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VEGETATION OF THE SANTA CATALINA MOUNTAINS, ARIZONA

IV. LIMESTONE AND ACID SOILS

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INTRODUCTION

In south-eastern Arizona scattered mountain ranges rise above the arid lowlands which prevail across much of the south-western United States. The forests and woodlands of the upper elevations of these ranges are islanded in deserts and desert grasslands, and form an archipelago of wooded areas in which mountain floras of the western United States and of Mexico are variously combined into plant communities. One of these ranges, the Santa Catalina Mountains, has been subject to intensive study (Shreve 1915; Whittaker & Niering 1964, 1965; Niering, Whittaker & Lowe 1963). This paper uses techniques of direct gradient analysis and floristic comparison to study the vegetation of limestone *vs* acid parent materials, on the north side of the range.

CHARACTERISTICS OF THE RANGE

The Santa Catalina Mountains are located north-west of Tucson, Arizona, near the south-eastern corner of the state, and about 140 km north of the Mexican border. The range is shaped roughly as a triangle with the apex to the north. Previous research of Shreve (1915) and the authors has dealt with the south slope, the base of the triangle; the present study concerns the north-east side of the range. Elevations in the mountains range from 2766 m at the summit of Mt Lemmon down to 850–980 m at the base of the mountains on the south, and around 1200 m at the base of the north-east side. The topography is maturely dissected by streams, with predominantly steep slopes, but an upland of less rugged terrain occurs above 2100 m. A single complex of granitic parent material (Catalina granite-gneiss, Du Bois 1959b) forms the greater part of the south slope of the mountains. The north-east slope, in contrast, is a mosaic of diverse materials including granite and diorite, schist, andesite, shale and slate, quartzite, and limestone (Du Bois 1959a; Wilson, Moore & O'Haire 1960). Contiguity of extensive areas of limestone (Marble Mountain area, Phot. 1) and diorite (Leatherwood quartz diorite) near the Oracle Road on the north-east slope has made possible the detailed comparison of vegetation on limestone and acid soils in the 1830–2130 m (6000–7000 ft) elevation belt. More limited data are presented for other elevations and parent materials.

Climatic data from the study areas on limestone and diorite are not available. It is assumed that climates of the two areas are alike because of their proximity to one another and because of the consistency of woodland vegetation on diorite on both sides (east and west) of the limestone area. Precipitation in the area increases with elevation from 27.8 cm/annum at Tucson, in desert on the south side of the range at 730 m elevation, and 49.2 cm at Oracle, in desert grassland on the north side of the range at 1370 m, to values

around 80 cm for short records at high elevations (McDonald 1956; Mallery 1936). These data, and a precipitation increase with elevation of about 2.9 cm/100 m in this area (Turnage & Mallery 1941), suggest 65 cm as an approximate mean annual precipitation supporting the vegetation of the study areas at 1830–2130 m elevation. There are two rainy seasons, one in winter produced by cyclonic storms from the Pacific Ocean, and a second in summer from convective storms (Sellers 1960); this dual precipitation regime may be responsible for some of the floristic richness of the vegetation. Mean monthly temperatures for January and July and mean annual temperatures are 10.0, 30.1 and 19.6° C for Tucson, 7.7, 26.5 and 16.7° C for Oracle (Sellers 1960). Shreve (1915) found that temperatures decreased with elevation at an average rate of 7.5° C/1000 m; year-round soil temperatures measured for the present study decreased at an even steeper mean rate of 8.9° C/1000 m (Whittaker *et al.* 1968).

Gradients of soil characteristics with elevation are described for the nearby Pinaleno Mountains by Martin & Fletcher (1943), and for the Santa Catalina Mountains by Whittaker *et al.* (1968). Soils of the woodlands on diorite at 1830–2130 m are shallow lithosols, dark to very dark greyish-brown gravelly cobbly, sandy loams, with rock forming 5–20% of the ground surface; soils on limestone are even stonier dark grey gravelly loams, with rock forming 20–60% of the ground surface. Measured soil characteristics on diorite (means of four samples of different exposures and elevations in the 1830–2130 m belt, Whittaker *et al.* 1968) and a sample on limestone were: pH 7.0 (decreasing with depth to 5.5 near bedrock) and 8.0, organic matter content 4.4 and 5.1%, nitrogen content 0.12 and 0.21%, carbon/nitrogen ratio 20.0 and 14.2, cation exchange capacity 17.1 and 25.8 m-eq/100 g.

Fires started by the lightning of summer storms are frequent in these mountains, although the spread of these fires is now effectively controlled by the Forest Service. Probably all the woodland and grassland vegetation described has been burned and is fire-adapted. Much of the vegetation has been subject to grazing by cattle which range upward from ranches around the base of the mountains. On the north side grazing disturbance is severe on some more level grasslands at lower elevations, generally moderate in open woodlands and grasslands of steeper slopes at middle elevations, and mostly slight in denser woodlands and forests of higher elevations. Although some cattle reach the areas of the transect studies above 1830 m, grazing disturbance of the communities sampled is considered slight (except for samples *k* and *l*).

METHODS

This study was designed to complement the intensive gradient analysis of the south side of the range (Whittaker & Niering 1964, 1965) with a more limited treatment of the northeast side. In the 1830–2130 m elevation belt chosen for detailed study, sets of sixty quantitative vegetation samples were taken from limestone (calcareous) and from acid soils (predominantly quartz diorite, but including some granite and quartzite). In addition, sets of five quantitative samples were taken from other woodland, desert grassland, and desert communities (samples *g–q*), and about 200 estimative samples were taken to represent other vegetation and provide data for the vegetation charts (Figs. 1 and 2).

The quantitative samples used by the authors in mountain vegetation (Whittaker 1960; Whittaker & Niering 1965) are based on a 50-m tape which is used to lay out a 0.1 ha (20 × 50 m) quadrat. In the quadrat trees are measured and recorded by dbh and species; shrubs also are counted in the quadrat or (for species with dense populations) in a

narrower strip. Tree seedlings, shrubs, and herbs are counted and coverages estimated by species in twenty-five 1 m² subquadrats along the tape. Coverages are recorded also by line intercept along the tape and at the 100 points at the corners of subquadrats; and location, elevation, exposure and inclination, parent material, and evidence of community history and disturbance are recorded. In the estimative samples tree dbh values, shrub individuals, apparent coverage per cents for all species, and environmental data are recorded for areas of approximately 20 × 20 m, without laying out bounded quadrats.

The samples from limestone and diorite in the 1830–2130 m belt were arranged into transects by a two-step ordination (Whittaker & Niering 1965). Samples were first grouped by nine classes of topographic positions, in a sequence approximately representing a moisture gradient: (1) deeper canyon bottoms, (2) shallower, open canyons and lower slopes; open slopes facing, (3) north, north-north-east and north-east, (4) east-north-east and north-north-west, (5) east and north-west, (6) east-south-east and west-north-west, (7) south-east and west, (8) south-south-east and west-south-west, and (9) south, south-west, and south-south-west. Relations of species distributions to one another in this first transect were used to define ecological groups of species along the gradient from most mesic to most xeric. These ecological groups were assigned weights (which are given by Whittaker & Niering 1964, 1968); and weighted averages (Ellenberg 1948; Whittaker 1951, 1956; Curtis & McIntosh 1951) were computed for each sample to indicate its relative position along the gradient. Weighted averages were separately computed for stems of trees and arborescent shrubs, and for quadrat frequencies of smaller shrubs and herbs. The two weighted averages were used to indicate samples deviant from the rest of the set for reasons of disturbance or special parent material effects (Whittaker 1960, Fig. 2, 1967) and to arrange fifty samples of each set into a second transect of ten steps, each with five vegetation samples. In each step data were summed to give composite samples with tree and shrub densities in 0.5 ha, herb frequencies and densities in 125 m², and mean coverage per cents. Data for the groups of five samples representing other community-types have been similarly summed as composite samples *g–q*.

