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FLORISTICS AND PHYTOSOCIOLOGY OF THE PAVEMENT PLAINS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

A Thesis
Presented to the
Faculty of
California State
College, San Bernardino

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Biology

by
Jeanine A. Derby
March 1979

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Dean

ABSTRACT

Three pavement plains in the San Bernardino Mountains, California were studied to determine the floristic and phytosociologic similarities existing among pavements and to correlate these with physical site conditions. Importance Values were assigned to each perennial species on each study area as a result of quantitative sampling. Successional trends on pavement plains were also examined.

The following floristic and phytosociologic similarities were found among all pavement plains studied. One half of the perennial species present on any one pavement plain were common to all others studied. Perennial grass plays a dominant role in pavement plain phytosociology and perennial species, in general, tend to be evenly spaced throughout pavement plains. Two plant species which are pavement plain endemics ranked high in Importance Value on each study site. Densities for the pavement plain endemics are inversely correlated with litter buildup and light intensity under tree canopies. Some perennial species in the pavement plain flora are definitely restricted to microhabitat niches within pavement plains.

Site conditions which favor pavement plain endemics act to exclude or inhibit tree encroachment within pavement plains and thus, maintain them as physiognomically discrete units within a forest climax.

ACKNOWLEDGEMENTS

I am particularly indebted to the U. S. Forest Service, San Bernardino National Forest, for providing technical and financial support, without which this study would not have been possible. Wes Hamilton, Resource Officer and Hugh Black, Wildlife Biolgist, offered continuing encouragement and support throughout the study. Keith Anderson, Geologist and Jim Retelas, Soil Scientist, offered technical expertise, adding immeasurably to the quality of this study. Jere Mitchell, Big Bear District Ranger, offered the complete cooperation of his staff during the on-site phase of the study.

I further wish to extend my appreciation to the faculty of California State College, San Bernardino, particularly to Dr. Ruth C. Wilson who served as my advisor from the first inception of the study. Dr. Dalton Harrington and Dr. Alfred Egge identified problem areas through their critical review of the thesis. All three faculty members offered meaningful insights into various aspects of the study through their graduate seminars.

Finally, my sons have been extremely supportive during the past three years while I have attempted to balance the demands of career, education and family life. They, especially, have my sincere thanks.

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INTRODUCTION

Pavement plains observed in the San Bernardino Mountains support a unique vegetation including some rare endemics. Perhaps the most unusual and notable feature of these sites is that they do not support trees. They appear as islands of sparse low growing vegetation with a surface feature of Saragosa Quartzite rock pavement within forests of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf, in A. Murr.) or woodlands of pinyon pine (*Pinus monophylla* Torr. & Frem.). Among the 33 plant species of the pavement plain flora are five San Bernardino Mountain endemics. At least two of the endemics occur only on pavement plains (Derby and Wilson, 1978).

The first reported observations of these unusual land features with their unique associated vegetation were made in July 1975 (Derby, 1975). Thorne (1976) compared Table Mountain in the San Gabriel Mountains to the San Bernardino Mountain sites. However, neither the same plant association nor similar underlying geology exist in the San Gabriel Mountains, therefore that comparison cannot be fully substantiated.

Expanding upon the earlier floristic descriptions (Derby and Wilson, 1978), this study examines three individual pavement plains to determine whether floristic and phytosociologic similarities exist. This study proposes that there <u>are</u> unique floristic and phytosociologic similarities among pavement plains in the San Bernardino Mountains and further that soil substrate conditions along with other physical parameters interact to maintain pavements as discrete vegetative units. This work will prepare the way for further ecological studies, including the interactions between pavement associations and adjacent plant communities through time.

STUDY AREA

Location and Habitat

All pavement plains presently documented are found within an area of approximately 240 square kilometers in the northeastern San Bernardino Mountain range. The main range for pavement plains centers around Big Bear Basin and Holcomb Valley. An isolated portion of the range is shown centered around Coxey Meadow (Figure 1). Elevations of the plains range from 1,830 to 2,288 meters. Each is a level or gently sloping site, ranging from one to sixteen hectares in size (Figure 2). Distinctive physical features are soil color and texture, vegetation physiognomy and rock pavement surface of Saragosa Quartzite (Figures 3, 4, and 5). Though pavements existing at high elevations on Sugarloaf and Onyx peaks appear similar in some respects, a comprehensive geomorphologic investigation of San Bernardino Mountain pavements as land features is needed before these sites can be placed in proper perspective.

The dominant vegetation types within the Big Bear Basin are Jeffrey Pine, Mixed Conifer and Pinyon Pine Series (Derby, *et. al*, 1978). Associated tree and shrub species are *Juniperus occidentalis* Hook, ssp. *australis* Vasek, *Cercocarpus ledifolius* Nutt., and *Amelanchior pallida* Greene. Nomenclature corresponds to Munz (1974).

The climate in the northeastern San Bernardino

Fig. 1. Infrared photography (scale of 1:131,000 or approximately 1/2 inch = 1 mile) showing the northeastern San Bernardino Mountains. Three study sites, 1) Sawmill, 2) Van Duesen and 3) Arrastre Flat are indicated within the heavy black line outlining the range of those pavement plains presently documented. Dotted lines indicate high elevation "pavements" on Sugarloaf Ridge. Onyx Peak is just off the photo.

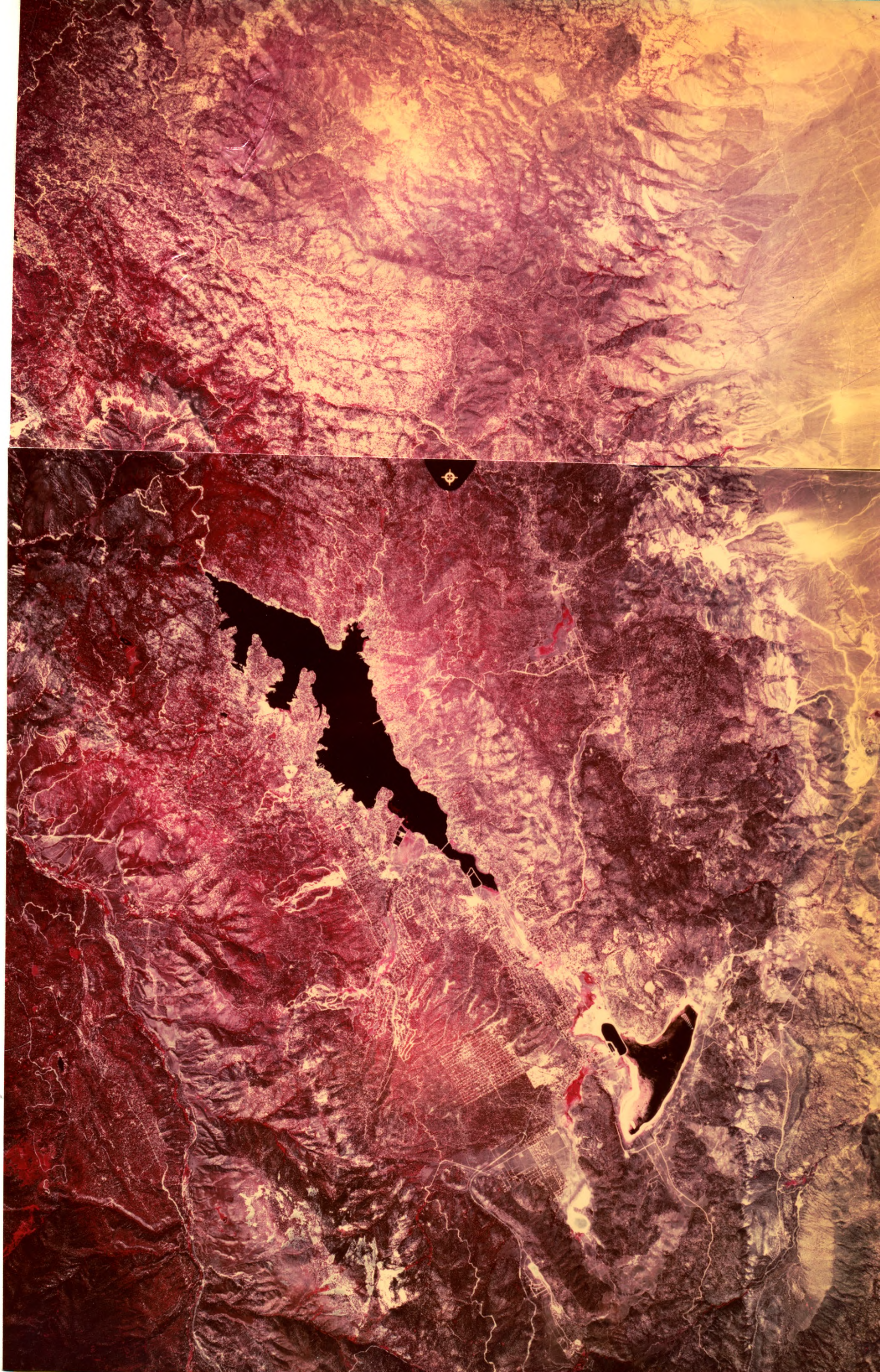

Fig. 2. A typical pavement plain in the San Bernardino Mountains, Sawmill study area, surrounded by pinyon and Jeffrey pines.

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Fig. 3. Van Duesen Canyon pavement with snow drifts lingering on the north side of trees in early spring. Snow melt produces a very wet soil which rapidly drys to a brick-hard surface within one month.

Fig. 4. Van Duesen Canyon pavement showing the characteristic low growing vegetation, reddish clay soil and surface rock pavement of Saragosa Quartzite.

Fig. 5. A soil profile from a soil pit on Van Duesen pavement, San Bernardino Mountains. Soils contain greater than 60% clay particles in the B2 layer.


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Mountain range is heavily influenced by the Mohave Desert. Annual precipitation drops rapidly from 102 cm mean annual rainfall at the Big Bear Dam to 25 cm at the west end of Bladwin Lake, just 16 km to the east. (Brown and Associates, 1975). Most of the precipitation occurs as snowfall. Pavement plains generally lie in an area of less than 38 cm of precipitation per year. East-west trending ridges bounding the basins tend to reduce wind velocities. A night time temperature inversion exists throughout the Big Bear Basin, creating a colder, more continental environment than that which is typical in an upland Mediterranean climate (Minnich, 1971). Though no data exist to substantiate it, similar land form and air drainage patterns suggest similar colder minimum temperature conditions for parts of Holcomb Valley. Lodgepole pine (Pinus murrayana Grev. & Balf. in A. Murr.) at Bluff Lake, 2316 meters elevation, is evidence of the southwestern extent of the temperature inversion.

The topography within Big Bear and Holcomb Valley is relatively gentle compared to the rugged peaks and ridges surrounding the area on all sides. The normal level of Big Bear Lake is 2055 meters. The ridge south of Bear Valley includes 2984 meter Sugarloaf Ridge, forming a rain shadow which separates the Basin from the upper Santa Ana River drainage. The north and east bounding ridges, ranging from heights of 2100 meters to 2440 meters, drop steeply down to the Mojave Desert floor.

Geologic History

The San Bernardino Mountains are part of the Transverse Ranges Geomorphic Province of California. Recent evidence suggests a minimum age of 6.2 million years for the early regional compression which ultimately raised the San Bernardino Mountain Range (Woodburne, 1975). Active uplift has continued from Pliocene through the present, a result of the relatively northwestern movement of the Pacific lithospheric plate against the North American plate with the San Andreas and San Jacinto faults acting as the principal discontinuities which accomodate plate movement (Crowell, 1975).

