation cover were calculated. The number of individuals of each species in the fifteen one-meter^2 quadrats (five plots per each of three 30-meter lines) was recorded. An individual was any plant rooted inside the one-meter^2 quadrat with a distinct stem and crown. Relative percent frequency and relative percent density were calculated from combined quadrat data. Values of relative percent cover, relative percent density, and relative percent frequency were summed to obtain importance values (I.V.) (Bray and Curtis 1957) for each species on each study site.

Table 1. Distribution of surface components on pavement plains in the San Bernardino Mountains, California.

Surface component	Average percent frequency		
	Sawmill	Van Duesen	Arrastre Flat
Living vegetation	38%	31.68%	34.44%
Litter	15.56%	8.91%	10%
Rock pavement	45.56%	47.52%	47.78%
Bare soil	0.89%	11.88%	7.78%
RATIO			
Percent living vegetation / Percent litter	2.44	3.56	3.44

Additional transects were used at the Sawmill study site to measure microhabitat differences. This site slopes slightly to the northeast on one side and to the southwest on the other side (less than 4% slope). The northeast and southwest aspects were sampled to determine any floristic or phytosociologic differences relative to microhabitat preference. Three sets of "belt transects" one meter by four meters long and divided into four one-meter^2 quadrats at intervals one meter apart, were placed on both the northeast and the southwest following the downslope contour. Relative percent frequency and relative percent density for each species were calculated to characterize and compare vegetation on the two aspects with the average for the site as a whole.

The apparently abrupt change in herbaceous species composition at the pavement's edge was examined by placing four "belt transects" consisting of six adjacent one-meter^2 quadrats on compass lines (N, S, E, W) around the base of a western juniper tree. Plant densities and frequencies for the 24 quadrats were recorded by species. Litter cover and depth were recorded in each quadrat as well.

Results

Derby and Wilson (1978) reported 31 species on these pavement plains. The flora is now revised to 33 species; 20 perennials and 13 annuals (Derby 1979). Additions are an annual, *Navarretia breweri* (Gray) Greene and *Sitanion hystrix* (Nutt.) J. G. Sm. *Navarretia breweri* did not appear on the plots during 1977 but appeared at Arrastre Flat in 1978 (O'Brien, personal communication). *Sitanion hystrix* like *Artemisia* was found only at Arrastre Flat, but appeared frequently enough in phytosociologic sampling there to rate an importance value, and thus was added to the flora. *Artemisia tridentata* reported by Derby and Wilson (1978) has been determined to be a

Table 2. Importance Values ranked numerically by species for three pavement plains in the San Bernardino Mountains.

	Sawmill		Van Duesen		Arrastre Flat	
Rank	Species	I.V.	Species	I.V.	Species	I.V.
1	*Poa incurva*	110.89	*Eriogonum kennedyi*	91.60	*Draba douglasii*	61.14
2	*Viola douglasii*	32.57	*Ivesia argyrocoma*	54.27	*Poa incurva*	49.92
3	*Erigeron aphanactis*	25.57	*Arenaria ursina*	51.66	*Artemisia nova*	47.65
4	*Arenaria ursina*	25.19	*Poa incurva*	22.75	*Eriogonum kennedyi*	35.41
5	*Eriogonum kennedyi*	23.83	*Antennaria dimorpha*	18.15	*Arenaria ursina*	23.27
6	*Antennaria dimorpha*	22.03	*Arabis parishii*	16.92	*Ivesia argyrocoma*	21.05
7	*Arabis parishii*	18.78	*Erigeron aphanactis*	16.44	*Lomatium nevadense*	15.31
8	*Draba douglasii*	17.75	*Lomatium nevadense*	16.08	*Astragalus purshii*	9.72
9	*Ivesia argyrocoma*	10.10	*Viola douglasii*	6.72	*Arabis parishii*	7.88
10	*Astragalus purshii*	8.85	*Lewisia rediviva*	3.29	*Bouteloua gracilis*	7.04
11	*Castilleja cinerea*	4.05	*Stipa × Oryzopsis*	1.16	*Viola douglasii*	4.91
12	*Lomatium nevadense*	0.06	*Allium fimbriatum*	1.0	*Sitanion hystrix*	4.57
13					*Erigeron aphanactis*	4.01
14					*Antennaria dimorpha*	3.61
15					*Lewisia rediviva*	3.20
16					*Castilleja cinerea*	1.08

Table 3. Frequencies and densities for nine species common to all pavement plain study sites in the San Bernardino Mountains.