RESULTS

Tables

The resulting data are summarized in Tables 1–3. Plant names follow Kearney & Peebles (1960). For publication purposes the transects have been shortened to six steps by combining pairs of steps in the ten-step transects. The six steps, with their approximate positions along the topographic moisture gradient and steps of the ten to which they correspond are: (*a*) ravines (step one only), (*b*) mesic lower slopes and open canyons (two, three), (*c*) open northerly slopes (four, five), (*d*) open intermediate, east- and west-facing, slopes (six, seven), (*e*) open southerly slopes (eight, nine), and (*f*) most xeric open south and south-west slopes (ten). Densities of trees and shrubs (Table 1) and frequencies of herbs (Table 2) in the six steps of a transect are followed by constancy per cent (in the fifty samples of the transect), mean coverage per cent, and mean density for the transect as a whole (computed from the ten steps of the original transect). Growth-form coverages and floristic comparisons in terms of life-forms, areal types, and species diversities are given in Table 3. The tables thus permit comparison of species distribution and community characteristics in the 1830–2130 m belt on diorite (Transect XI) and limestone (Transect XII), and for related communities of other elevations on acid soils (supplementary samples *g–l*) and calcareous soils (samples *m–q*). Comparable data for vegetation of

Table 3. Summaries of community composition, samples from the north side of the Santa Catalina Mountains, Arizona

	Supplementary samples											XV												
	Group XIII					Group XIV					XV													
	Transect XII (limestone)					Transect XIII (diortite)																		
A. Growth-form coverage (%)	a	b	c	d	e	f	a	b	c	d	e	f	Trans-sect mean	g	h	i	j	k	l	m	n	o	p	q
Trees	23.2	39.4	16.2	12.2	4.9	1.7	17.0	8.8	3.5	1.0	1.3	0.6	2.1	50.6	0.4	0.4	1.1	2.7	3.5	1.2	0.4	.	.	.
Needleleaf evergreen	54.7	7.7	0.5				7.1	1.6	1.2				0.4	1.8										
Broadleaf, deciduous	16.4	42.0	63.4	63.6	36.5	27.6	45.5	25.1	14.7	1.7	0.1	0.3	5.8	54.1	11.7	10.0								
Broadleaf, evergreen	8.7	0.4	0.3	0.3	0.9	2.3	1.4	23.9	49.4	34.3	28.0	24.2	31.2	1.3	1.0	5.2	0.4		1.3	3.9	22.1	24.7	23.6	
Broadleaf, deciduous	.	0.2	1.8	2.6	6.7	12.8	3.5	19.4	14.8	5.1	4.2	1.8	0.8	7.2	0.8	9.4	6.2	0.1	8.5	2.9	8.3	8.5	3.5	
Broadleaf, evergreen	.	0.4	0.02	0.1	0.2	1.8	0.3	.	.	0.1	2.2	2.3	0.7	0.8	1.4	4.9	1.6	0.01	1.5	9.4	0.1	0.7	0.7	
Pinnate legume	0.02		0.004	.	0.1	0.1	0.4	1.0	0.9	0.1	0.1	1.2	0.1	0.8	16.1	1.1	0.6	2.1	0.4	
Narrowleaf dicot	.	.	0.3	4.8	8.8	10.2	3.8	6.4	13.3	10.5	14.3	9.7	4.5	10.7	8.2	32.2	0.3	0.1	0.6	3.9	2.3	1.8	4.4	
Rosette monocot	0.004	.	0.1	0.7	0.3	0.3	.	0.2	0.1	0.2	0.6	0.3	2.4	0.2	0.3	0.1	1.0	
Succulent	1.6	0.1	0.2	1.5	0.5	0.3	0.3	0.4	1.1	0.6	0.5	1.3	17.3	0.7	0.3	1.1	0.6	2.6	0.9	
Liana	0.03	0.1	0.2	.	0.3	0.9	0.2	0.1	0.4	0.3	0.3	0.4	1.1	0.4	0.5	1.3	17.3	0.7	0.3	1.1	0.6	2.6	0.9	
Suffrutescent	0.3	4.1	10.1	9.0	7.8	2.1	6.4	5.8	6.7	13.1	11.8	14.6	11.9	11.0	3	14.8	0.9	21.3	46.8	4.5	36.6	15.1	8.3	
Herbs	2.2	2.1	2.0	0.7	1.8	1.2	1.7	4.3	2.4	2.5	1.9	2.4	1.6	2.4	1.2	1.5	1.8	1.2	0.7	0.3	3.5	1.0	0.8	
Grass	0.03	1.0	2.7	0.8	0.6	0.1	1.0	0.2	0.3	0.2	0.1	0.5	0.2	0.3	1.0	0.03	0.5	0.06	0.03	0.9	1.8	0.01	0.05	
Forb	1.0	0.6	0.2	0.1	0.02	0.002	0.3	0.5	0.5	0.1	0.1	0.4	0.3	0.3	0.3	0.3	0.3	0.3	0.01	0.01	0.01	0.01	0.02	
Fern	1.4	1.6	1.5	0.5	0.4	0.05	1.0	0.3	0.6	0.3	0.1	0.1	0.02	1.7	0.4	0.2	0.2	
Moss	0.002	0.001	.	0.001	.	.	0.0004	0.03	0.001	0.3	0.1	0.1	0.02	0.003	
Lichen	0.002	0.001	.	0.001	.	.	0.0004	0.03	0.001	0.3	0.1	0.1	0.02	0.003	
Liverwort	0.002	0.001	.	0.001	.	.	0.0004	0.03	0.001	0.3	0.1	0.1	0.02	0.003	
B. Life-forms (no. of species in samples)	4	2	2	1	1	2	1.9	2	2	14	12	8	13	17	20	17	13	6	10	14	12	9	15	
Phanerophytes	21	2	2	19	25	17	18.3	17	20	16	15	13	14	15.2	11	14	14	11	1	1	1	3	1	
Chamaephytes	1	1	1	1	1	1	0.5	3	4	4	5	3	3	4.5	4	4	5	6	5	5	5	12	9	
Chamaephyte-suffrutescents	2	2	3	6	6	2	0.1	1	1	1	1	1	0.5	3	2	2	2	1	2	4	2	2	2	
Chamaephyte-hemicryptophytes	4	7	7	11	11	11	7.1	4	5	4	4	8	4	5.0	2	8	9	9	1	2	6	8	13	
Hemicryptophytes	38	27	23	29	29	15	27.9	28	34	27	24	29	19	27.5	19	19	16	15	12	27	28	14	22	
Geophytes	2	2	1	1	1	1	0.8	2	2	2	1	1	1	0.7	1	1	1	1	1	1	1	2	1	
Therophytes, summer only	2	1	1	1	1	2	1.2	1	2	1	1	1	0.7	1	1	3	4	1	1	4	5	1	1	
C. Areal types (no. of species)	4	2	2	1	1	2	1.9	2	2	14	12	8	13	17	20	17	13	6	10	14	12	9	15	
Endemic	21	2	2	19	25	17	18.3	17	20	16	15	13	14	15.2	11	14	14	11	1	1	1	3	1	
Madrean	1	1	1	1	1	1	0.5	3	4	4	5	3	3	4.5	4	4	5	6	5	5	5	12	9	
Chihuahuan	1	1	1	1	1	1	0.1	1	1	1	1	1	0.5	3	2	2	2	1	2	4	2	2	2	
Sonoran	16	16	14	17	21	18	17.0	21	25	20	19	21	16	20.7	11	23	21	22	9	11	24	25	16	
Southwestern	7	8	6	4	4	3	5.7	3	4	5	4	4	5	4	5	4	4	3	2	2	4	3	2	
Rocky Mountain	11	8	7	5	4	3	6.2	10	6	5	1	4	2	4.4	2	2	2	4	3	2	2	2	3	
Western Plains	8	11	4	1	1	1	4.2	3	1	1	1	1	1	2.1	1	1	1	1	1	1	1	1	1	
Temperate	2	2	2	2	2	2	0.4	1	1	1	1	1	0.2	2	2	4	3	2	2	10	9	5	4	
Holarctic	2	2	2	2	2	2	0.4	1	1	1	1	1	0.2	2	2	4	3	2	2	10	9	5	4	
Latin American	2	2	2	2	2	2	0.4	1	1	1	1	1	0.2	2	2	4	3	2	2	10	9	5	4	
Introduced	2	2	2	2	2	2	0.4	1	1	1	1	1	0.2	2	2	4	3	2	2	10	9	5	4	
D. Species diversity (vascular plants)	27.6	21.2	19.7	17.5	21.9	24.4	21.3	31.0	23.0	18.9	21.9	23.7	20.0	22.6	19.8	27.8	24.4	25.6	17.8	14.6	32.4	31.4	23.0	
Species per quadrat	68	70	57	50	65	48	60	65	73	54	49	53	45	57	39	57	50	55	30	30	70	65	43	
In combined samples																								

acid soils on the south side of the range are available on the tables of Whittaker & Niering (1965).