Dibblee (1975) described two major blocks forming the San Bernardino Mountain range, separated by the north branch of the San Andreas Fault. He further suggests that the north block is geologically part of the Mojave crustal block and was a part of the Mojave Desert Floor during Tertiary and early Quaternary time. Interpreting the geomorphology of the San Bernardino Mountains, Dibblee (1975) proposes that prior to uplift the surface of the northeastern part of the range was eroded to low relief and was traversed by a small valley that now contains Big Bear Lake. When the north block was elevated in late Quaternary time that old erosion surface became a plateau.

Other authors (Brown and Associates, 1975, Stout, 1976) interpret the formation of the Big Bear and Holcomb

Valleys as a relatively recent event, created by localized thrust faulting during the mid to late Pleistocene. Holcomb Valley is described as part of an early quaternary surface, once contiguous with the area around Bluff Lake, located approximately 3.5 km southwest of Big Bear Lake (Brown and Associates, 1975).

McJunkin (1976) hypothesized that Big Bear Valley was formed through the pull-away of a mega-landslide in the northern part of the San Bernardino Mountains. However, evidence of thrust faulting on the north side and east side of the Valley and a continuity of high level erosion surfaces to the north and west of the valley lead Stout (1976) to contradict the landslide theory.

Big Bear Valley itself is a bedrock enclosed basin filled with more than 152 meters of lacustrine and alluvial debris (Stout, 1976). Stout (1976) also cites evidence for at least two earlier lakes in the Big Bear Valley. The presence of a nearly flat terrace, 18 to 24 meters above the present high water level is particularly well developed on the south side of Big Bear Lake. No terraces are evident around Baldwin Lake at this elevation. A thick section of blue-gray clay up to 60 meters thick appears to represent a second lake which may have filled both Big Bear and Baldwin Lake Basins and probably spilled over the drainage divide to the east. Baldwin Lake remains today as a closed basin of internal drainage. Bear Creek, a young stream with a steep gradient, created the outlet for Bear Valley to the west, probably in late Pleistocene (Brown and Associates, 1974).

Geologists disagree when describing the age of major rock formations in the northeastern San Bernardino Mountains. Richmond (1955) described the oldest of three distinct formations north of Big Bear Lake as carboniferous to pre-carboniferous sedimentary rocks. This group includes the Chicopee Canyon formation which is predominantly quartzite and the Furnace formation of calcitic and dolomitic marbles. He describes the second oldest group, including rocks of volcanic origin, as Mesozoic age. Diorite, hornblende, quartz monzonite, and granite porphyry are included in the Mesozoic group and are part of a composite batholith which extends under the southeastern Mojave Desert. Richmond (1955) describes the most recent group as clastic sedimentary deposits of late Cenozoic age. However, McJunkin (1976) describes the geology of Sugarloaf ridge, the major ridge south of Big Bear Basin, in a much older context; as an uplifted block of Precambrian Baldwin Gneiss unconformably overlain by the late Precambrian to Cambrian Saragosa Quartzite, equivalent to the Chicopee Formation described by Richmond (1955). Stewart and Poole (1975) propose lithological correlation of the San Bernardino Mountain Saragosa Quartzite Formation with other units in the eastern Mojave Desert and Southern Great Basin, thus providing for extension of the Cordilleran Miogeosynclinal Belt to the

San Andreas Fault. This correlation supports a Precambrian age for deposition of Saragosa Quartzite and middle Cambrian through Permian for Furnace limestone.

McJunkin (1976) suggests two periods of thermal metamorphism of the Precambrian and Paleozoic sedimentary rock in the Sugarloaf Mountain Block, coinciding with the Mesozoic volcanism and metamorphism described by Richmond (1955).

Richmond (1955) suggests conditions of sedimentation for the Chicopee Canyon Quartzite as nearshore marine deposition for most of the body with some cross bedding and relict ripple marks in the lower member. He describes an abundance of clay minerals, possible formed under marine conditions after deep subaerial weathering of micaceous sandy sediments, but states that relict structures which would help explain the concentration of clay are absent.

Difference of opinion regarding the age of the major rock formations as well as the dating of more recent geomorphological changes in the Big Bear - Holcomb Valley areas will not be resolved here. Therefore, the origin of pavement plains as land features will be addressed only speculatively.

MATERIALS AND METHODS

Sample sites were selected from areas which have similar vegetation physiognomy and surface rock pavement. Probable sites were distinguished on infrared or color aerial photography. Verification on the ground and a further sorting followed, using the following criteria: 1) a minimum of past manmade disturbance; 2) no natural disturbance such as fire within 50 years; 3) uniformity in elevation, slope, exposure, soils and geology; 4) no introduced vegetation present. The three study sites selected provide a triangular sample representing the geographic center of pavement plain distributions. All three study sites are located within National Forest lands. The study sites: 1) Sawmill, 2) Van Duesen and 3) Arrastre Flat, are located relative to the total distribution of pavement plains in the San Bernardino Mountains in Figure 1. Sawmill (3 hectares) and Van Duesen (1 hectare) typify the dwarf perennial pavement plain vegetation, with no overstory trees or shrubs (Figure 6). Arrastre Flat (16 hectares) was included because it typifies another less frequent type of vegetation; the usual dwarf perennials are present along with a low growing form of _Artemisia nova_ A. Nels. (Figure 7 and 8).

Herbarium specimens were collected at about two week intervals from February to September, 1977. Voucher specimens (numbers 77-407-1, 77-425-1 through 77-425-7, 77-504-1 through 77-504-5, 77-525-1, 77-603-1 through

Fig. 6. Sawmill pavement plain, San Bernardino Mountains, typically lacks shrubs and trees throughout but is beginning to show some shrub encroachment at left center.

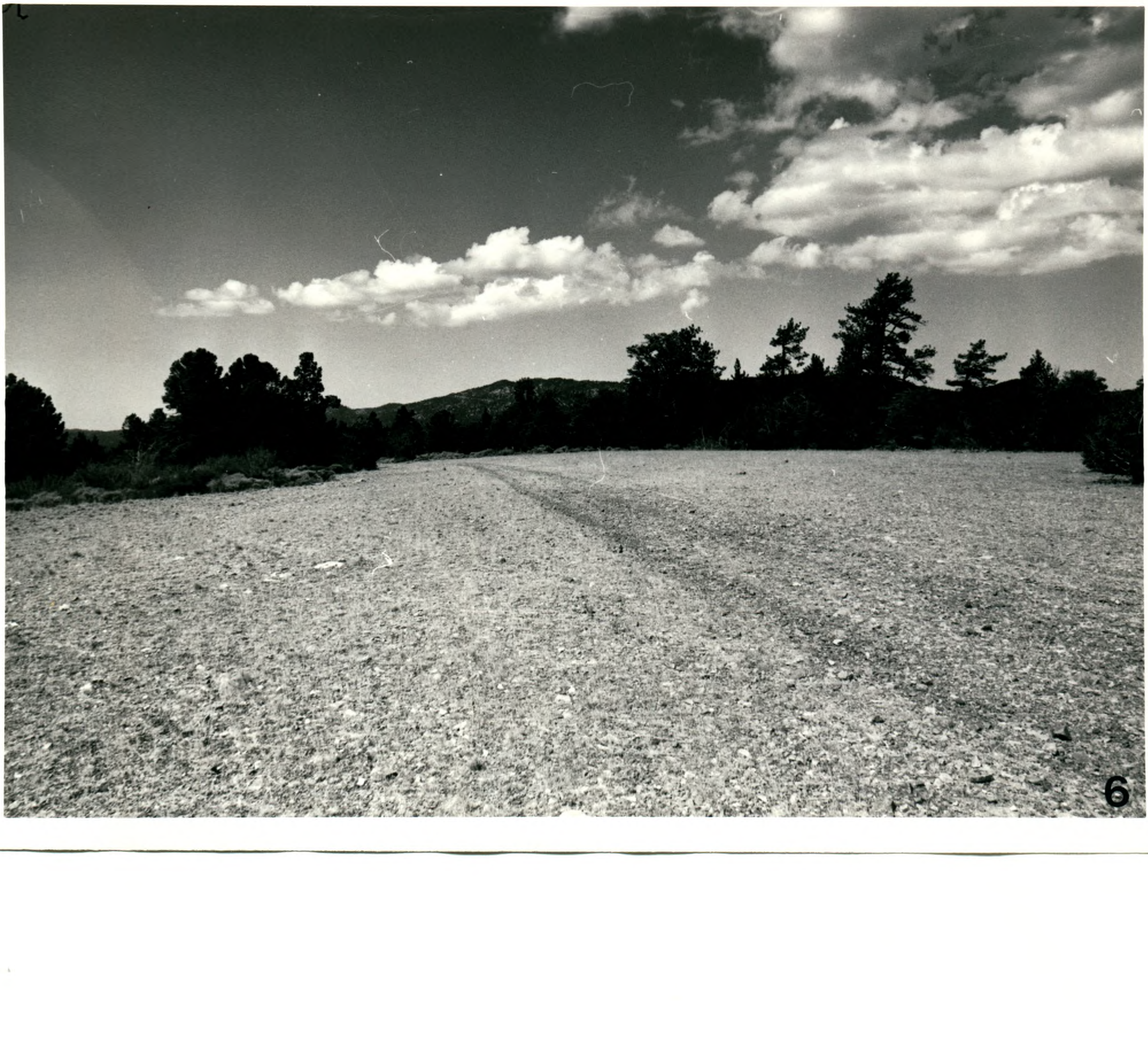

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Fig. 7. Arrastre Flat in Holcomb Valley, San Bernardino Mountains showing the even distribution of dwarfed Artemisia nova throughout the pavement plain. Pavement species, though not visible, are evenly distributed between shrubs.

Fig. 8. Hummocks on Arrastre Flat pavements, San Bernardino Mountains support a variety of species; those appearing as regular components of the adjacent forest floor, larger Artemisia shrubs and occasionally some typical pavement species. Though origins of the mounds are unknown, they may be the result of mining activities in the area. These mounds were avoided when placing sample transects.


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77-603-19, 77-725-1 through 77-725-13, 77-808-1, 77-912-1) are on file at the Rancho Santa Ana Botanic Gardens Herbarium. Nomenclature of plant species follows Munz (1973, 1974).