Species	Sawmill study site		Van Duesen study site		Arrastre Flat study site	
	Mean density/ meter^2	Frequency	Mean density/ meter^2	Frequency	Mean density/ meter^2	Frequency
Poa incurva	48.73	1.0	7.87	0.53	18.07	0.93
Arenaria ursina	11.50	0.93	22.20	1.00	8.00	0.67
Eriogonum kennedyi ssp. *austromontanum*	7.33	0.93	47.93[b]	1.00	11.07	0.87
Ivesia argyrocoma	2.80	0.33	20.00	0.93	6.47	0.47
Eriogeron aphanactis var. *congestus*	15.73	0.93	4.40	0.67	1.27	0.20
Viola douglasii	15.67	0.93	1.93	0.27	1.73	0.20
Antennaria dimorpha	12.67	0.80	3.87	0.80	0.20	0.20
Arabis parishii	7.20	0.93	3.80	0.67	1.80	0.40
Lomatium nevadensis[a]	0	0	5.20	0.60	2.60	0.73
Total mean density, all species	131.57		117.60		96.30	

[a] *Lomatium* appeared only as cover on the line, not in quadrats on Sawmill, therefore no comparison of density or frequency for this species is available from Sawmill.

[b] High density for *Eriogonum kennedyi* reflects large number of young plants or seedlings at Van Duesen.

form of *A. nova* A. Nels. The *Stipa* sp. collected at Sawmill is now thought to be an undescribed hybrid or intermediate *Stipa* sp. and *Oryzopsis hymenoides* R. & S. Ricker.

Strong similarities among the three study sites exist in frequencies of the surface pavement rock component and the ratio of living vegetation to litter present (Table 1). The greatest difference between sites is in percent frequency of bare soil.

The magnitude of importance values (I.V.'s) for the individual species varies among the three study sites. When I.V.'s are numerically ranked, the top five species from each site contain three species in common, *Poa incurva* Scribn. & Will., *Arenaria ursina,* and *Eriogonum kennedyi* ssp. *austromontanum*. Significantly, the latter two are San Bernardino Mountain endemics and occur only within pavement plain habitats (Table 2).

Nine perennial species or one half of the perennial species present in the pavement plain flora are common to all three study sites. Frequencies and densities for those nine species are compared in Table 3. Each of the nine species common to all sites exists with a frequency of 0.67 or greater on at least one study site, thus any one of them can be found on at least one pavement in two out of every three random one-meter^2 plots. *Arenaria*

Table 4. A comparison of microhabitats on Sawmill study site, San Bernardino Mountains, using density and frequency values for perennial species existing on the site.

	Total Sawmill sample		Northeast Sawmill microhabitat sample		Southwest Sawmill microhabitat sample	
Species	Mean density/meter^2	Frequency	Mean density/meter^2	Frequency	Mean density/meter^2	Frequency
Antennaria dimorpha	12.67	0.80	6.83	0.83	28.58	1.0
Arabis parishii	7.20	0.93	10.75	1.0	—	—
Arenaria ursina	11.50	0.93	21.33	1.0	18.58	1.0
Astragalus purshii var. *lectulus*	2.40	0.53	—	—	1.08	0.5
Bouteloua gracilis	—	—	2.17	0.17	4.92	0.33
Castilleja cinerea	0.4	0.27	3.92	0.83	—	—
Draba douglassii var. *crockeri*	7.07	0.60	—	—	6.67	0.92
Dudleya abramsii	—	—	5.08	0.50	—	—
Erigeron aphanactis var. *congestus*	15.73	0.93	36.42	1.0	32.58	0.92
Eriogonum kennedyi ssp. *austromontanum*	7.33	0.93	6.42	1.0	11.33	1.0
Ivesia argyrocoma	2.8	0.33	10.08	0.5	0.25	0.25
Poa incurva	48.73	1.0	44.92	1.0	38.17	1.0
Stipa × *Oryzopsis*	—	—	—	—	7.0	0.67
Viola douglasii	15.67	0.93	0.58	0.33	2.58	0.83