Vegetation patterns on limestone and acid soils

Vegetation of the south side of the range forms a physiognomic and floristic continuum from subalpine forest through montane fir and pine forest, pine-oak forest and woodland, open oak woodland, and desert grassland, to Sonoran desert (Whittaker & Niering 1965). A largely similar pattern for acid soils on the north side is represented in Fig. 1.

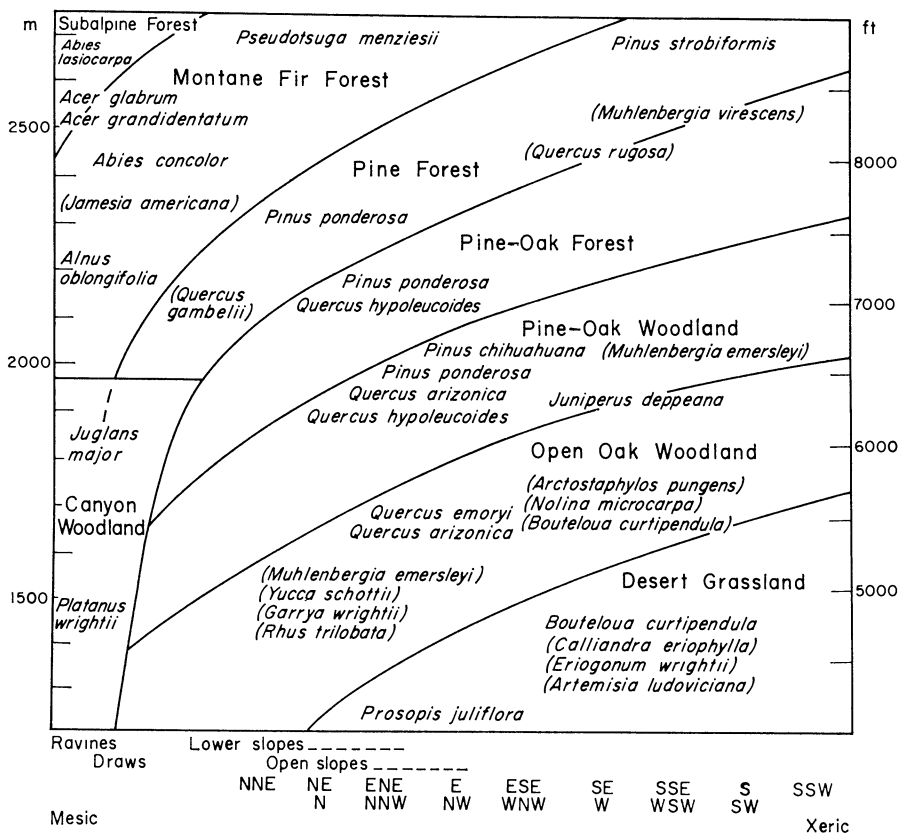


FIG. 1. A mosaic chart of vegetation on granitic and other acid parent materials, north-east side of the Santa Catalina Mountains, Arizona, based on 180 vegetation samples.

The figure is a mosaic chart (Whittaker 1956, 1960) based on plotting 180 vegetation samples in relation to elevation and topographic position and drawing boundaries at average positions of the transitions between community types defined by physiognomy and species dominance.

The pattern differs from that of the south side of the range in that: (a) *Cupressus arizonica* is lacking as a dominant of canyon woodlands on the north side; (b) the pygmy conifer-oak scrub of more xeric steep slopes in the pine-oak woodland belt of the south side (and two of its major species, *Pinus cembroides* and *Arctostaphylos pringlei*) are almost lacking from the north side, where equivalent topographic positions are occupied by apparently less xerophytic pine-oak woodlands; (c) open oak woodlands and desert

grasslands of the north side differ in composition, with some major south-side species (*Agave schottii*, *Selaginella* spp.) apparently absent and others (*Quercus oblongifolia*, *Vauquelinia californica*, *Haplopappus laricifolius*) much less important in the north-side communities; (d) at elevations around 1220 m the open oak woodlands and desert grasslands of lower mountain slopes on the north side contact the desert grasslands of more level situations of the San Pedro Valley. Sonoran desert communities, which occur as a spectacular and floristically rich high desert scrub with giant cactus (*Carnegiea gigantea*), palo verde (*Cercidium microphyllum*) and ocotillo (*Fouquieria splendens*) on the lower slopes of the south side (Niering *et al.* 1963; Whittaker & Niering 1965) are of very restricted occurrence on the north side.

These differences appear not to be simply a rain-shadow effect; vegetation belts are not displaced to different elevations as would be expected with a significant rainfall contrast. In general the vegetation is of comparable mesophytism at corresponding elevations on the two sides, in the more mesic half of the topographic moisture gradients at least. The more xerophytic character of vegetation of open xeric slopes on the south side (notably the occurrence of pygmy conifer-oak scrub there) may be attributed to factors other than precipitation difference—somewhat steeper slopes and rockier soils, and exposure to arid winds off the Sonoran desert during periods of moisture stress, these factors combining to require greater drought adaptation and to render the communities more susceptible to fires.

Fig. 2 represents a parallel pattern of vegetation on limestone, for a range of elevations 1000 ft lower than that of Fig. 1. The pattern is based on 118 samples, and the samples at high and low elevations are too few to clarify relations among forest and desert scrub types on limestone to our satisfaction. Pine forests and pine-oak woodlands occur above 2000–2500 m on limestone and extend downward into canyon forests in a manner similar to that in Fig. 1. The pine-oak woodlands, however, occur at elevations which would support pine forests on diorite. Mountain mahogany, *Cercocarpus breviflorus* (*C. montanus* var. *paucidentatus*), scrub occupies a range of environments similar to that of the pine-oak woodlands on diorite, but prevails over a broader elevation range than that of these woodlands. The open oak woodland belt on diorite is replaced by a desert grassland belt on limestone, and the desert grassland belt on diorite by a desert scrub of *Fouquieria splendens*, *Agave palmeri* and *Acacia constricta*, a community different from the Sonoran desert mentioned. Below 1200 m a number of other desert scrub types, which also are not of primarily Sonoran affinities, occur on limestone.

Systems of plant formations for this area have been suggested by Lowe (1961, 1964) and Gehlbach (1966, 1967). We believe (though continuity of the limestone pattern is not established by transect data) that both patterns form physiognomic and floristic continua from coniferous forest to desert. The vegetation patterns (apart from the canyon woodlands) may consequently be interpreted as formation-series in the sense of Beard (1955), with a sequence of formations from high elevations to low on both limestone and acid parent materials:

1. Subalpine forest (*Abies lasiocarpa*, *Picea engelmanni*, the latter not present in the Catalinas).
2. Montane fir forest (*Abies concolor*, *Pseudotsuga menziesii*).
3. Montane pine forests (*Pinus ponderosa*, *P. strobiformis*).
4. Pine-oak forests (*P. ponderosa*, *Quercus hypoleucooides*, etc.).
5. Pine-oak woodlands (woodlands with smaller trees of *Pinus chihuahuana*, *P.*

ponderosa, *Quercus arizonica*, *Q. hypoleucoides*, etc.; and pygmy conifer-oak scrub of *Pinus cembroides*, *Juniperus deppeana*, *Quercus arizonica*, *Q. emoryi*, *Arctostaphylos pringlei*, *A. pungens*, *Nolina microcarpa*, etc.).