Each of the three study sites was sampled quantitatively by three random 30 meter line-intercepts (Cain and Castro, 1959 and Phillips, 1959). Five one meter^2 quadrats were placed at 5 meter intervals along each 30 meter line (Figure 9). 150 points per line (one every 20 cm on the 30 m lines) were sampled and presence of vegetation, rock pavement, bare ground or litter were recorded. In addition to the point frequency measurements, total number of centimeters for all plants intercepting the 30 m line was recorded by species. Overlapping species were recorded separately, although overlap was very infrequent. On each study site data from the three 30 meter lines were combined and relative percent cover for each plant species was calculated as well as frequency of rock pavement, bare ground and litter relative to total vegetation cover. The number of individuals of each species in the fifteen one meter^2 quadrats (five plots per each of three 30 meter lines) was counted. An individual was any plant rooted inside a one meter^2 quadrat and with a stem and crown distinct from other stems and crowns. Relative percent frequency and relative percent density were calculated from combined quadrat data. Values of relative percent cover, relative percent density

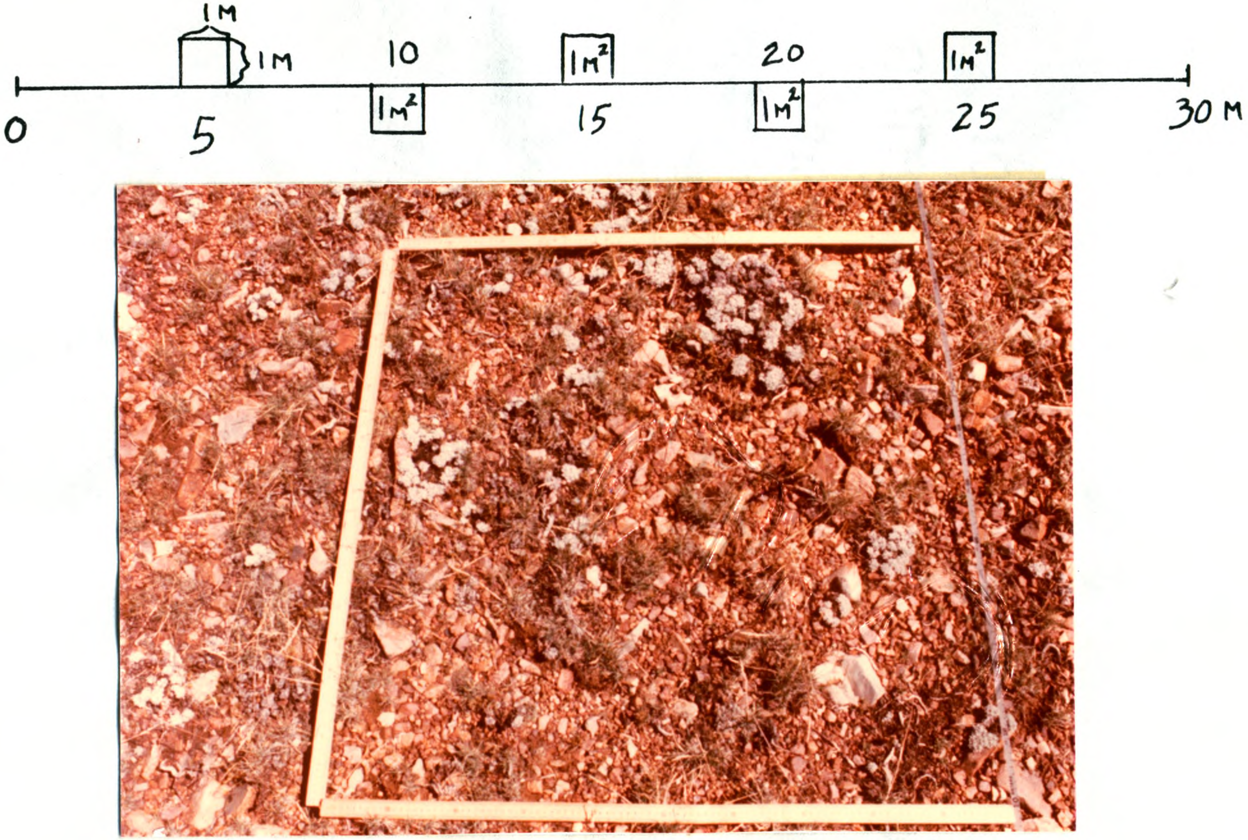

Figure 9. An example of one 30 meter transect with five one meter^2 quadrats placed at five meter intervals on the line.

and relative percent frequency were totaled to obtain Importance Values (I.V.) (Bray and Curtis, 1957) for each species on each study site.

The Sawmill study site was sampled with additional transects to measure microhabitat differences. The site slopes slightly to the northeast on one side and the southwest on the other side (less than 4% slope). The northeast and southwest aspects were sampled to determine any floristic or phytosociolgic differences relative to microhabitat preference. Three sets of "belt transects" (Figure 10) one meter by four meters long and divided into four one meter^2 quadrats, were placed at intervals one meter apart, following the downslope contour to the southwest. This procedure was repeated on the northeast contour.

A species presence list was prepared for each microhabitat measured. Relative percent frequency and relative percent density for each species were calculated to characterize and compare vegetation on the two different aspects with the average for the site as a whole. Selaginella watsonii Underw. could not be easily separated into individual plants, therefore an estimation of the number of square centimeters of ground covered by Selaginella divided by the total area of the quadrat gave a direct estimate of percent cover. No relative percent frequency or density could be calculated for this species.

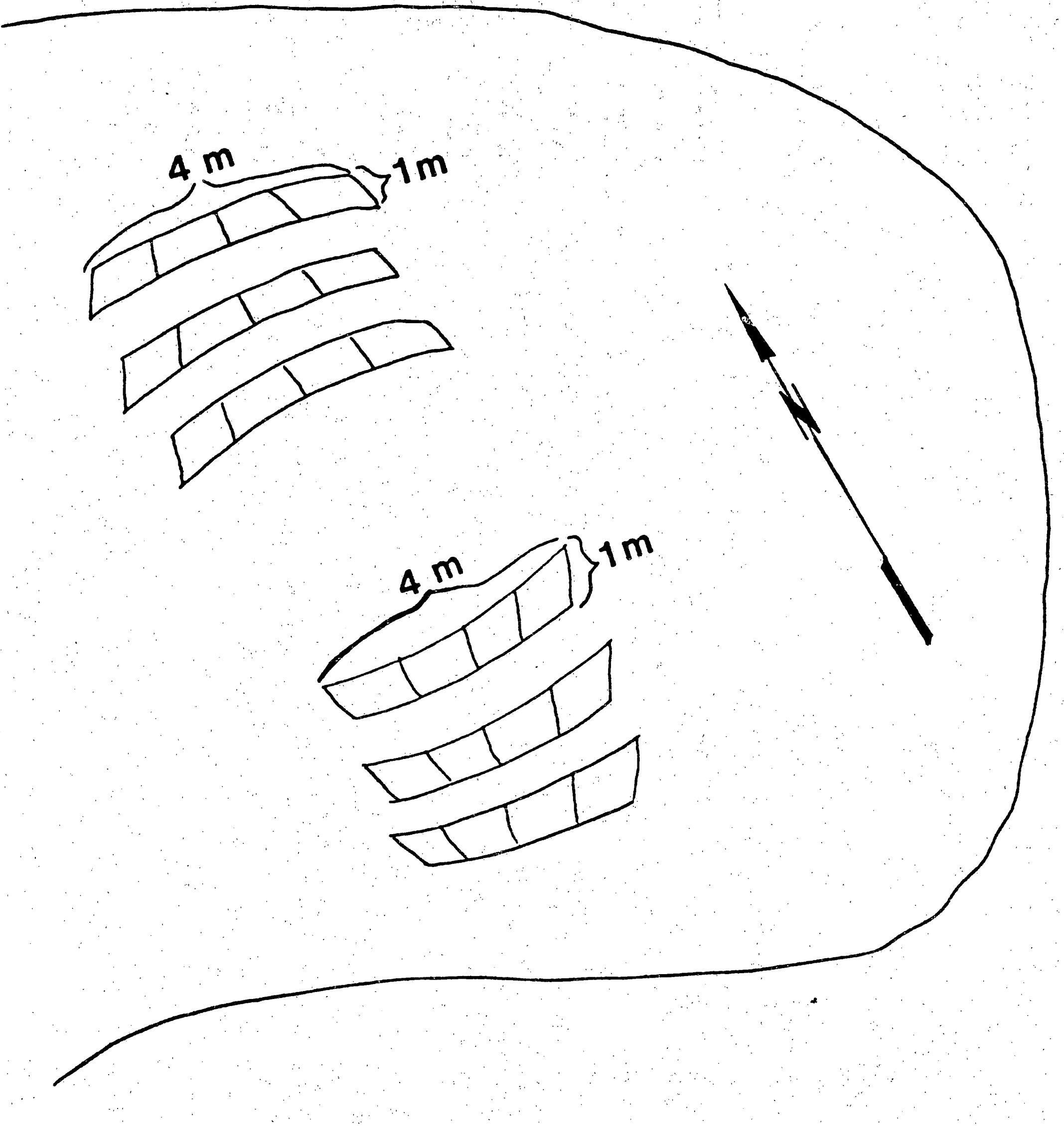

Figure 10. Example of microhabitat sampling using "belt transects" on Sawmill, a three hectare pavement plain on a flat ridgetop, San Bernardino Mountains.

Twelve samples of tree and shrub reproduction were tabulated at pavement edges on the Sawmill site. A sample represented a circle under existing trees with a diameter equal to the diameter of the tree canopy. Five samples were taken under western juniper growing side by side with interlocking crowns and one at the base of a weathered juniper stump. Individual seedlings growing within the projected tree canopy line were counted.

In order to examine the apparently abrupt change in species composition which occurs at the pavement's edge, measurements were taken of herbaceous species under one western juniper tree. The tree was located such that four 6 meter long "belt transects" could be placed in each of four different compass directions. The sampling consisted of six adjacent one meter^2 quadrats within each belt transect. These were placed on compass lines (N, S, E, W) extending from the base of the tree toward open pavements. Plot number one was placed as close as possible to the base of the tree and plot number six was then six meters distant from the tree base. Plant densities and frequencies for the 24 quadrats were recorded by species. Litter cover and depth were recorded in each quadrat as well.

Calculations

Calculations as adapted from Bray and Curtis (1957) and used in determining the percent frequency of surface components; vegetation, rock pavement, bare ground and litter for all sample sites follow:

$$\text{Percent Frequency} = \frac{\text{Number of points with component x present}}{\text{Total number of points sampled}} \times 100$$

Example: Sawmill Study Site

Surface Components	NUMBER OF OCCURRENCES Transects 1	2	3	Totals	Mean Percent Frequency
Living Vegetation	61	49	61	171	171/450 = 38%
Litter	35	14	21	70	70/450 = 15.56%
Rock Pavement	52	87	66	205	205/450 = 45.56%
Bare Ground	2	0	2	4	4/450 = 0.89%
TOTALS	150	150	150	450	100.01%

Note that the sum of the mean percent frequency for living vegetation, litter, rock pavement and bare ground equals 100%.

Importance Values (I.V.) for each species were calculated on each of three study sites as follows:

$$\text{Frequency of Species X} = \frac{\text{Number of quadrats with species x present}}{\text{Total number of quadrats sampled on study site A}}$$

$$\text{Relative Percent Frequency for species x} = \frac{\text{Frequency value of species x}}{\text{Total of frequency values for all species on study site A}} \times 100$$

$$\text{Density of Species x per meter}^2 = \frac{\text{Total number of individuals of species x present in quadrats on study site A}}{\text{Total number of one meter}^2\text{ quadrats sampled on study site A}}$$

$$\text{Relative Percent Density for Species x} = \frac{\text{Density value for species x}}{\text{Sum, density values for all species on study site A}} \text{ X } 100$$

Cover, Species x = Sum of number of centimeters for Sum of number of centimeters for species x covering the line transects measured on study site A

$$\text{Relative Percent Cover} = \frac{\text{Cover for species x}}{\text{Total cover (sum) for all species on study site A}} \text{ X } 100$$

$$\text{IMPORTANCE VALUE (I.V.) for Species x} = \text{Relative Percent Cover for Species x} + \text{Relative Percent Density for Species x} + \text{Relative Percent Frequency for Species x}$$

The sum of Importance Values for all species on any one sample site (Sawmill, Van Duesen or Arrastre Flat) must equal 300%.

RESULTS

Floristics

The pavement plain flora, sampled from three study sites, includes 33 species from 18 plant families (Table 1). Several species common to forest or woodland habitats and only occasionally occurring within open pavements are not considered as a part of the pavement flora. The field work was conducted in 1977, a year of low rainfall. In 1978 one additional annual, *Navarretia breweri* (Gray) Greene was collected and added to the list (O`Brien, 1979). Twenty pavement species are perennials and thirteen are annuals. Thirty nine percent of the species in the pavement plain flora are annuals (Table 1).