ursina is present in at least two out of every three random one-meter^2 plots on any of the pavements studied. *Eriogonum kennedyi* ssp. *austromontanum* is present in at least four out of every five random one-meter^2 plots on any pavement. Perennial species on pavement plains tend, in general, to be evenly distributed throughout the pavement plains (Derby 1979).

Floristic and phytosociological changes appear to be correlated with changes in slope (less than 4%) and in aspect. From data (Table 4) on the northeast and southwest aspects of the Sawmill study site one can infer habitat preferences relative to changes in microhabitat. Generally the plant distribution follows relative temperature and/or mesic to xeric gradients. For example, *Antennaria dimorpha* (Nutt.) T. & G. is a wide-ranging western species which shows a decided preference for more xeric and hotter sites. An overall average of 12.67 plants per meter^2 drops by one half on the northeast aspect and increases more than two times on the southwest aspect. In opposition to this general trend, *Arabis parishii,* a San Bernardino Mountain endemic, is absent from southwest aspects and increases in density on the northeast aspect. *Stipa* × *Oryzopsis* occurs only on southwest aspects while *Dudleya abramsii* and *Selaginella watsonii* are restricted to the northeast aspect of pavement plains.

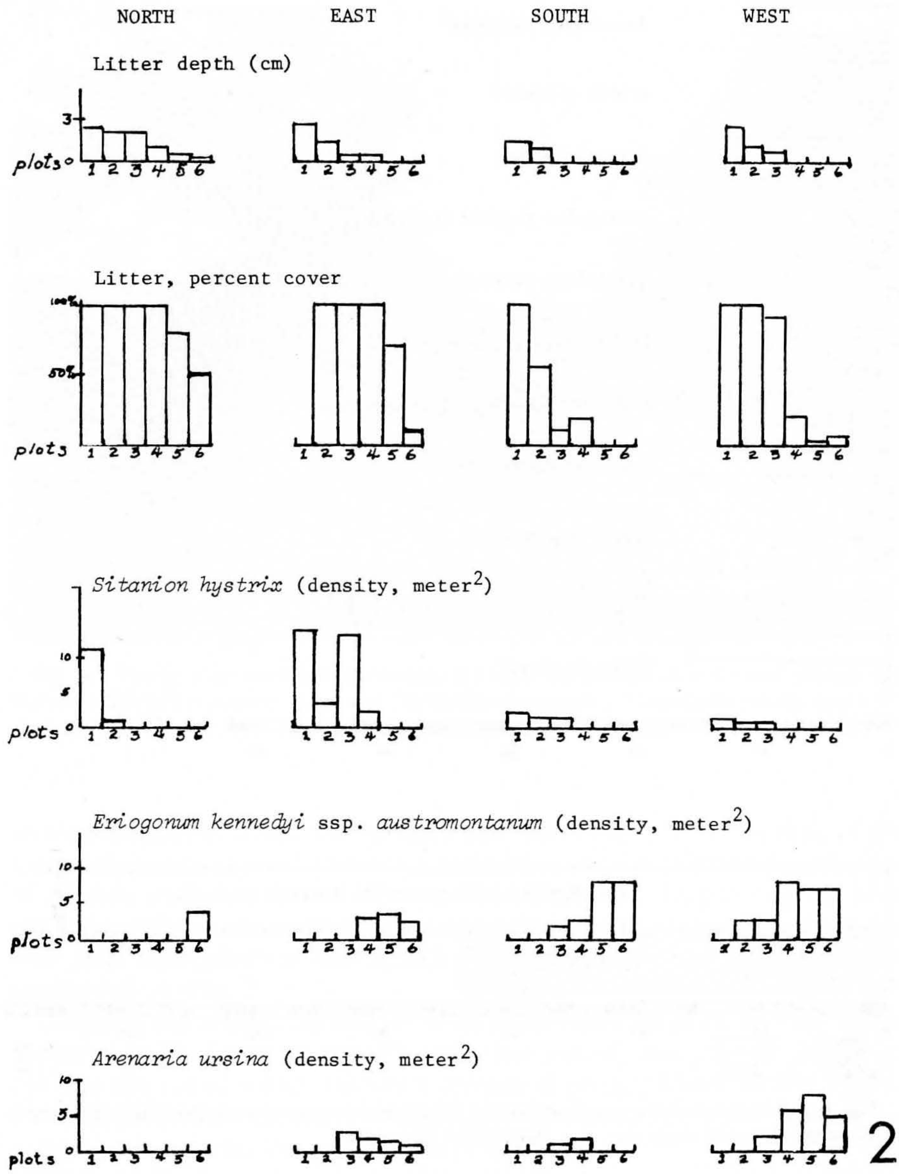

Fig. 2. Plant densities (meter²) compared to litter and percent cover under a western juniper tree, Sawmill site, San Bernardino Mountains.

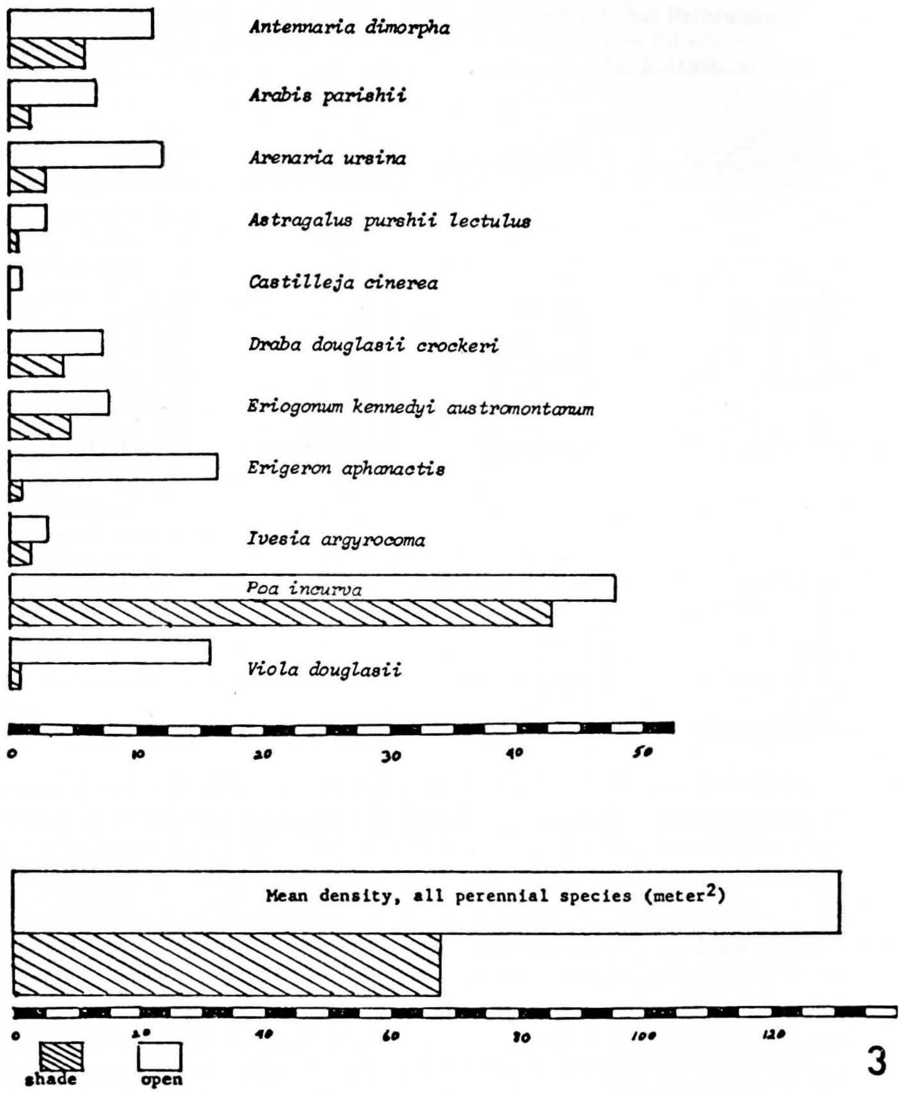

Fig. 3. Comparison between plant density values on open pavements and within tree understory at the Sawmill study site, San Bernardino Mountains.