6. Open oak woodlands (with small, spaced *Quercus arizonica*, *Q. emoryi* and *Q. oblongifolia*, and a grassy floor). *Juniperus* species occur with the oaks in some situations and in some others replace the oaks. On limestone, these woodlands are replaced by *Cercocarpus* scrub, and in other areas chaparral may occupy the corresponding position in the sequence.

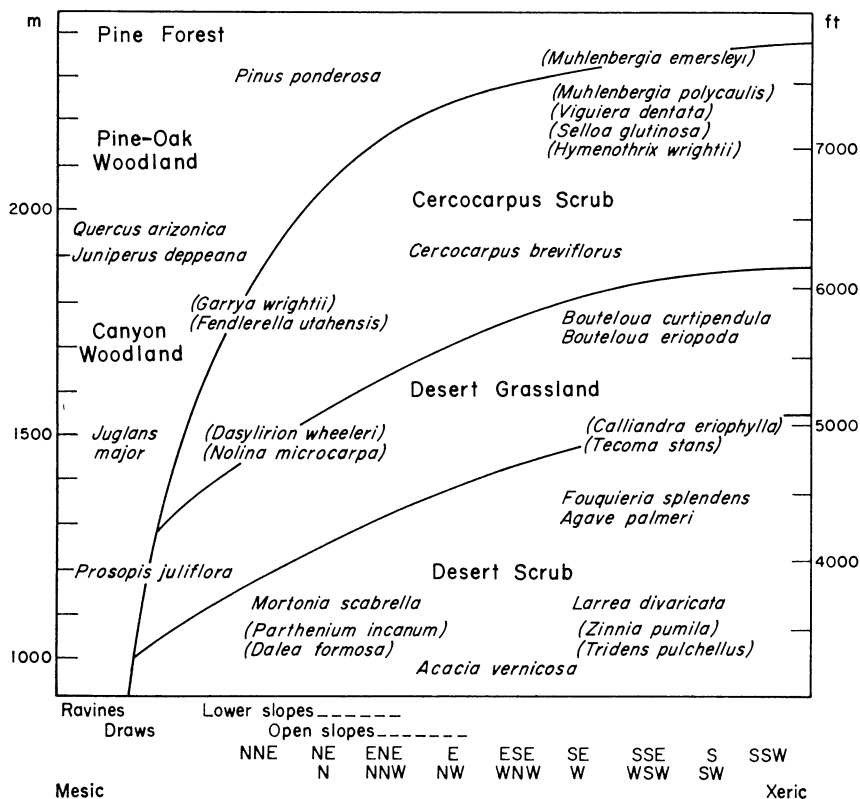


FIG. 2. A mosaic chart of vegetation on limestone, north-east side of the Santa Catalina Mountains, Arizona, based on 118 samples.

7. Desert grasslands (many grass species, often with scattered monocot rosette and other shrubs, similar physiognomy on acid and limestone soils).

8. Upper (spinose) desert scrub (*Carnegiea gigantea*, *Cercidium microphyllum*, *Fouquieria splendens*, etc., on acid soils, *F. splendens*, *Agave* spp., etc., on limestone).

9. Lower (microphyll) desert scrub. (*Larrea divaricata* is the principal species, usually with associated suffrutescent shrubs; *Mortonia scabrella* occurs on limestone and *Atriplex* spp. on some soils.)

For lack of high-elevation limestone in our area, the first two formations could not be observed on limestone; and only limited observations are available for formations 3 and 4 on limestone. Pygmy conifer-oak scrub is not known to occur on limestone; whereas

the *Cercocarpus breviflorus* scrub is not known to occur, as a type strongly dominated by this species, except on limestone. A salient feature of the physiognomic treatment is the manner in which the formations are displaced one step upward in relation to the elevation gradient, on limestone as compared with diorite. In this desert mountain range the vegetational gradient from forest to desert is strongly affected by moisture as well as temperature; this gradient of mass, production and coverage of plant communities may be thought most essentially a response to moisture conditions. A given elevation and topographic position on limestone is thus occupied by vegetation which is one step more xeromorphic than that of a corresponding position on acid parent materials.

Limestone and diorite vegetation, 1830–2130 m

Vegetation of the 1830–2130 m belt may be described in terms of community gradients, or coenoclines, in relation to the topographic moisture gradient. Supporting data on species importances and stratal coverages are given in Tables 1–3.

Vegetation of this belt on the south side of the range has been described (Whittaker & Niering 1965) as a coenocline from canyon fir forest through pine and pine–oak forest on lower slopes to pine–oak woodland on mesic open slopes and pygmy conifer–oak scrub on xeric open slopes. On diorite on the north side, mixed forests of *Pseudotsuga menziesii*, *Pinus ponderosa*, *P. strobiformis*, *Juglans major*, *Alnus oblongifolia*, etc., occur in canyons (transect XI, column *a*). On the canyon slopes these gradate into pine–oak forests dominated by *Pinus ponderosa* with *Quercus hypoleucoides*. These in turn gradate into pine–oak woodlands (Phot. 3) which occupy the rest of the topographic gradient (*c–f*), with changing composition and decreasing tree coverage toward more xeric slopes. *Pinus ponderosa* occurs in the more mesic of these woodlands, but *P. chihuahuana* occurs throughout and is the dominant conifer in the more xeric stands. Among the oaks dominance shifts from *Quercus hypoleucoides* in more mesic (*c*) to *Q. arizonica* in less mesic (*d*, *e*) and *Q. emoryi* in more xeric (*f*) stands. As coverage of both pines and oaks decreases toward the xeric sites, undergrowth coverage increases. The most xeric stands have few pines, an open oak stratum, and well-developed undergrowth. Extension of the coverage and composition trends beyond these stands leads to open oak woodlands such as represented in sample XIII-*h*.

On limestone open woodlands of smaller trees and arborescent shrubs occur in canyons (transect XII, *a*). Up the canyon walls this woodland, which includes *Cercocarpus breviflorus*, gives way to the scrub dominated by *Cercocarpus* (Phot. 4), which occupies the rest of the gradient. Character of the scrub changes markedly along the gradient, however. On mesic slopes the shrubs are tall (2–3 m) and of relatively high coverage (40–60%), with *Garrya wrightii* important along with *Cercocarpus*. In the undergrowth beargrass (*Nolina microcarpa*) and the small shrub *Fendlerella utahensis* are most important. From mesic through intermediate slopes (*c–e*) the height and coverage of the shrub stratum decrease progressively, and the densities of *Garrya*, *Nolina*, *Fendlerella* and *Yucca schottii* decrease. On xeric slopes (*f*) *Cercocarpus* is strongly dominant in the shrub stratum, but in a very open stratum of 15–25% coverage of shrubs mostly 1.5 m or less tall. Rosette shrubs (*Nolina*, *Dasyliirion wheeleri*, *Yucca schottii*) are conspicuous and grass cover is 10–20%. Extension of these trends of decreasing shrub and increasing grass cover leads to the desert grasslands of drier limestone slopes (sample XV-*m*), with grass cover of 30–50% and more widely scattered shrubs.

Supplementary samples

Woodlands on non-calcareous soils (group XIII)

Composite sample *g* is for the high-elevation (2100–2200 m) woodlands below the San Pedro lookout on the Mt Lemmon highway, on steep northerly slopes on Catalina granite-gneiss. As in the diorite canyon woodland (sample XI-a), *Pinus ponderosa* and *Pseudotsuga menziesii* are dominant in an open upper tree stratum above an open lower tree stratum of oaks. Species centred in higher-elevation forests predominate in the sparse shrub and herb layers. The communities are of interest for the occurrence in them of *Quercus chrysolepis* var. *palmeri*, a narrowly endemic oak population disjunct by many kilometres of desert from the species in California.