Six pavement species appear on the California Native Plant Society`s rare and endangered list (Powell, 1974). Five species are currently considered sensitive by the U. S. Forest Service. These will be considered for federal listing (threatened or endangered) by the U. S. Fish and Wildlife Service. Five pavement species are San Bernardino Mountain endemics and at least two perennials, *Eriogonum kennedyi* Porter ex. Wats. ssp. *austromontanum* (M. & J.) Stokes and *Arenaria ursina* Rob. are believed to be restricted to pavement habitats in the San Bernardino Mountains.

Species composition and vegetation physiognomy at Arrastre Flats differed somewhat from the other two study sites. The most obvious difference is the presence of

Table 1. Flora of the pavement plains, San Bernardino Mountains.

Perennial Species	Species Present		
	Sawmill	Van Duesen	Arrastre Flat
Allium fimbriatum Wats. var. *fimbriatum*	x	x	x
Antennaria dimorpha (Nutt.) T. & G.	x	x	x
Arabis parishii Wats.[a, b]	x	x	x
Arenaria ursina Rob.[a, b]	x	x	x
Artemisia nova A. Nels	-	-	x
Astragalus purshii Dougl. var. *lectulus* Jones	x	x	x
Bouteloua gracilis (HBK)lag.	x	x	x
Castilleja cinerea Gray[a, b]	x	-	x
Draba douglasii Gray var. *crockeri* (Lemmon) C.L. Hitchc.	x	x	x
Dudleya abramsii Rose	x	-	x
Erigeron aphanactis (Gray) Greene var. *congestus* (Greene) Cronq.	x	x	x
Eriogonum kennedyi Port. in Wats. ssp. *austromontanum* (M.&J.) Stokes[a, b]	x	x	x
Ivesia argyrocoma (Rydb.) Rydb.[b]	x	x	x
Lewisia rediviva Pursh var. *minor* (Rydb.) Munz	x	x	x
Lomatium nevadense (Wats.) Coult. & Rose var. *parishii* Jeps.	x	x	x
Poa incurva Scribn. & Will.	x	x	x
Selaginella watsonii Underw.	x	-	-
Sitanion hystrix (Nutt.) J. G. Sm.			
Stipa X *Oryzopsis hymenoides*	x	x	-
Viola douglasii Steud.	x	x	x

Percent perennials in pavement plain flora = 60.61%

Annual Species

Arenaria pusilla Wats. var. *diffusa* Maguire
Chaenactis glabriuscula DC. var. *curta* (Gray) Jeps.
Collinsia childii Parry ex Gray
Cryptantha simulans Greene
Epilobium paniculatum Nutt. ex T.&G.
Gilia diegensis (Muna) A. & V. Grant
Linanthus breviculus (Gray) Greene
Linanthus killipii Mason[a, b]
Microsteris gracilis (Dougl. ex (Hook.) ssp. *humilis* (Greene) V. Grant
Muhlenbergia minutissima (steud.) Swall.
Navarretia breweri (Gray)Greene
Plagiobothrys tenellus (Nutt.) Gray
Plantago purshii R. & S. var. *oblonga* (Morris) Shinners

Percent annuals in pavement plain flora = 39.39%

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[a] Endemic to San Bernardino Mountains

[b] California Native Plant Society's rare and endangered plants list

Artemisia nova. This species has achieved an even distribution of dwarfed plants throughout the pavement plain. Other of the more ubiquitous perennials, such as *Eriogonum umbellatum* Torr. and *E. wrightii* Torr. ssp. *subscaposum* (Wats.) Stokes, may extend onto pavement edges but are not considered to be true components of the pavement flora. *Eriogonum umbellatum* appeared in one of the density plots at Arrastre Flat but since this plot was near an area of apparent past disturbance, the species was not included in the pavement plain flora. The species was not present within samples taken from either of the other two study sites. *Sitanion hystrix* (Nutt.) J. G. Sm. is unique in its appearance only at Arrastre Flat, though with a low Importance Value (I.V.).

Phytosociology

Percent frequency for categories of ground surface components: pavement rock, bare ground, living vegetation and litter or dead vegetation are compared in Table 2 for the three study sites. Strong similarities exist among the three sites in frequencies of pavement rock component. The ratio of living vegetation to litter present varies only about one percent between sites. The greatest difference between sites is in percent frequency of bare soil.

I.V.'s for perennial species are ranked numerically for each study site in Table 3. Quadrats and line transects

Table 2. 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			
$\frac{\text{Percent Living Vegetation}}{\text{Percent Litter}}$	2.44	3.56	3.44

Table 3. Importance values ranked numerically by species for all pavement plains studied 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* X *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

were measured In June and only perennial species were tabulated. Some early perennials had no foliage visible above ground at the time of sampling but remnants of flowering parts were usually evident. The data may show a slight bias against those early perennials which include *Allium fimbriatum* Wats. and *Lewisia rediviva* Pursh. var. *minor* (Rydb.) Munz.

The magnitude of I.V.`s for species varies among the three study sites. However, it is significant that 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.

Nine perennial species, almost half of the perennial species present in the pavement plain flora, are common to all three study sites (Table 3). Frequency and densities for the nine species are compared in Table 4. The frequencies infer distribution patterns for species and when displayed with density figures, offer a conceptualization of spatial distribution for comparison among the three study sites. A comparison of the spatial distribution for the two pavement plain endemics illustrates significant similarities between pavements (Table 4). *Arenaria ursina* is present in at least two out of every three random one meter^2 plots on any of the

Table 4. 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
Erigeron 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 plants/meter^2		117.60 plants/meter^2		96.30 plants/meter^2	

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[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.

pavements studied. Eriogonum kennedyi ssp. austromontanum is present in at least four out of every five random one meter^2 plots on any pavement. Densities for Eriogonum kennedyi vary significantly according to age of plants ranging from seven to 48 plants per meter^2 on the three pavements sampled. Van Duesen contains an unusually high number of Eriogonum kennedyi seedlings.

In Figure 11 the range of frequencies and percentages of species in common occurring at any given frequency for the three study sites is compared. The Sawmill site had a greater percent of species occurring at higher frequencies, thus with even distributions, than either of the other two sites. Van Duesen, with a greater range of frequencies, also has more plant species at the higher end of the frequency scale. Thus, the tendency at Van Duesen is also toward even plant distributions. Arrastre Flat shows a tendency toward uneven plant distribution or "clumping" of species.

Each of the nine species which are common to all sites exists with a frequency of 0.67 or greater on at least one study site. Therefore, one of the common species can be found on at least one pavement in two out of every three random one meter^2 plots. The dashed lines on Figure 11 divides the graphs for each study site into groups; percent of species above and below the frequency of 0.67. The percent of species occurring at a frequency equal to or greater than 0.67 ranges from 78% at Sawmill to 44% at

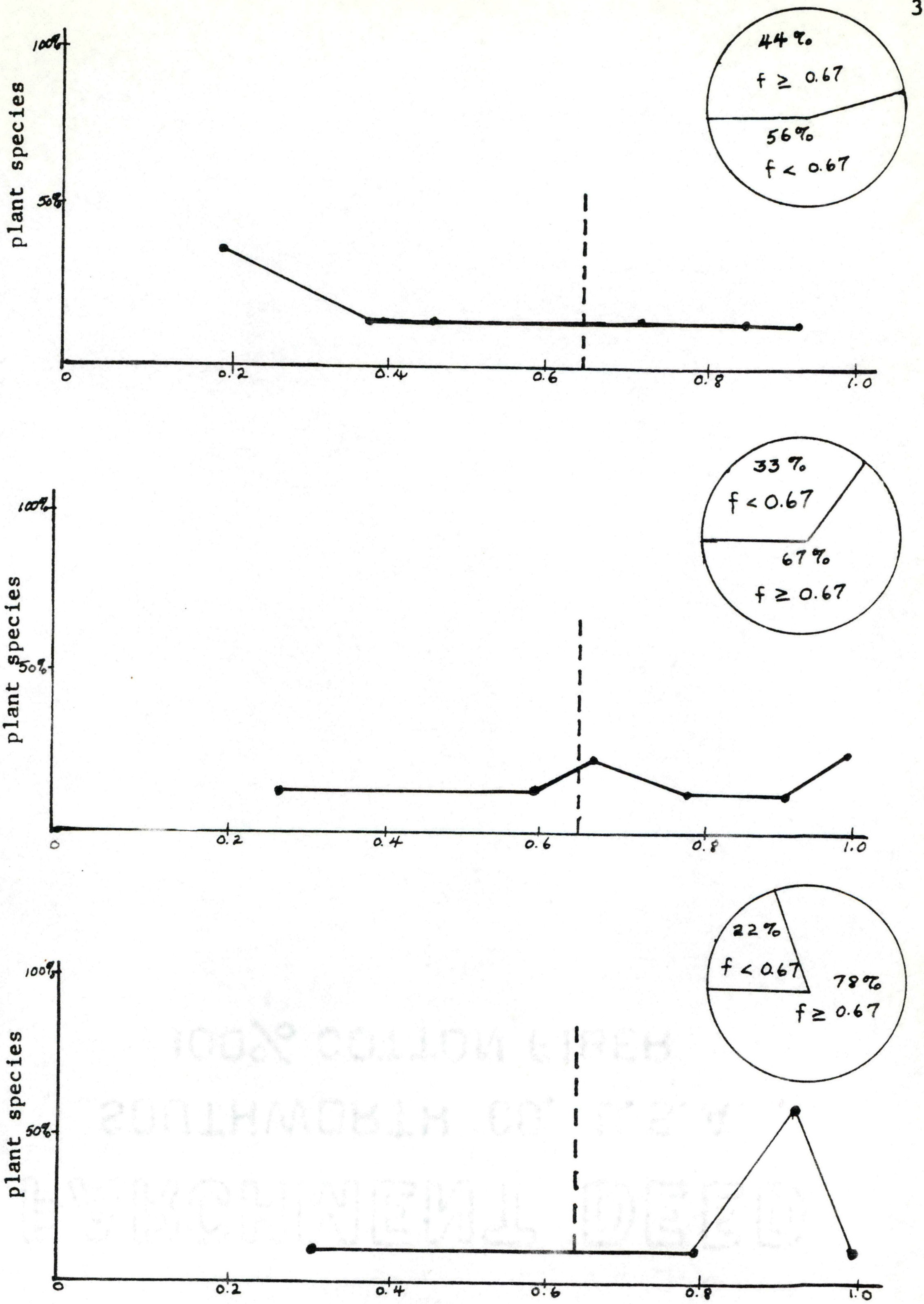


Fig. 11. Percent of nine species (see Table 4) occurring at any given frequency compared for three pavement plains studied in the San Bernardino Mountains.

Arrastre Flat. The differences in plant physiognomy at Arrastre Flat may account for the tendency toward an uneven plant distribution. Therefore, it can be predicted that typical pavements tend toward an even distribution of plant species and that the species which occur as a common component on pavements will occur with a frequency of 0.67 or greater.

Though pavement plains are generally flat, a slight change in slope (less than 4%) and thus in aspect caused vegetation changes. Samples of the northeast and southwest aspects of the Sawmill study site illustrate microhabitat differences reflected in the vegetation (Table 5). Though species composition changes on different aspects at Sawmill, total plant cover and total grass cover remain at approximately the same density. Average plant density, overall species diversity and density of grasses on the Sawmill site are compared in Table 6.