Data from studies under western juniper tree canopy reveal that percent cover and depth of litter increase on north and east aspects, and that the south aspect is most sparsely covered by litter (Fig. 2). Furthermore, the pavement-plain endemics, *Arenaria ursina* and *Eriogonum kennedyi* ssp.

Fig. 4. Pinyon pine seedlings are abundant under the canopy of a western juniper tree (right) on Sawmill pavement plain, San Bernardino Mountains. The mature pinyon pine (left) produces significantly more litter than the western juniper of comparable size.

austromontanum, occur with greater densities farther from the base of the tree. *Eriogonum kennedyi* shows a preference for the south and west sides of the tree where shade and litter are less abundant. *Arenaria ursina* does not appear within the north transect and achieves its greatest density on the west side. Both plants exhibit a preference for low levels of shade and litter accumulation (Fig. 2).

Densities are always greater on open pavements for plant species which appeared in the "belt transects" under the juniper tree canopy, but were consistently found within the open pavement plains. Mean density values for total perennial vegetation within open pavements are twice those from samples taken under the juniper tree (Fig. 3).

Tree and shrub seedlings becoming established at pavement edges usually occur under existing mature trees (Fig. 4). Seedlings of *Pinus monophylla* are the most frequent tree species and seedlings of *Artemisia nova* are the most frequent shrub species encroaching into open pavements (Derby 1979). In general, three times as many seedlings grow beneath mature western junipers than under pinyon pines.

Discussion

Pavements exist worldwide as land features at all elevations and in many environments coincident with two common conditions. First, particle concentration at the surface is uninhibited by vegetation and secondly, both coarse and fine particles co-exist in the underlying soil deposit. Furthermore, three processes contribute to pavement formation: 1) deflation of fine material by wind, 2) removal of fines by water at the surface and 3) processes causing upward migration of coarse particles to the surface (Cooke and Warren 1973). The sparse vegetation cover on pavement plains provides little barrier to wind or to impact of raindrops on the ground. The upward migration of coarse particles can be accomplished through two mechanisms; cycles of freezing and thawing, and cycles of wetting and drying (Springer 1958; Corte 1963; and Inglis 1965). Thus pavement plains, like alpine communities, are subject to active frost heaving, extreme annual and daily temperature fluctuations, high light intensities, and dessicating winds. They differ from alpine communities in their longer growing season, warmer overall temperature regime, and lower intensity of ultraviolet radiation. Existing vegetation patterns along with fossil-flora evidence suggest that the pavement-plain flora evolved under colder, perhaps near alpine conditions (Derby 1979). Physiognomically, pavement plains are much like any alpine community in existence today. Pavement perennial plants form compact rosettes or cushions whereas annual plants are dwarfed ephemerals. Although physiological evolution is implied, the pavement-plain species may have been physiognomically and morphologically preadapted to the rigors of their present habitat.

Pavement endemics apparently have evolved a specific competitive advantage for their particular specialized habitat but lack that advantage in adjacent forest habitats. Successional trends involve both the mechanisms which tend to keep pavement endemics confined to their narrow habitats and the mechanisms preventing trees and shrubs from becoming easily established. Pavement endemics show an inverse correlation to shade or a positive correlation for higher light intensities (Fig. 2). Soil temperatures can be expected to increase with increased light intensities. Factors producing a favorable niche for pavement-plain endemics are therefore presumed to be increased soil temperatures and greater light intensities such as those found in the open treeless pavements.