Composite sample *h* represents open oak woodlands of north-facing slopes on shales above Rattlesnake Canyon, 1500–1600 m. Two of the more xeric oaks (*Q. arizonica*, *Q. emoryi*) are dominant in very open growth (10% and 2% coverage, respectively), with moderate shrub coverage (*Garrya wrightii* 7%, *Nolina microcarpa* 6%, *Arctostaphylos pungens* 2.3%, *Yucca schottii* 1.4%, *Rhus trilobata* 0.7%) and grass coverage (12–35%) in which *Bouteloua curtipendula* and *Muhlenbergia emersleyi* are most important species.

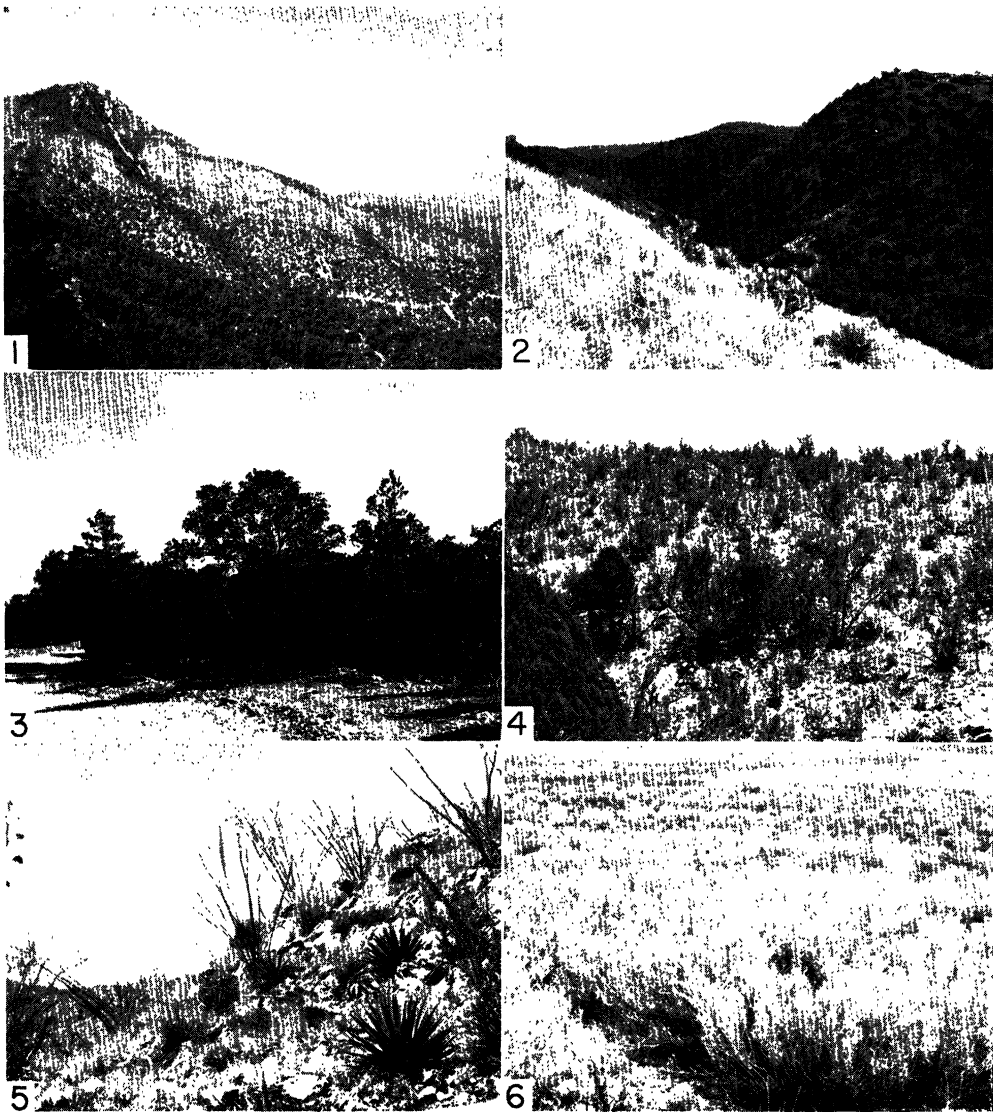
Composite sample *i* is from lower-elevation (1370–1400 m) open oak woodlands on gentle slopes of an area of dissected granite near the town of Oracle. Major species are similar to those of the preceding sample: *Quercus emoryi* 6.3% and *Q. arizonica* 3.7%; *Nolina microcarpa* 31%, *Arctostaphylos pungens* 6%, *Rhus trilobata* 5%, *Mimosa biuncifera* 3.5%, *Yucca schottii* 0.7%. Sample *i* differs from *h* in somewhat more xeric species composition, high coverage of the liliaceous beargrass (*Nolina*) and low of true grasses (1% average), and occurrence of some species of the desert grasslands and deserts (*Calliandra eriophylla* 1.0%, *Haplopappus laricifolius* 0.8%, *Krameria parviflora* 0.5%, among the shrubs).

Desert grasslands on non-calcareous soils (group XIV)

Composite sample *j* is from south-facing slopes on quartzite above Rattlesnake Canyon, 1450–1600 m; these grasslands form a north–south slope contrast or alterne with the woodlands of sample *h*, though on a different parent material (Phot. 2). *Prosopis juliflora* (mesquite) 2.7%, *Juniperus monosperma* 1.1% and widely scattered oaks occur in a grassland of 21% mean grass coverage. Principal shrubs are the low suffrutescents *Artemisia ludoviciana* ssp. *albula* 10% and *Eriogonum wrightii* 6%; the principal grass is *Bouteloua curtipendula*.

Composite sample *k* represents grasslands on level soils at the Page Ranch, San Pedro Valley, 1160 m. The grassland has been protected for some years since earlier grazing, and has relatively good grass cover (47% mean), with *B. gracilis*, *B. eriopoda*, *Andropogon barbinodis*, and *Aristida ternipes* among the major species. *Yucca elata* occurs in the area, but *Eriogonum wrightii* 0.7% is the only shrub of more than trivial coverage in the quadrats.

Composite sample *l* represents contrasting grasslands, exposed to severe grazing, in a similar environment. Grass coverage is limited to 3–6% and exceeded by that of suffrutescent shrubs (of the narrow-leaf dicot grouping of Table 3) associated with grazing disturbance—*Gutierrezia sarothrae* 12% and *Haplopappus tenuisectus* 4.6%. Coverages of *Prosopis juliflora* 3.5% and *Opuntia engelmannii* 1.4%, which are higher than in sample *k*, probably also represent grazing effects.



PHOT. 1. A view of the limestone study area on Marble Mountain in the Santa Catalina Mountains, Arizona. Mountain mahogany scrub prevails on the limestone slopes of the mountain, contrasted with pine-oak woodlands on acid soils in the foreground.

PHOT. 2. Desert grassland on quartzite, south-east-facing slope of 28° inclination, 1550 m elevation, Santa Catalina Mountains. *Bouteloua curtipendula* is dominant, *Dasyllirion wheeleri* and *Opuntia engelmannii* are visible on the slope. The opposite, north-west-facing slope across the canyon bears open oak woodland dominated by *Quercus arizonica* and *Q. emoryi*.

PHOT. 3. Pine-oak woodland on diorite, south-facing slope of 9° inclination, 2040 m elevation, from the Oracle Road on the north-east side of the Santa Catalina Mountains. *Pinus chihuahuana*, *Quercus hypoleucoides* and *Q. arizonica* are dominant.

PHOT. 4. Mountain mahogany scrub on limestone, south-west-facing slope of 20° inclination, 2130 m elevation, Marble Mountain, Santa Catalina Mountains. *Cercocarpus breviflorus* is dominant, monocot rosette shrubs (*Dasyllirion wheeleri*, *Agave palmeri*, *Nolina microcarpa*) are conspicuous. *Juniperus deppeana* occurs on the lower slope to the left.

PHOT. 5. Spinose desert scrub on limestone, south-facing slope of 26° inclination, 1460 m elevation, Santa Catalina Mountains. *Fouquieria splendens* and *Agave palmeri* are dominant, *Dasyllirion wheeleri*, *Cercocarpus breviflorus* and grass cover are visible.