The microhabitat data for individual species infers a habitat preference which can be generalized to a temperature related and/or mesic to xeric continuum. For example, Antennaria dimorpha (Nutt.) T. & G. is a wide ranging western species which shows a decided preference for more xeric and hotter sites. The average density of 12.67 plants per meter^2 drops by one half on the northeast aspect and increases more than two times the overall average on the southwest aspect. Arabis parishii, a San Bernardino Mountain endemic, shows the

Table 5. 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 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 X *Oryzopsis*	-	-	-	-	7.0	0.67
Viola douglasii	15.67	0.93	0.58	0.33	2.58	0.83

Table 6. A comparison of microhabitats on the Sawmill Study site using density values for total vegetation, perennial grass species and a measure of perennial species diversity.

Species	Sawmill Sample density meter^2	Northeast Microhabitat density meter^2	Southwest Microhabitat density meter^2
Bouteloua gracilis	-	2.17	4.92
Poa incurva	48.73	44.92	38.17
Stipa X Oryzopsis	-	-	7.0
TOTAL (grasses/meter^2)	48.73	47.09	50.09
Mean density for perennials (plants per meter^2)	131.6	148.5	151.75
Perennial Species Diversity (total perennials present)	11	11	11

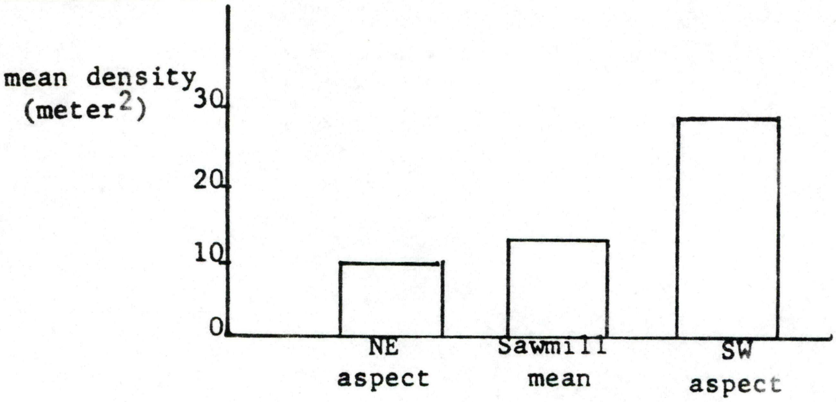
opposite trend through its absence on southwest aspects and increasing in density on the northeast aspect (Figure 12).

Successional Trends

Species composition and plant distributions appear to change abruptly at pavement edges, however a transition is sometimes apparent in the tree understories at pavement edges. At the Sawmill study site one large western juniper measuring approximately 10.7 meters tall and 35 cm diameter at breast height grows within a pavement plain edge such that measurements extending from the open pavement habitat toward the base of the tree were taken in four compass directions (N, S, E, W). Plant densities and frequencies from the four transects are displayed in Table 7. A study of the relationships between key species and litter cover under the western juniper tree revealed that percent cover and depth of litter increase on north and east aspects, and that the south aspect is more sparsely covered by litter (Figure 13).

Sitanion hystrix (Nutt.) J. S. Sm. was not usually found as a member of the pavement plain flora but frequently exists as a component of the forest understory. This grass species occurs with greater density on north and east aspects always close to the base of the tree and well within the shade canopy and litter zone. In contrast, the pavement plain endemics, *Arenaria ursina* and *Eriogonum kennedyi* ssp. *austromontanum* occur with greater densities farther from the base of the tree. *Eriogonum kennedyi* shows a preference for

Antennaria dimorpha



Arabis parishii

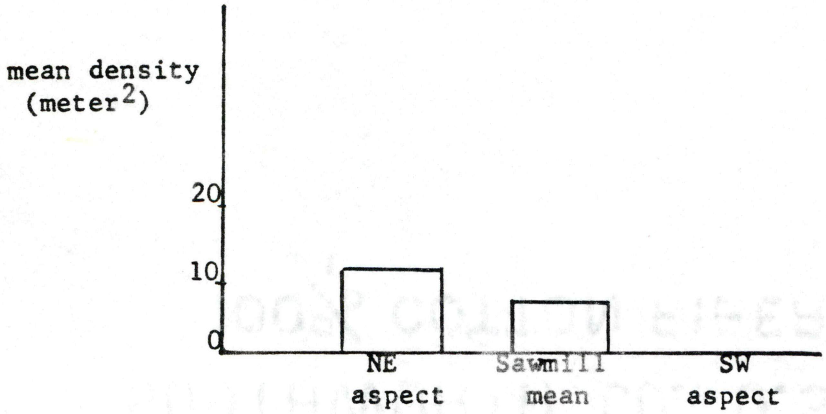


Figure 12. Comparison of density values for two representative species from microhabitats on the Sawmill study site, San Bernardino Mountains.

Table 7. Plant densities and frequency values from quadrats under a western juniper tree on the Sawmill study site, San Bernardino Mountains.

Species	SOUTH		WEST		NORTH		EAST	
	Mean Density meter^2	Frequency	Mean Density meter^2	Frequency	Mean Density meter^2	Frequency	Mean Density meter^2	Frequency
Sitanion hystrix	1.67	0.5	0.67	0.5	4.0	0.33	9.33	0.67
Poa incurva	12.83	0.83	62.33	1.0	47.33	0.5	48.67	1.0
Koelaria macrantha	0.33	0.17	-	-	-	-	-	-
Arabis parishii	1.5	0.67	3.17	0.67	0.5	0.5	-	-
Astragalus purshii lectulus	0.33	0.17	0.83	0.33	0.67	0.33	0.33	0.17
Eriogonum kennedyi ssp. *austromontanum*	6.67	0.83	6.0	0.67	1.5	0.17	3.0	0.5
Erigeron aphanactis congestus	-	-	0.5	0.33	-	-	1.0	0.5
Arenaria ursina	0.83	0.33	6.83	0.67	-	-	2.5	0.67
Draba douglasii crockeri	0.67	0.33	9.33	0.67	4.0	0.33	0.83	0.17
Viola douglasii	0.33	0.33	-	-	-	-	-	-
Antennaria dimorpha	1.5	0.67	4.0	0.67	3.0	0.33	12.33	0.67
Ivesia argyrocoma	1.33	0.5	1.5	0.33	1.83	0.33	1.0	0.5
Artemisia nova	0.17	0.17	-	-	-	-	0.17	0.17
Pinus monophylla	0.33	0.33	-	-	-	-	0.17	0.33

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 greatest density on the west side. Both plants exhibit a preference for low levels of shade and litter accumulation (Figure 13).

Densities for those plant species which appeared in the "belt transects" under the juniper tree and in addition are consistently found within the pavement plains are compared in Figure 14. All species which commonly occur on open pavements have a lower density value under the tree canopy. The mean density value for total perennial vegetation cover within open pavements is twice that for samples taken under the juniper tree canopy (Figure 14).

Tree and shrub seedlings becoming established at pavement edges usually occur under the canopies of existing mature trees. A general trend can be observed at the northeast end of Baldwin Lake where the vegetation overstory appears as synchronous "waves" of increasingly taller and presumably older trees (Pinus monophylla) as the distance from open pavements increases (Figure 15). In order to document seedling establishment on the Sawmill study site, tree and shrub seedlings under 10 representative trees at the pavements outer edge were recorded (Table 8). Five overstory trees were pinyon and five were western junipers. Tree seedlings were also recorded beneath a pair of trees (one pine and one western juniper). Of 25 seedlings in this under-

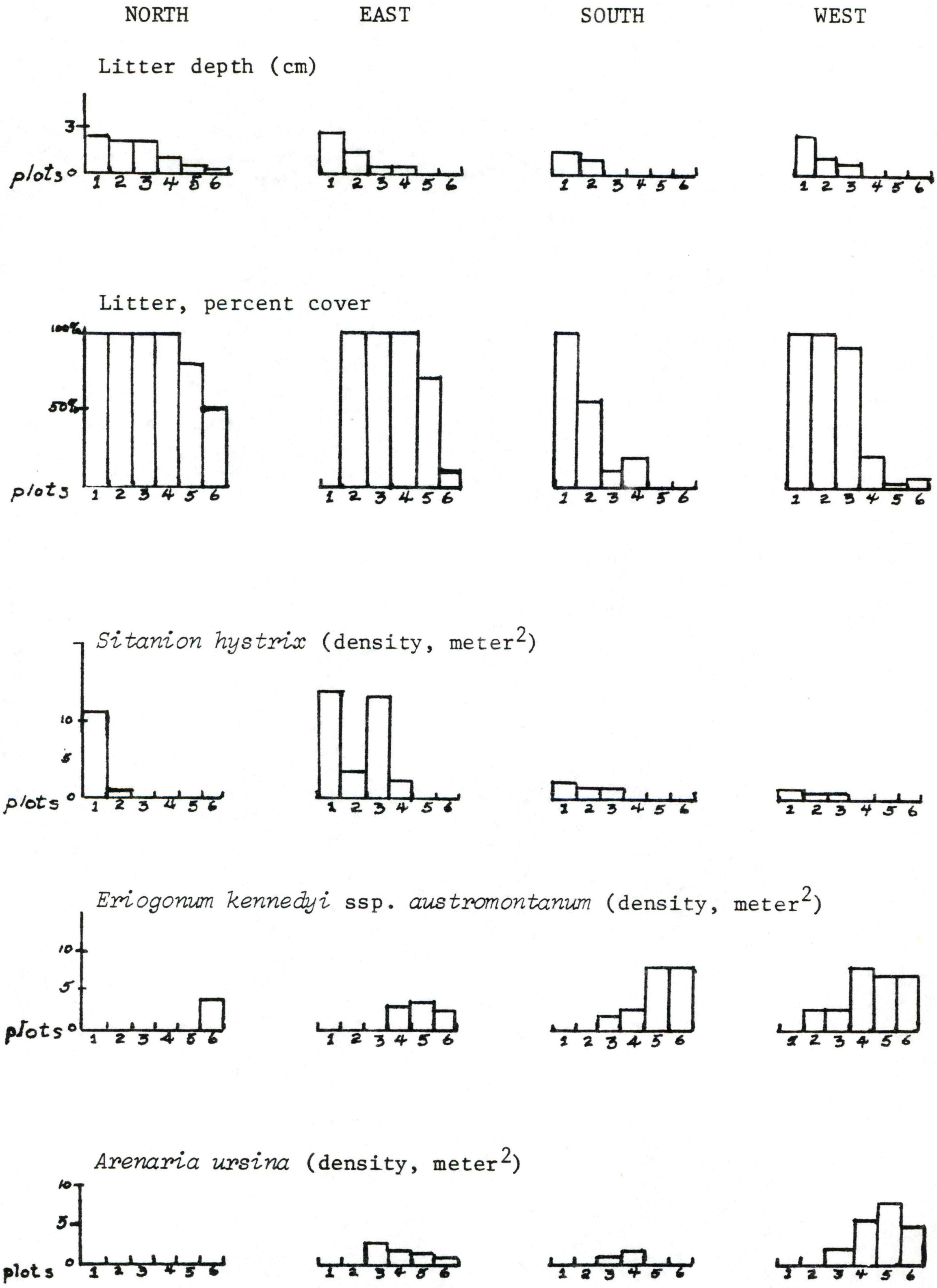


Fig. 13. Plant densities (meter^2) compared to litter and percent cover under a western juniper tree, Sawmill site, San Bernardino Mts.