Factors inhibiting tree and shrub establishment on pavement plains appear related to the high percentage of clay in B2 soil horizons (Derby 1979) as well as the inhospitable habitat on open pavements. Pavement-plain habits differ physically from those of surrounding forests in several aspects: 1) timing and duration of available soil moisture, 2) soil temperature, 3) action of frost heaving, 4) presence or absence of mycorrhizal fungi, and 5) available soil nutrients. Any one or a combination of these factors can have an adverse effect on successful tree establishment and survival. Pinyon seeds require a relatively low temperature for germination, 7 C, while 15 to 24 C is the lethal threshold for pinyon seedlings (Erdman 1970). Unshaded sites can easily exceed the lethal temperatures even 15 cm below the surface. Tree litter, by contributing insulation, is believed to have a greater effect on soil temperatures than shade afforded by the tree canopy (Oosting 1956). If the pavement areas have been barren of trees for up to 8000 years or since the proposed redistribution of Jeffrey pine and pinyon pine during the xerothermic period (Raven and Axelrod 1978), the mycorrhizal relationships may become especially important. If this is the case, then we may be witnessing the primary advancement of the dominant forest cover type within the northeast San Bernardino Mountain Range.

Conclusions

The combination of soils, geology, and plant association on pavement plains is unique in the world. The following floristic and phytosociologic features are common to all pavements studied, and thus it is inferred, common to all pavement plains in the San Bernardino Mountains.

1) At least one half of the perennial species present on any one pavement plain are common to all others.
2) Importance values for individual species may vary between pavement plains but the two endemic species are always among the dominant species present.
3) Grass has a dominant role in pavement-plain phytosociology.
4) Perennial species present on pavement plains tend toward evenly spaced overall distributions.
5) Densities of pavement-plain endemics are inversely correlated with litter buildup and light intensity under tree canopies.
6) Some species occurring on pavement plains are restricted to microhabitat niches within the habitat.

Mechanisms acting to exclude or inhibit tree encroachment onto pavement plains are also responsible for habitat conditions favoring pavement-plain endemics. Pavement plains, as they exist today, represent a topographic-edaphic subclimax which is apparently succeeding to *Pinus monophylla*-dominated forests. Habitat management, such as selective overstory removal, may eventually be required if the two endemic species, *Eriogonum kennedyi* ssp. *austromontanum* and *Arenaria ursina,* are to be maintained through time within their limited natural range.

Literature Cited

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Cooke, R. U., and A. Warren. 1973. Geomorphology in Deserts. University of California Press, Berkeley, California. 374 p.

Corte, A. E. 1963. Particle sorting by repeated freezing and thawing. Science 142:499–501.

Derby, J. A. 1979. Floristics and phytosociology of the pavement plains in the San Bernardino Mountains, California. Unpublished master's thesis, California State College, San Bernardino, California. 82 p.

Derby, J. A., and R. C. Wilson. 1978. Floristics of pavement plains of the San Bernardino Mountains. Aliso 9(2):364–378.

Erdman, J. A. 1970. Pinyon-juniper succession after natural fires on residual soils of Mesa Verde, Colorado. Brigham Young University Science Bulletin, Biological Series XI(2):1–24.

Inglis, D. R. 1965. Particle sorting and stone migration by freezing and thawing. Science 148:1616–1617.

Minnich, R. A. 1971. Minimum temperatures in Big Bear Basin, California. Association of the Pacific Coast Geographers Yearbook V(33):83–106.

Munz, P. A. 1973. A California Flora and Supplement (combined edition). University of California Press, Berkeley, California. 1681 p. and 224 p.

———. 1974. A Flora of Southern California. University of California Press, Berkeley, California. 1086 p.

Oosting, H. J. 1956. The Study of Plant Communities. W. H. Freeman, San Francisco, California. 440 p.

Raven, P. H., and D. I. Axelrod. 1978. Origin and Relationship of the California Flora. University of California Press, Berkeley, California. 134 p.

Springer, M. E. 1958. Desert pavement and vesicular layer of some desert soils in the Lahonton Basin, Nevada. Proc. Soil Scientists Society of America 22:63–66.

Stewart, J. H., and F. C. Poole. 1975. Extension of the Cordilleran miogeosynclinal belt to the San Andreas fault, southern California. Geological Society of America Bulletin V(86):205–212.

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