PHOT. 6. Sandpaperbush scrub on limestone, north-west-facing slope of 12° inclination, 1475 m elevation, Mule Mountains south of Tombstone, Arizona. *Mortonia scabrella* is strongly dominant; the darker scrub in the background is formed by *Larrea divaricata*.

Desert grassland and scrub on calcareous soils (group XV)

Composite sample *m* includes desert grassland samples from south-facing slopes on limestone, Rattlesnake Canyon, 1500–1600 m, which are from environments comparable to those of sample *j* though on a different parent material. Grass coverage was higher than in *j* (37%) and of more mixed species composition, with *Bouteloua curtipendula*, *B. eriopoda*, *Aristida glauca*, and *A. parishii* as dominant species. The principal shrub was the small legume *Calliandra eriophylla* 8.5%, growing on the same level as the grass cover. Taller shrubs include *Dasyliirion wheeleri* 3.5%, *Fouquieria splendens* 1.5%, *Tecoma stans* 0.5%, *Aloysia wrightii* 0.5% and *Cercocarpus breviflorus* 0.3%. As coverage of some of the shrubs increases, while that of grasses decreases, the community gradates into the following of more xeric and rockier slopes.

Composite sample *n*, spinose desert scrub, limestone slope phase (Phot. 5), was taken also from south-facing slopes of Rattlesnake Canyon, 1500–1600 m. Dominant shrub species—*Fouquieria splendens* 9%, *Agave palmeri* 1.7%, *Cercocarpus breviflorus* 2.8%, *Calliandra eriophylla* 2.9%, *Tecoma stans* 1.1%, *Dasyliirion wheeleri* 0.8%—are mostly shared with Sonoran deserts and woodlands on acid soils in the area; but the physiognomy of the community is more nearly that of Chihuahuan desert on limestone. Grass coverage is around 15%, of mixed composition (Table 2), and the drought-adapted fern *Notholaena sinuata* var. *cochisensis* 1.8% is conspicuous in the herb stratum.

Composite sample *o* represents sandpaperbush (*Mortonia scabrella*) desert scrub on dissected calcareous valley-fill soil, Reddington road, 1070–1130 m. *Mortonia* is strongly dominant at 21% coverage; other shrubs are *Acacia constricta* var. *vernica* 2.7%, *Larrea divaricata* 1.1%, *Calliandra eriophylla* 4.8%, *Dasyliirion wheeleri* 1.2%, *Parthenium incanum* 0.8%, *Yucca elata* 0.5% and *Polygala macradenia* 2.0%. The community is a low (0.7–1.0 m) open, evergreen scrub with little herb coverage (grass 8%, with *Tridens muticus* and *T. pulchellus* as major species). *Mortonia* is a shrub of the Chihuahuan desert, but these stands are geographically marginal and floristically depleted for the type, and the following was taken for comparison.

Composite sample *p* is from the *M. scabrella* desert scrub (Phot. 6) of north-facing limestone slopes, Mule Mountains near Tombstone, Arizona, about 100 km south-east of the Catalinas, at 1400–1450 m. The *Mortonia* scrub is one type of the complex and highly developed Chihuahuan desert vegetation pattern on limestone of these mountains (Lowe 1964). *Mortonia* is dominant at 23% coverage, with *Acacia constricta* var. *vernica* 8%, *Nolina texana* 3.1%, *Aloysia wrightii* 2.6%, *Rhus choriophylla* 1.0%, *Dasyliirion wheeleri* 0.9%, *Parthenium incanum* 0.8% and *Menodora scabra* 1.5%, as other major species, and grass coverage (11%) and composition comparable to the preceding.

Composite sample *q* represents creosotebush (*Larrea divaricata*) desert scrub on dissected calcareous valley-fill soil, Reddington Road, 1070–1130 m. The community-type forms alternates with *Mortonia* scrub in part of the area, with *Mortonia* on north- and *Larrea* on south-facing slopes. *Larrea* is strongly dominant (24% coverage) in a scrub of height and coverage similar to that of the *Mortonia* desert; other important shrubs are *Cercidum microphyllum* 1.7%, *Acacia constricta* var. *vernica* 1.4%, *Opuntia phaeacantha* 0.9% and *Fouquieria splendens* 0.7%. Grass coverage is 2%, predominantly *Tridens pulchellus*.

Species distributions

Relations of species populations to the topographic moisture gradient can be directly compared between transects XI and XII (Tables 1, 2). Many of the species present in both

transects show a marked distributional shift—the population is displaced toward the left, that is toward more mesic topographic positions, on limestone compared with diorite. When modes or population maxima on the ten-step transects are compared, the amounts of these shifts are three to five transect steps in some species (*Quercus arizonica*, *Garrya wrightii*, *Agave palmeri*, *Nolina microcarpa*, *Selloa glutinosa*, *Yucca schottii*, *Bouteloua curtipendula*, *Eragrostis intermedia*), but others shift by one or two steps, or apparently none. Similar shifts in relation to parent material were observed in the Siskiyou Mountains (Whittaker 1960) and White Mountains (Wright & Mooney 1965). The shifts in distribution from diorite to limestone are comparable with those from diorite to gabbro in the Siskiyou in number of steps, but they are less consistent in amount between species. The amount of the shift, and degree of floristic contrast, is much less than that from diorite to serpentine in the Siskiyou (the gabbro being chemically intermediate to diorite and serpentine).

Many species which occur in one transect are absent from the other. *Abies concolor*, *Pseudotsuga menziesii*, *Quercus hypoleucoides*, *Q. rugosa* and other mesic species of high-elevation forests are present in the diorite transect and absent from the limestone transect (but not necessarily absent from limestone at higher elevations). Some less mesic species (*Pinus chihuahuana*, *Arbutus arizonica*, *Quercus emoryi*, *Dalea albiflora*, *Andropogon cirratus*) are apparently excluded from limestone, rather than occurring on it with a distributional shift, in this study area. In the reverse relationship a number of limestone species are absent from the diorite transect. One group of these (*Fouquieria splendens*, *Melampodium leucanthum*, *Tragia nepetaefolia*, *Aristida glauca*, *Leptochloa dubia*) occurred in drier situations of lower elevations on acid soils but extended to the 1830–2130 m elevation belt only on limestone. Another group of species—among them *Asclepias macrotis*, *Fendlerella utahensis*, *Maurandya antirrhinifolia*, *Hymenothrix wrightii*, *Thelesperma longipes*, *Viguiera dentata* at higher elevations, *Mortonia scabrella*, *Parthenium incanum*, *Polygala macradenia*, *Nolina texana* and a number of grasses at lower elevations—were recorded only on limestone, on the north side of the Catalinas. Some of these are known to occur on other soils elsewhere. Most species show only relative restriction to limestone or acid soils; and, as observed for limestone in Europe (Walter 1949) and parent materials in the Siskiyou Mountains (Whittaker 1960), species form a continuous sequence from restriction to one parent material, through varying degrees of relative ‘preference’, to restriction to the other parent material.

Many species occur at higher elevations on limestone than on acid soils. Displacements of distribution in relation to elevation, comparing parent materials, were also observed in the Siskiyou (Whittaker 1960). In the White Mountains of California and Nevada certain species extend to higher elevations on dark parent materials than on the light-coloured dolomitic limestone (Wright & Mooney 1965; Mooney 1966), a displacement in the reverse direction from that observed in the Catalinas. In the White Mountains the communities of both parent materials are very open, and the greater heat absorption of the dark parent material may be responsible for the difference in distribution. In the Santa Catalina Mountains the limestone communities are much more open, with greater exposure of undergrowth plants to sunlight and to effects of atmospheric drought without the protection of a woodland canopy. Microclimatic effects may thus be partly responsible for the distributional shifts and the extent of desert and desert-border species to higher elevations on limestone.

When composite samples for the diorite transect are compared with those of the limestone transect by coefficient of community, it is found that the closest similarity for the

xeric diorite sample (XI-*f*) is with an intermediate (XII-*d*) limestone sample. The similarity expresses the distributional shift of diorite species toward the mesic on limestone and the predominance of other (more distinctively limestone, or desert-border) species in the drier situations on limestone. The limestone vegetation is thus more xeric in species composition as well as in physiognomy.