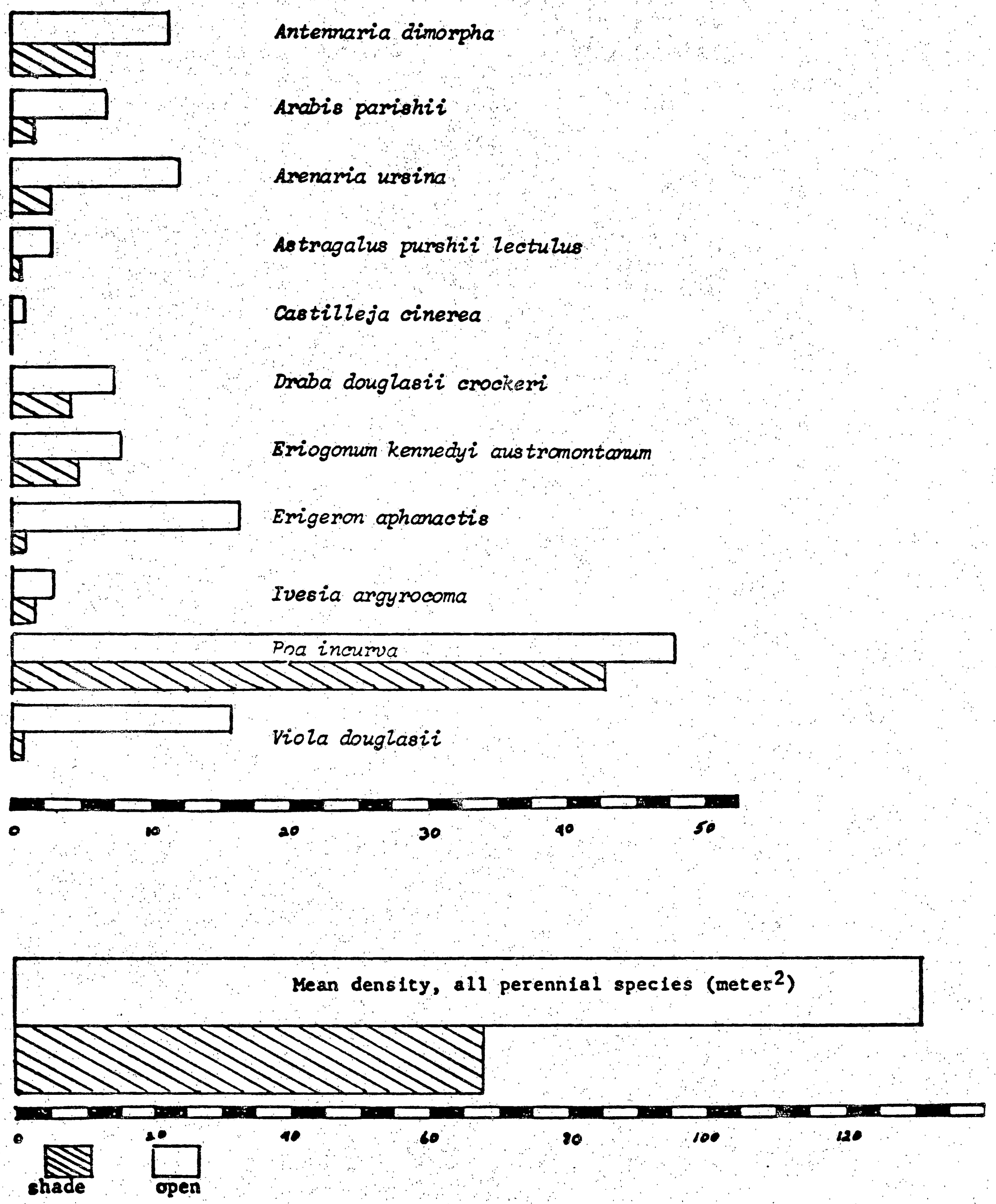


Figure 14. Comparison between plant density values on open pavements and within tree understory at the Sawmill study site, San Bernardino Mountains.

Fig. 15. Baldwin Lake in the San Bernardino Mountains, where several generations of pinyon pines exist in discrete bands, gradually extending the tree line onto pavement plains.

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Table 8. **Comparison of tree and shrub seedling establishment under pinyon and juniper trees at pavement edge, Sawmill study site, San Bernardino Mountains.**

Species	Pinyon Overstory (No. of seedlings)	Mean for 5 Trees	Juniper Overstory (No. of seedlings)	Mean for 5 trees
Pinus monophylla	13	2.6	60	12
Artemisia nova	15	3	21	4.2
Amelanchior pallida	1	0.20	7	1.4
Fremontodendron californicum	1	0.20	3	0.6
Ceanothus leucodermis	1	0.20	-	-
TOTALS	31	6.2	91	18.2

story, 24 were pinyons (Pinus monophylla) and one was sagebrush, Artemisia nova[1]. In most cases tree seedlings occurred beneath the shaded canopy of an overstory tree. However, one old juniper stump was surrounded by 21 seedlings; five pinyon pines and 16 sagebrush. The stump is weathered, indicating that the seedlings may have become established after the tree was cut down. In general, three times as many seedlings grew beneath western junipers as pinyons. The five sample pinyons sheltered a total of 31 seedlings, an average of 6.2 per tree while the five western junipers sheltered a total of 91 seedlings, an average of 18.2 per tree. Crown diameters on all ten overstory trees were of similar size. Litter accumulation is greater under pinyon pines than junipers in trees of comparable size (Figure 16).

While tree seedlings occurred at greater densities under mature trees, several shrub species have become established at pavement edges outside of the tree canopy cover. Once established, the shrubs may be followed by trees (Figure 17) but in no case was a tree seedling found outside of existing tree or shrub canopies. Shrubs frequently found at pavement edges include Artemisia nova, Fremontodendron californicum (Torr.) Cov., Amelanchior pallida, Ceanothus

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[1] Artemisia seedlings at Sawmill are assumed to be A. nova because mature shrubs existing on Arrastre Flat are A. nova.

Fig. 16. The litter accumulation under _Pinus monophylla_ (left) is considerably more than under _Juniperus occidentalis_ for trees of comparable size at the Sawmill study site, San Bernardino Mountains.

Fig. 17. A group of mixed shrubs on Sawmill pavement, San Bernardino Mountains, established at pavement's edge with young _Pinus monophylla_ (left) and _Juniperus occidentalis_ (right) growing within the shrub line.

16

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greggii Gray var. vestitus (Greene) McMin and C. Leucodermis Greene. Of these, Artemisia nova seems to have the greatest success in establishing first. The distribution of dwarfed Artemisia nova shrubs across open pavements at Arrastre Flat and other Holcomb Valley sites attests to the greater tolerance of this species for varying ecological conditions.

Soils

Soils mapping by Retelas (1978) assign pavement plain soils to the Hodgson Family of fine mixed mesic typic haploxeralfs. Observations made on road cuts in the Big Bear Basin show an abrupt soil texture change at the B2 horizon (Figure 18). The sparse vegetation allows fine clay particles to be eroded from the soil suface easily. Rock cobbles left behind in a pavement formation are generally less than 7 cm in diameter (Figure 19).

Fig. 18. Soil profile from a roadcut south of Big Bear Lake, San Bernardino Mountains, illustrating the abrupt textural change at the B2 horizon located 35.56 cm below the surface or about the level of the man`s thumb in the photograph. This particular pavement plain supports scattered sagebrush and other pavement species.


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Fig. 19. Rock cobbles surface pavement at Sawmill study site, San Bernardino Mountains showing clumps of *Poa incurva* rising above the surface suggesting that fine surface particles have eroded away.


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DISCUSSION

Initially, an attempt was made to select study areas which represented the geographic means and extremes of existing pavements. However, application of the selection criteria, particularly the necessity to exclude areas subjected to unnatural disturbances, narrowed the possible choices. The three study sites utlimately selected for phytosociologic study represents the triangular center of pavement plain distribution, located in Bear Valley and Holcomb Valley.

Pavements easily accessible to the Bear Valley floor have a history of disturbance. Many are now covered with commercial and residential developments. Other which are still intact, such as at the northeast end of Baldwin Lake, contain the introduced Mediterranean grass Bromus tectorum L. (cheat grass). Early records report intensive grazing of sheep to the conclusion of native grasses (Leiberg, 1900) in the basin. This undoubtedly explains the invasion of cheat grass on pavements.

Snow Forest Ski Lodge (now Crystal Ridge) originally constructed ski runs in the late 1950's on the south side of Big Bear Lake where pavement plains once existed. After grading slopes, clearing trees and planting introduced grasses, a significant change in species composition is apparent. Eriogonum wrightii Torr. ex Benth. var. subscaposum (Wats) Stokes may have replaced Eriogonum kennedyi ssp.

austromontanum in some areas, probably those where the surface disturbance was greatest. On undisturbed pavements the two are mutually exclusive, *Eriogonum kennedyi* occupying open pavements and *E. wrightii* replacing it at the pavement's edge beneath the trees. The two species are almost identical in vegetative characteristics but differ in flowering habit. Their phylogenetic relationship is close (Reveal, 1969) and gene flow might be inferred from intermediate floristic characters observed within this unnaturally mixed population.

Another disturbance to the natural landscape has occurred in the Coxey Meadows area 16 km northeast of Holcomb Valley where the U. S. Forest Service has type-converted native vegetation to perennial grass pastures following a fire in 1955. Pavement plains are still visible within these type conversions but contain introduced grasses, *Agropyron* ssp.

Native pavement species may have been displaced as a result of this disturbance. A point of interest for possible future study is that the Coxey Meadows pavements appear to support a different and wider ranging ssp. of *Eriogonum kennedyi*, *Eriogonum kennedyi* ssp. *kennedyi* Porter ex Wats., rather than the Big Bear Valley endemic, *Eriogonum kennedyi* ssp. *austromontanum*. Coxey pavements are separated geographically and geologically from the main body of pavement distribution by an intrusion of quartz monzonite rock (Figure 1).

The prediction can be made that those pavement plains containing introduced grasses or Eriogonum wrightii rather than E. kennedyi may have a past history of unnatural disturbance. Pavements exhibiting these characteristics were not considered as potential study sites.

High elevation pavements (above 2590 meters) on Sugarloaf Ridge and Onyx Peak were excluded from consideration as study sites because they do not meet the uniformity criteria. An obvious floristic difference between high elevation "pavements" and those selected for study is the absence of Eriogonum kennedyi ssp. austromontanum at higher elevations. Some floristic similarities do exist, including the presence of other elements of the pavement plain flora such as Castilleja cinerea and Arabis parishii. Specific information on the underlying soil and geology is not available at this time and is beyond the scope of this study.

Initial soil studies of pavement soils, conducted at University of California, Riverside (M. Lund, 1977) show that the depth of the A1 (gravelly loam) horizon is 20 cm within pavement plains on the Van Duesen site and increaes to 35 cm (loam) at pavement`s edge beneath a tree overstory. The clay content changes abruptly to greater than 60% at the $B2_1$ horizon in both soil pits, while no significant difference in pH exists between the two test pits (Appendix A and B).

Soil studies are currently in progress by the U. S.

Forest Service to examine the percentage of clays in the B2 soil horizon and depth to the upper limit of the B2 horizon. Samples are being examined both on pavement plains and on adjacent sites where similar appearing soils exist within tree overstory (Anderson, 1979).

Dibblee (1964 a, b) has mapped the geology underlying the pavement plains either as quartzite or older alluvium. Though the surface rock fragments on pavements are almost 100% Saragosa Quartzite, they cannot be explained relative to present topography and source areas for Saragosa Quartzite. The following is proposed as a possible explanation for the evolution and present positions of the pavement plains. The metamorphism of Precambrian or Paleozoic sediments into quartzite rock during the Mesozoic Era and subsequent weathering into clay soils probably occurred within the geographic and topographic vicinity of the Mojave Desert floor. Alluviation and weathering, coinciding with the Pliocene mountain building activities may have redeposited some of the clays and quartzite gravels in terraces. Continuing alluviation, uplift and erosion through the Pleistocene period produced the present landscape with pavements now existing on isolated ridgetops and sometimes appearing in basins or flats. Displacement of pavements by uplift and local subsidence can be hypothesized for Gold Mountain where several large open pavements exist on the ridgetop and smaller fragments appear at the south base of this abrupt mountain. Pavements scattered from Arrastre Flat to Burnt Flat are apparently subsiding to the northeast due to movement along the Helendale Fault. These may have been a continuous land feature at an earlier time. A local fracture has displaced segments of the Arrastre Flat pavement. Juxtaposition of sites could also be proposed for areas south of Big Bear Lake. The fact that similar clay soils are buried beneath younger sandy loams throughout much of Big Bear and Holcomb Valley (Retelas, 1978) also suggests a once more extensive and perhaps more continuous land feature.

Soil genesis is partially dependent upon continentality of climate (Major, 1953) and relief (Petrie, et. al, 1929). The origin of the clay pavement soils is obscured in geologic history but the biological and physical processes which presently contribute to soil building and help to maintain pavements as surface land features can be explored. Soil textures and pH have been described for pavements and adjacent woodland (Appendix A and B) but soil chemistry has not been examined. Changes in soil chemistry as well as texture can be produced by the vegetation growing on a site (Major, 1953). If there are onsite changes produced by conifer trees, these are precluded for the present on pavement plains due to the complex mechanisms which preclude tree establishment.

Pavements exist worldwide as land features, at all elevations and in many environments. Wherever they occur, two common conditions exist. Particle concentration at the surface is uninhibited by vegetation and both coarse and fine particles co-exist in the underlying soil deposit (Cooke and Warren, 1973). 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. Surface erosion can be easily inferred from the clumps of bunch grasses (*Poa* and *Stipa* spp.) which stand on pedestals several centimeters above the eroded pavement surface (Figure 19). 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) has described a mechanism for the wetting and drying cycle, logically suggesting that when clays are wet they expand, lifting rock fragments slightly. As the soil shrinks upon drying, the size of the rock prohibits it from dropping down into the depression below but finer particles can sift down, thus resulting in upward displacement of the rock. There is disagreement on the mechanism for upward movements caused by frost heaving (Corte, 1963 and Inglis, 1965) but agreement that it is a powerful process. On some of the more remote pavements where disturbance is rare, dead cushion plants of *Eriogonum* kennedyi ssp. austromontanum stand above the pavement surface like miniature flat topped trees with their tap roots forming the "trunk". These have apparently been forced out of the ground by one or both of the heaving processes when there is no longer a living root to hold them in place.

The pavement plain flora is reminiscent of an alpine flora but occurs at mid-elevations. In exploring this phenomenon it is helpful to consider the time period when the flora may have been evolving. There is no question that climate within the Transverse Ranges was colder and wetter during the Pleistocene Epoch. Mt. San Gorgonio, 3506 meters, was glaciated (Sharp, et al, 1959). The Soboba Flora in interior southern California shows that a mixed conifer forest existed on the floor of the San Jacinto Valley at 450 meters (Axelrod, 1966). The area now supports semi-desert taxa including Yucca schidigera roezl. ex Ortgies, Encelia farinosa Gray ex Torr. and Eriogonum fasciculatum Benth. Climate changes inferred from the vegetation changes indicate that the mean temperature was 5° C lower and the precipitation about 38 to 50 cm greater than it is today (Axelrod, 1976). The forest zones shifted down in elevation at least 900 meters, making it safe to assume a subalpine forest flora within the Big Bear Basin.

Elevation shifts in overstory vegetation can also be inferred from present day evidence. Very old (greater than 400 years) pinyon pines exist at approximately 1220 meters on the north side of the San Bernardino Mountains, along the interface between Pinyon Pine and Blackbrush Series (Derby, et al, 1978). Some of the younger pinyon generations can be observed at 2135 meters near the east end of Baldwin Lake. At least two relict stands of limber pine (Pinus flexilis) exist at 2135 meters; one on the north rim of the San Bernardino Mountain range near Crystal Creek and another in Van Duesen Canyon between Bear and Holcomb Valleys. In both areas the trees are not reproducing and are losing branches and needles in the crown. Existing vegetation patterns along with the fossil flora evidence suggest that the pavement plain flora evolved under colder, perhaps near alpine, conditions.

The vegetation of the plains represents several vegetative life forms; phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes (Raunkiaer, 1934), but the physiognomy of this community is strikingly uniform. The plants, as a group of widely unrelated species, comprise what Jepson (1925) called Simulophytes, plants of habital similarity. Perennials are compact rosettes or cushion plants and annuals are dwarfed ephemerals, certainly much like any alpine community in existence today. Present alpine communities occur above 3050 meters in the San Bernardino Mountains but pavement plains still share some of the same extremes of physical environment as the alpine habitats. They are subjected to 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. Some evolution in physiologic processes is implied but the pavement plain species may have been physiognomically and morphologically pre-adapted to the rigors of their present habitat.

The pavement plain flora contains a high percentage (39.39%) of annual species (Table 1). The California floristic province contains 27.4% annual species (Raven and Axelford, 1978) and Raunkiaer (1934) reported that 13% of the world flora is annuals. Arid regions of the old world, particularly the Mediterranean region, support higher proportions (greater than 40%) of annuals in their floras, whereas locally the pavement plains can best be compared to the Mojave Desert which has 44.1% annual species in the flora (Raven and Axelrod, 1978). The greatest concentration of these occur on the southern and western highlands of the desert (Shreve and Wiggins, 1964).

Using the Mojave Desert as a model, some similarities may be drawn between pavement plains and the desert with respect to the factors favoring development of an annual plant flora. Water is limiting in both cases. Success of desert annuals is dependent upon adequate rainfall with proper timing. Annuals are adapted to respond rapidly, completing their life cycles before dessication occurs. Snow melt supplies soil moisture on pavement plains and again a relatively short period of time presumably exists when both soil temperature and moisture conditions are favorable for annual plant growth. The upper soil layers are at first too saturated for germination to occur. Though clay holds water longer than sandy desert soils, the water soon becomes unavailable to ephemerals due to the structure and physical properties of the soil.

Spatial distribution and percent cover for perennial species on pavement plains could be likened to that of deserts (Table 2). The sparse cover produces an open habitat in terms of available light and space.

Floristic studies of the Mojave Desert show both a cismontane and transmontane influence in the annual flora (Shreve and Wiggins, 1964) as well as endemism (Powell, 1974). The annual flora of the pavement plains contains cismontane plants such as Plagiobothrys tenellus (Nutt.) Gray and also transmontane high desert species such as Plantago purshii R. & S. var. oblonga (Morris) Shinners, as well as at least one endemic to the northeast San Bernardino Mountain range. Therefore, both desert and pavement habitats appear to bridge some of the geographic geologic and climatic barriers to plant distributions, while retaining some of the isolating mechanisms required for local endemism.

Endemism of both annuals and perennials in the pavement plain flora deserves particular attention.

Examining endemism as it occurs in other regions may again provide a model. Stebbins and Major (1965) have described a trend toward increased endemism from the northern to the southern Sierra Nevada Mountains as being related to the natural decrease in boreal elements at lower latitudes, thus providing a greater opportunity for local speciation. The Transverse Ranges of southern California fit this pattern particularly well, existing at even lower latitudes as well as being physically isolated from the southern Sierra Nevada and other mountain ranges. Contributing to endemism is the inherent diversity of mountain habitats. Mid-elevations can be presumed to provide the most hospitable climatic environments. Thus adaptive radiation and speciation occurring at mid-elevations will probably result in successfully established plant populations, whereas extinction is more probable in harsher environments.

The high proportion of endemism in the northeast San Bernardino Mountain range may be explained on the basis of isolating characters of climate and landform, inherent habitat diversity and the presence of a mid-elevation ecotone. Dramatic changes in climate at the western entrance to Bear Valley produce a colder, dryer environment than the typical mid-elevation climate within the mountain range. High rising Sugarloaf Ridge to the south provides a physical barrier to plant dispersal. The Mojave Desert to the north and east provides an inhospitable habitat barrier. Habitat diversity in Big Bear and surrounding valleys is expressed by the underlying geology with parent materials ranging from Pre-Cambrian to Quaternary age (Dibblee, 1964a b). Edaphic conditions vary accordingly and dolomite endemics are present as well as Saragosa Quartzite pavement endemics. Some habitats within the area are decreasing through time. Vast meadows existed in Big Bear Valley prior to construction of a dam at the turn of the century. Subsequently increased development and lowering water tables have altered much of the remaining meadow habitat. However, one patroendemic, <u>Sidalcea pedata</u> Gray (Stebbins and Major, 1965), remains in the few isolated remnants of a once vast meadow.

Recent geologic history as well has had its effect on endemism. The present distribution of Jeffrey Pine and Pinyon Pine Forest was largely determined during the xerothermic period 8000 to 4000 years ago (Raven and Axelrod, 1978). Those new distributions occupying wholly new environments have produced a wealth of opportunity for plant speciation into new and narrower habitats. The northeast region of the San Bernardino Mountains is a vast ecotonal gradient between Jeffrey Pine or Mixed Conifer Forests and Pinyon Pine or Western Juniper Forests; a mesic to xeric transition extending north and east through 1609 km^2 from a point near Big Bear Dam.

The northeast region of the San Bernardino Mountains provides a classic example of climatic and edaphic diversity occurring within an ecotone between different biotic provinces, described by Stebbins and Major (1965) as the condition most actively promoting evolution and speciation in California.

Edaphic endemism is a more specific case which can be examined relative to species studies on the pavement plains. Kruckeberg (1951) proposes that edaphic endemism is controlled by competition, there being less competition for space within specialized edaphic niches. Pavement plain soils could differ from surrounding forest soils in several aspects; timing and duration of soil moisture availability, soil temperature, action of frost heaving, presence or absence of mycorrhizal fungi and available nutrients. At least some of these differences are implied through the absence of tree/shrub overstory. Any one or a combination of those factors can have a significant effect on successful plant establishment and survival. The very fact that pavement endemics exist suggests that they have evolved a specific competitive advantage for their particular specialized habitat but lack that advantage in adjacent forest habitats. Distribution of pavement endemics to the several small island-like habitats is difficult to explain without acceptance that the habitat was once more continuous. Seeds of pavement endemics are not wind disseminated, but drop close to parent plants. The seeds are too small to be very important as food to birds or mammals. However, the specific question of distribution, adaptation and speciation of endemics cannot be satisfactorily addressed without comprehensive monographic studies.

There are several basic similarities between the three pavement plains studied. The similarity between sites in percent frequency of the pavement rock component relative to total surface components (vegetation, litter and bare soil) is significant (Figure 11), providing evidence to support the hypothesis that all pavement plains originated from a single source and were formed under similar conditions. Less similarity exists between soils in relative frequency of living vegetation, litter and bare soil (Table 2). However, these can vary due to disturbance conditions. The Van Duesen study site and Arrastre Flats both show evidence of gopher activity. All sites have some illegal off-road vehicle use occurring with the Arrastre Flat site being most accessible to this activity. The ratios between percent frequency of living vegetation and litter were similar for all study sites. The higher ratio found at Van Duesen and Arrastre Flat, as well as a greater percentage of bare soils, suggests that some litter is being removed through disturbance activities. Many seedlings of Eriogonum kennedyi ssp. austromontanum at Van Duesen suggest that a disturbance factor has moved the system to an earlier successional stage, while the Sawmill site could be viewed as typical of a relatively stable condition.