Life-forms

Life-form data are summarized in terms of numbers of species in samples in Table 3, B. The class of 'Chamaephyte-hemicryptophytes' is used in this area for primarily herbaceous plants which are suffrutescent to near, but above, ground level, and which are thus transitional between surface-deciduous perennial herbs and suffrutescent chamaephytes or semishrubs. Because the samples are based on a single visit to a stand in summer, the records of geophytes and therophytes are incomplete.

There is general consistency of life-form representation in the transect samples and most of the supplementary samples, with hemicryptophytes first, phanerophytes second and suffrutescent plants third. The predominance of hemicryptophytes in species number, combined with dominance in coverage of phanerophytes, is consistent also with other forest and woodland areas of temperate, subhumid climates. The strong representation of suffrutescents is a more distinctive feature of this area with its two rainy seasons and sharing of some suffrutescent species between woodlands and the desert margin. Mean Raunkiaer spectra for the transects (assuming two species each of geophytes and therophytes) are—on diorite Ph 30, Ch 7, Ch-H 12, H 45, G 3, Th 3%, and on limestone Ph 25, Ch 15, Ch-H 8, H 46, G 3, Th 3%. The reduction in phanerophytes and increase in chamaephytes from diorite to limestone is in the same direction as shifts in spectra toward drier environments in this area (Whittaker & Niering 1964, 1965).

The supplementary samples are so arranged as to represent an approximate elevation gradient from high-elevation woodlands through open woodlands and grasslands to desert. The same trends of decreasing phanerophyte and increasing suffrutescent representation may be observed, though with marked differences between communities. These trends may be noted also along the moisture gradient within the transects. A further trend which cannot be shown here is the increase in number of therophytes toward lower elevations, from none or few in some high-elevation forests and woodlands, to several species per sample in grasslands and many in deserts (Whittaker & Niering 1964, 1965).

Geographic relations of floras

Representation of broad areal or distributional types in the samples is given in Table 3 C; the types are defined by Whittaker & Niering (1964, 1965). Madrean species (with greatest extent southward in the Mexican mountains) predominate in the woodland communities along with Southwestern species (mostly with broader distributions from Texas to California and southward). These woodlands are northern representatives of the widespread pine-oak and open oak woodlands of Mexico, though less rich in evergreen oaks and other species than the Mexican woodlands. Rocky Mountain, Western and Temperate (widespread across the United States) species form together a third important fraction of the woodland floras, linking them with other forests and woodlands of the western United States. These groups decline in parallel along the moisture gradient in the two transects. The two transect floras differ in the greater representation of Chihuahuan and Latin American species on limestone.

Rocky Mountain, Western, Temperate and Madrean species decrease toward lower elevations in the supplementary samples (cf. Whittaker & Niering 1964, 1965). Counterbalancing these decreases are increases in Chihuahuan species (extending eastward to Texas and southward into or beyond Chihuahua and Coahuila) and Latin American species (extending into Central America or occurring also in South America). A few Plains species in desert grasslands samples *k-m* indicate weak floristic relation of these with the grasslands of the Middle West. Sample *q*, the *Larrea* desert, departs from some of the elevation trends. Both here and on the south side of the mountains (Whittaker & Niering 1964, 1965) widespread south-western species predominate in samples of this most widespread dominance-type of the south-western deserts. Chihuahuan species are much more numerous in sample *q* from the north side of the range, however, and the *Larrea* desert of the north side may be thought floristically continuous with the extensive *Larrea* communities of the Chihuahuan desert region to the south-east, that of the south side with the *Larrea* desert of the Sonoran region to the south-west.

Location of the Santa Catalina Mountains is such that high-elevation communities represent part of the floristic gradation from Western (U.S.) to Mexican mountain floras, whereas low-elevation communities show the contact or gradation of the two major south-western desert floras, the Sonoran and Chihuahuan. The most marked floristic contrast between the two sides of the range is the increase in Sonoran species toward lower elevations on the south side, but in Chihuahuan species on the north-east side. The contrast is much affected by parent material, however. The deserts and desert grasslands of the south side of the range are, like a large part of the Sonoran desert, on non-calcareous soils; the north-side samples with strong Chihuahuan representation are, like a large part of the desert and mountain vegetation of the Chihuahuan region, on limestone. Regional occurrence of parent materials, and of communities and floras adapted to those parent materials, may have provided evolutionary background for the floristic contrast of adjacent plant communities on different parent materials in the Santa Catalina Mountains.

Contrasts in geographic relations of floras were shown also for serpentine and other parent materials in the Siskiyou Mountains (Whittaker 1960). The limestone vegetation of the Santa Catalina Mountains does not show the concentration of narrow endemism that is conspicuous in many serpentine floras (Whittaker 1954). Another characteristic of some distinctive parent materials, the 'xerothermic' character of their floras, is of doubtful application here. Grassland and pine steppe communities on serpentine, gypsum and limestone in Europe show concentrations of species whose major distributional areas lie to the south (Klika 1933; Suza 1935; Gams 1938; Meusel 1939, 1941; Medwecka-Kornaś 1959; Medwecka-Kornaś, Kornaś & Pawłowski 1966). Differently considered, species which are specialists on limestone or other distinctive parent materials in northern Europe occur on more varied parent materials in the south (Brenner 1930-31; Eklund 1946). The limestone vegetation of the Catalinas contains many species with distributional centres to the south, in the Chihuahuan region; but the acid-soil vegetation is equally rich in occurrence of Sonoran species. No contrast is apparent when mean extents of species southward are compared (by the technique of Whittaker 1954, 1960).

Species-diversities

Species-diversities for vascular plants are given in Table 3, D, first in the form of mean numbers of species per quadrat sample (trees and shrubs in 0.1 ha plus herbs in 25 m²), second in combined species (total number of trees, shrubs and herbs in one or more of

five such samples, excluding additional species recorded outside quadrats). Most of the composite samples have between twenty and thirty species per quadrat. Such values are intermediate for temperate-zone communities the authors have studied—lower than the richest eastern forests (Whittaker 1965) and the rich Sonoran desert of north-facing mountain slopes (Whittaker & Niering 1965), higher than many mountain forests and more arid deserts. Community-types richest in species are the canyon woodland of the limestone transect (XII-*a*) with a good number of riparian plants in its well-lighted canyon bottoms, the desert grasslands of limestone slopes (XV-*m, n*), conspicuously richer than grasslands of a level plain (XIV-*k, l*), and the *Mortonia* scrub of the Mule Mountains (XV-*p*), which is richer than the outliers of this community-type in the Santa Catalina Mountains (XV-*o*).

Species-diversities increase from denser forests toward more open woodlands and grasslands (Whittaker 1960; Whittaker & Niering 1965). The data of Table 3, D, suggest, however, that there is no significant difference in 'alpha' species-diversity between the samples of the diorite and limestone transects, despite the more open structure of the latter vegetation. The two transects are in marked contrast in a different aspect of diversity. 'Alpha' species-diversity refers to the richness in species of a particular community or sample, 'beta' diversity to the degree of floristic differentiation of a community pattern (Whittaker 1960, 1965; MacArthur 1965). 'Beta' diversity, the degree of floristic change from the mesic to the xeric, is much less in the limestone transect than in the diorite transect (or in the granite-gneiss transect of comparable elevations on the south side of the range). The difference may be observed by comparing, for the different transects, percentage similarities (means of values for the three strata) of steps *a* and *f* from the extremes of the topographic moisture gradient. Resulting values are 37.8% for the limestone transect, 8.8% for the woodlands of the diorite transect, 0.9% for the granite-gneiss transect on the south side.

Extent of floristic differentiation along the gradient may also be expressed as half-changes (Whittaker 1960; Whittaker & Niering 1965), and these are 0.92 for the limestone, 2.78 for the diorite and 3.14 for the granite-gneiss transects. Because the floristic differentiation along the gradient is less in the limestone coenocline, the number of species in the transect (comparing all species occurring in one or more of the fifty quadrats as an expression of 'gamma' diversity) is lower than on diorite—112 compared with 142 species. Decreases of beta and gamma diversity of coenoclines (for similar ranges of topographic situations) from continental to maritime climates have been observed (Whittaker 1960; Whittaker & Niering 1965). We cannot, however, suggest a reason for the contrast in beta diversity of the limestone and diorite vegetation in the Santa Catalina Mountains.