Physiognomic similarity between pavement plains has been emphasized. Other similarities between sites are evident in the phytosociologic relationships. When Importance Values are used as a measure of plant relationships (Table 3), any bias which might exist from a single measure of frequency, line cover or density, is removed. Of the twenty perennial species present on pavements only nine appeared with regularity, receiving an I.V. on all three study sites. Thus, almost one half of perennial species present on any pavement plain studied was present on <u>all</u> those studied. Those nine species and their assigned I.V.'s then become a measure of similarity among study sites (Table 4). When the species present on each study site are ranked in order of I.V., the top five species for any one site has three species which are common to all sites (Table 3). Two of those three are pavement endemics. Thus, it can be concluded that two perennial cushion plants endemic to pavements and a bunch grass native to high elevation, open sites characterize pavement plains. Though annual species were documented in the floristic description of pavements (Table 1), they were not included in site characterization because one season's response is not a sufficient sample for comparison.

Not only is the species presence and rank of importance a measure of similarity between the study sites but the spatial distribution of characteristic species is also significant. The densities for total number of perennial species are lowest at Arrastre Flat (Table 4) where the presence of Artemisia nova affects the competition for soil moisture. The general trend toward uneven distribution of species at Arrastre Flats as opposed to even distributions at the other two sites can be attributed to this competition (Figure 11). Using an arbitrary frequency of 0.67 as a measure of even distribution, the Sawmill study site had the most evenly distributed vegetation and Van Duesen is only slightly less so. However, Arrastre Flat has slightly more than half of those species common to all sites occurring with frequencies of less than 0.67, tending toward uneven distributions. Even so, the frequency of pavement endemics remains high on all sites (Table 4). This is a decidedly significant finding regarding similarities in plant relationships on pavement plains.

Preferences of individual species for specific habitat niches have been described (Table 5, 7, Figure 13). As additional studies regarding the distributions of some of the pavement species are completed, their habitat preferences can be interpreted with more confidence. The habitat of Arabis parishii, for example, has been studied recently (Krantz, 1978). Those findings support the interpretations made from the microhabitat data (Table 5). The density for Arabis parishii increased on the northest aspect and the plant was absent from the southwest aspect, suggesting a preference for the more mesic of the pavement habitats. The species extends throughout the northeast San Bernardino Mountains under trees when the crown cover is less than 40%. It is almost invariably found on south aspects when under a tree canopy (Krantz, 1978). The plant apparently has rather narrow habitat requirements for soil temperature, available light or both. Tree canopy is generally more sparse, more light is available and soil temperatures are warmer on the south aspects. However, within pavement plains the limits are apparently exceeded, since Arabis parishii cannot tolerate the hot xeric southwest aspect of the pavement habitat (Figure 12).

The major thrust of this study has been to describe the pavement plains as unique habitats supporting a unique plant association, to identify floristic and phytosociologic similarities between sites and to correlate these with physical site parameters. The intriguing questions of pavement origins and the mechanisms for maintaining them, including successional trends in overstory vegetation, can only be superficially addressed from present data. However, successional trends have become apparent and can be examined in future studies.

Successional trends involve both the mechanisms which tend to keep pavement endemics confined to their narrow habitats and the mechanisms perventing trees and shrubs from becoming easily established. The occurrance of pavement endemics under trees has been shown to be inversely correlated to presence and depth of litter, while there is a positive correlation for other non-pavement species to occur where litter accumulations are greatest (Figure 13). Litter accumulation through time can affect soil pH, texture, surface temperature and depth of the A1 horizon. Though shade canopies and light intensities were not measured, there obviously is less light closer to the tree trunk where litter accumulations are also greater. Shade has a greater effect on the north side of the tree. Thus pavement endemics also show an inverse correlation to shade or a positive correlation for higher light intensities (Figure 13). Soil temperatures can be expected to increase with increased light intensities and the south side of a tree provides a warmer niche than the north side. The factors which produce a favorable niche for pavement plain endemics are, therefore, presumed to be increased soil temperatures and greater light intensities found in the open, treeless pavements. Though soil chemistry has not been examined, geologists find no reason to believe an exotic chemistry exists within pavement plain soils.

Soil water relationships may be a factor in the general distribution of pavement species, if it can be assumed that tree root systems decrease the available soil moisture within their crown circumferences. However, conditions under a tree canopy also result in reduced evapotranspiration rates for the understory species, thereby balancing the effect to some extent. All members of the pavement plain flora must be able to tolerate soils which are saturated with water for a period of weeks in the spring as well as active frost heaving in the winter.

If pavement plain species, particularly pavement endemics, favor habitats with higher light intensities and increased soil temperatures relative to the surrounding forest habitat, their maintenance is also dependent upon those factors which inhibit tree and shrub encroachment upon their habitat. Billings and Mark (1957) addressed factors involved in the persistance of montane treeless balds from their experience in the southern Appalachian Mountains. Pavement plains do not fit their "typical pattern of ecotonal phenomenon existing near the elevational tolerance limits for prinicipal forest dominants". Pavements are, in fact, imbedded within the continuous matrix of <u>Pinus monophylla</u> forests. Pavement plain habitats are subject to wind exposure, temperature extremes, drought and snow removal through drifting; all conditions which are detrimental to tree seedling establishment and growth. Data collected by Anderson (1979) reveal that depth to the B2 soil horizon is significantly greater within forested areas than it is on open pavements. The percentage of clay rises dramatically at the B2 horizon (greater than 60%) and clay films are present (Appendix A, B). A ponding effect could develop after snow melt at this transition between B1 and B2 horizons. This supersaturated soil may prove hostile to the roots of developing tree seedlings. At pavement edges where depths to B2 soil horizons increase and microclimatic conditions are less severe, a tree seedling stands a better chance of developing a viable root system. If the susceptibility of seedlings to this stress is at all dependent upon age of the seedling, a deeper B1 horizon provides more time for successful root development before the seedling is subject to the saturation stress. Once the seedling root system has successfully penetrated the B1 - B2 transition, the supersaturation may no longer have an adverse effect on seedling establishment and growth. Though this is purely speculative, it is presented as an area for possible future study.

Dominance of established mature trees at pavement`s edge seems to be rather equally divided between Pinus monophylla and Juniperus occidentalis. However, most seedlings at pavement`s edge are pinyon pines (Table 8). This apparent anomaly may reflect a slower natural reproductive rate for western juniper which correlates with a longer physiological rotation cycle, or it may reflect some long term successional trends occurring within the Big Bear Basin. However, since pinyon pines are the overstory species most actively encroaching on pavement plains, we can examine their specific habitat requirements relative to pavement habitats. Pinyon requires a relatively low temperature for germination, 7°C, while 15°C is the lethal threshold for pinyon seedlings (Erdman, 1970). Unshaded sites can easily exceed the lethal temperatures even 15cm 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). Table 8 shows that total shrub/tree regeneration is greatest under western junipers where litter fall is moderate to low, thereby suggesting that too much litter inhibits regeneration responses. Mycorrhizal relationships, while not within the scope of this study, are recognized as a factor in tree establishment. They may be particularly important if it is assumed that the pavement areas have actually 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). If this were actually so, we may be witnessing the primary advancement of the dominant forest cover type within the northeast San Bernardino Mountain Range.

CONCLUSIONS

Pavement plains represent a distinctive landform whose soils and underlying geology are distinct from all other soils in the San Bernardino Mountain range. Though vegetation physiognomy is unusual in its uniformity, pavement plains support a diverse flora. The typical pavement plain plant association contains *Eriogonum kennedyi* ssp. *austromontanum*, *Arenaria ursina* and *Poa incurva*, as dominants. The combination of soils, geology and plant association 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) 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 among pavement plains but the two endemic species are always among the dominant species present.
3) Perennial grasses play 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 perenial 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.

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Appendix A. Profile descriptions of soils on Van Duesen pavement plain, San Bernardino Mountains, unpublished data from M. Lund, University of California, Riverside.

East Pit, Open Pavement Plain

A1	0-20 cm Dk Brown (7.5YR 4/3) gravelly loam; massive; abrupt smooth boundary.
B21t	20-39 cm Yellowish red (5YR 4/6) clay; strong, coarse prismatic breaking to strong, medium angular blocky; sticky, plastic; thick, continuous clay films on peds; gradual boundary.
B22t	39-55 cm Yellowish red (5YR 4/6) clay; strong, medium angular blocky; sticky, plastic; thick, continuous clay films on peds; gradual boundary.
B23t	55-70 cm Yellowish red (5YR 5/6) clay; moderate, medium angular blocky; sticky, plastic; thin, continuous clay films; gradual boundary.
B24t	70-88 cm Strong brown (7.5 YR 5/6) clay; moderate, medium angular blocky; sticky, plastic; thin, continuous clay films; gradual boundary.
B3t	80-110 cm Brown (7.5 YR 5/4) sandy clay; strong, fine angular blocky; thin, continuous clay films.

West Pit, Under Trees at Pavement's Edge

A11	0-20 cm Dark Yellowish brown (10YR 3/4) loam; moderate, fine granular; slightly plastic, slightly sticky; gradual boundary.
A12	20-35 cm Dark yellowish brown (10YR 3/4) loam; moderate, fine subangular blocky; slightly plastic, slightly sticky; abrupt boundary.
B21t	35-58 cm Reddish brown (5YR 4/4) clay; strong, coarse prismatic; sticky, plastic; thick continuous clay films; gradual boundary.
B22t	58-77 cm Dark brown (7.5 YR 4/4) clay; moderate, coarse angular blocky; sticky, plastic; few thin clay films; gradual boundary.
B23t	77-97 cm Dark brown (7.5 YR 4/4) clay; moderate, coarse subangular blocky; sticky, plastic; gradual boundary.
B3t	97+ cm Light yellowish brown (10YR 6/4) sandy clay; weak subangular blocky; sticky, plastic.

Appendix B. Particle size distribution and pH from Van Duesen pavement plain, San Bernardino Mountains, unpublished personnal communication, M. Lund, University of California, Riverside.

Horizon	Depth (cm)	Very Coarse Sand 2-1	Coarse Sand 1- .5	Medium Sand .5-.25	Fine Sand .25-.10	Very Fine Sand .10-.05	Silt .05-.002	Clay <.002	pH
		- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	PERCENT	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	
East Pit, Open Pavement									
A1	0-20	2.7	6.0	8.0	11.3	11.1	33.0	27.9	6.3
B21t	20-39	1.1	2.9	4.9	7.0	6.3	11.4	66.4	5.8
B22t	39-55	1.6	2.8	4.4	7.1	5.5	13.0	65.5	5.4
B23t	55-70	1.2	2.3	4.4	6.9	6.1	12.1	67.0	5.2
B24t	70-88	1.5	2.8	4.5	7.6	5.3	12.0	66.4	5.2
B3t	88-110	3.4	5.6	8.1	13.3	9.3	15.6	44.7	5.2
West Pit, Tree Overstory at Pavement's Edge									
A11	0-20	3.0	8.6	8.6	11.5	10.2	34.1	23.8	6.0
A12	20-35	3.8	6.7	8.0	10.5	9.1	31.2	30.7	5.8
B21t	35-58	1.3	3.2	4.6	6.7	6.3	14.8	63.0	5.0
B22t	58-77	1.7	3.3	5.4	7.4	6.3	9.5	66.3	4.9
B23t	77-97	2.0	3.8	5.1	8.0	6.4	10.9	63.9	5.1
B3t	97	3.2	6.3	8.6	11.4	8.4	14.8	47.4	5.4