CONCLUSION

It is of interest to compare effects of limestone on vegetation with those of serpentine and other distinctive soils. A study of serpentine vegetation (Whittaker 1954) observed that this was characterized by: (1) reduction of plant stature and community structure toward the lower strata; (2) xeromorphic physiognomy, and apparently more xeric species composition; (3) displacement of population distributions in relation to topography toward the mesic, and displacement of elevation distributions in both directions, among species occurring both on serpentine and on other soils; (4) ecotypic adaptation to the chemical conditions of serpentine, as well as more xeromorphic growth habit on serpentine, among species occurring both on serpentine and on other soils; (5) concentration of narrowly

endemic species largely or wholly restricted to serpentine soils; (6) concentration also of species near the margins of their geographic distributions, occurring in a wider range of soils and environments elsewhere but relatively limited to serpentine within the study area; (7) high proportions of species with their widest distributions to the south on serpentine, compared with floras of non-serpentine soil.

Of these characteristics of serpentine vegetation, numbers (1), (2) and (3) apply also to limestone vegetation in the Santa Catalina Mountains. The effects under (3) are of less apparent intensity on limestone, and no case of downward elevation displacement on limestone was observed in the Santa Catalina Mountains. Point (4) needs investigation for limestone, point (5) does not apply to this limestone flora. Points (6) and (7), while they apply to limestone vegetation elsewhere, do not appear in the form of contrast between limestone and other soils in this area.

The physiognomic contrast of limestone and acid-soil vegetation in this area is impressive, as striking as some of the effects of serpentine on vegetation. Observations on physiognomic effects of limestone soil in other areas are varied; they include:

(1) Diverse high-mountain communities of limestone and dolomite, in varying degrees distinct in composition from those on acid soils and in many areas, though not all, more open, barren, or xeric in character than those on other soils (Braun-Blanquet, Pallmann & Bach 1954; Wikus 1960; Ellenberg 1963; McVean 1964; Medwecka-Kornaś *et al.* 1966; Quézel 1967; Mooney, St Andre & Wright 1962).

(2) Open larch and larch-pine forests on limestone in areas of northern spruce forests (Sokolowa 1937; Leontjev 1937).

(3) Beech forests on limestone in Europe, in areas of beech or other forests on other soils. The limestone forests differ in floristic composition from, but may not be in physiognomic contrast with, other forests (Ellenberg 1963; Frehner 1963; Füllerkrug 1967).

(4) Open pine forests on limestone, in contrast with various kinds of forests on other soils in other, probably drier, areas of Europe (Gams 1930; Kaiser 1926; Schmid 1936).

(5) Grasslands on limestone in forest climates of Europe—the chalk and limestone downs of England (Hope-Simpson 1941; Tansley 1965; Anderson 1965; Gimingham, Pritchard & Cormack 1966), and alvar and other grasslands (Vilberg 1929; Turrill 1929; Brenner 1930–31; Klika 1932; Dziubałowski 1926; Meusel 1940; Gams 1938; Albertson 1950; Ellenberg 1963), many of them strongly influenced by grazing and fire.

(6) Oak-hickory forests on limestone *vs* oak-chestnut forests (now oak forests) on acid soils in the eastern United States (Braun 1950; Whittaker 1956).

(7) In drier parts of the eastern deciduous forests cedar glades and barrens (*Juniperus virginiana* in dense stand or in grassland) on limestone (Harper 1926; Erickson, Brenner & Wraight 1942; Quarterman 1950; Braun 1950); and, in the southern area of forest-grassland transition, grassland on limestone contrasted with oak woodland ('cross timbers') on sandstone (Braun 1950).

(8) Diverse and distinctive plant communities on limestone in southern Europe (Braun-Blanquet, Roussine & Nègre 1951; Braun-Blanquet 1964), some of xeric physiognomy relative to communities on other soils, most probably much influenced by man. Representation of Mediterranean flora on limestone among the Atlantic plant communities of western Portugal is observed by Pinto da Silva, Teles & Rozeira (1958).

(9) Contrasts of oak woodland with pine forests, of chaparral with woodland and grassland and of differing desert scrub types, on limestone versus other soils in Mexico (LeSueur 1945; Rzedowski 1960, 1966).

(10) Distinctive communities on limestone in other tropical areas such as the limestone scrub of Madagascar (Poisson 1921) and forests in Cuba (Smith 1954).

A pattern of physiognomic response to limestone in different climates may be suggested: (1) In more humid forest climates soil development permits development of forests on both limestone and acid soils. Floristic composition is in most cases different, and the limestone communities may be more vulnerable to conversion to grassland by man; (2) in marginal forest and woodland climates limestone in most cases supports vegetation which is more open, of lower stature, or both, and a step more xeric in physiognomy—open pine forest, scrub or grassland—and which is quite different in floristic composition and geographic relations from adjacent forests on other soils; (3) in grassland, desert and arctic-alpine climates open communities on acid soils are replaced by different open communities on limestone; the latter are not necessarily of lower coverage or lower stature but are usually the more xeric in physiognomic type and floristic composition.

The principal cause of xeric quality of limestone vegetation may be drying of the soil by drainage of water in cracks and channels of the limestone rock. Floristic composition and species responses to limestone involve much broader problems of ecosystem characteristics (Brenner 1930–31; Lundegårdh 1957), however, including not only direct effects of soil drought but effects of thin and rocky soils, of different nutrient levels and balances and their relations to soil moisture (Lloyd & Pigott 1967; Grime & Hutchinson 1967), different microclimates, different competitive and interference relations among species, and in some cases, differential effects of grazing and fire. It may be precarious to link these diverse, interrelated factors and the varied characteristics of limestone vegetation as causes and effects with the evidence available. Physiognomic differences of limestone from acid-soil vegetation may be thought, however, much affected by contrast of soil moisture conditions, the distributional shifts of species populations between parent materials by combinations of soil moisture factors with microclimatic effects of physiognomic difference, and floristic differences in the sense of presence and absence of species on different parent materials by differences in soil chemistry combined with competitive and interference relations.

It has been said that limestones and other distinctive parent materials cease to have effect on plant communities with the development of mature soils and climax vegetation (Daubenmire 1947). The effect of soil development, however, is to reduce, not to nullify, the difference of moisture availability and chemical character of soils formed on limestone and acid parent materials. The limestone vegetation of the Santa Catalina Mountains is considered climax in the sense of mature and steady-state condition in relation to its environment. With one exception—some indication of conversion of desert grassland into *Fouquieria* scrub with grazing—no evidence of successional alteration was found for the limestone communities described here. Evidence from the Santa Catalina Mountains and from the occurrence of limestone vegetation in other areas suggests that limestone, like other distinctive parent materials (Whittaker 1953, 1960), supports vegetation which is normally different in floristic composition, is often in physiognomic contrast, and in some cases forms climax patterns as distinctive in relation to the vegetation of acid soils as the *Cercocarpus* scrub and Chihuahuan desert complex of southern Arizona.

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SUMMARY

Vegetation of limestone and acid soils was compared by means of detailed transect studies in the 1830–2130 m elevation belt and more limited vegetation samples from other elevations. In the transects an open scrub of *Cercocarpus breviflorus* on limestone contrasted with pine-oak woodlands on diorite; at lower elevations Chihuahuan desert communities on limestone contrasted with grassland and with other desert types on acid soils. In general, the limestone vegetation shows: (1) more open and xeromorphic physiognomy, (2) distributional displacements of species populations in relation to elevation and topography, (3) different and more xeric species composition, (4) similar life-form composition and species diversity, in this area, (5) different geographic affinities, with strong representation of Chihuahuan species. The limestone vegetation is regarded as climax and as forming landscape patterns as stable as, but conspicuously in contrast with, those on other soils. Contrasts of limestone vegetation with that on other soils may be most striking in areas of marginal forest and woodland climates.

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