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VEGETATION OF THE SANTA CATALINA MOUNTAINS, ARIZONA.
V. BIOMASS, PRODUCTION, AND DIVERSITY ALONG THE ELEVATION GRADIENT[1]

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Abstract. Measurements were taken in 15 communities along the elevation gradient from fir forest at high elevations, through pine forest, woodlands, and desert grassland, to deserts at low elevations in the Santa Catalina Mountains, Arizona, and in a *Cercocarpus* shrubland on limestone. Eight small-tree and shrub species of woodlands and deserts were subjected to dimension analysis by the Brookhaven system. Aboveground biomass decreased along the elevation gradient from 36–79 dry kg/m^2 in fir and Douglas-fir forest to 0.26–0.43 kg/m^2 in the desert grassland and two desert samples. Net aboveground primary productivity similarly decreased from 1,050–1,150 g/m^2 · yr in mesic high-elevation forests to 92–140 g/m^2 · yr in desert grassland and deserts. Both biomass and production show a two-slope relation to elevation (and, probably, to precipitation), with a steeper decrease from the high-elevation forests to the mid-elevation woodlands, and a less steep decrease from dry woodlands through desert grassland into desert. The two groups of communities at higher vs. lower elevations also show different relations of leaf area index and chlorophyll to elevation and to productivity. The two groups may represent different adaptive patterns: surface-limiting, with low productivity in relation to precipitation but high production efficiency in relation to surface in the more arid lower elevations, vs. surface-abundant, with high productivity relative to precipitation based on high community surface area, but lower production efficiency in relation to this area, in the more humid higher elevations. Vascular plant species diversity shows no simple relation to productivity, but decreases from high-elevation fir forests to the pine forests, increases from these to the open woodlands, and decreases from dry woodlands through the desert grassland and mountain slope desert to the lower bajada (creosotebush) desert.

Key words: Arizona; biomass; desert; diversity; elevation; forest; grassland; productivity; Santa Catalina Mountains; woodland.

INTRODUCTION

The Santa Catalina Mountains are a range with strong Mexican affinities, northeast of the city of Tucson in southeastern Arizona. The south slope of the range bears an uninterrupted vegetational gradient from subalpine forest through woodlands and grasslands to desert. This gradient, described by Shreve (1915) and Whittaker and Niering (1964, 1965) is unique in the Southwest for its wide range of communities on largely consistent parent materials (Catalina gneiss and granite, and the bajada materials derived from these). On the north side of the mountains a vegetation pattern from fir forest to desert grassland occurs on a more complex mosaic of parent materials and includes distinctive communities on limestone among which mountain mahogany (*Cercocarpus breviflorus*) shrubland is most extensive (Whittaker and Niering 1968a, b). For this study production samples were taken in 14 climax vegetation types on the south slope of the range, and in a successional stand of aspen and a *Cercocarpus* scrub

on limestone. Some major species of the woodlands and deserts were subjected to dimension analysis by the Brookhaven system (Whittaker and Woodwell 1968, 1969, 1971). Primary purposes of the study were (1) to obtain measurements of aboveground net primary productivity and biomass for kinds of communities—woodlands and semideserts especially —for which few data are available, and (2) to observe interrelations of biomass, production, leaf area and chlorophyll, and species diversity along the extended physiognomic gradient from fir forest to desert.

BASIS OF THE STUDY

The elevation gradient

Elevations range from 2,766 m at the summit of Mt. Lemmon to 850–980 m at the southwestern base of the range near Tucson, and down the desert plain or bajada to 730 m at Tucson. The gradient of vegetation extends from subalpine fir forests near the summit of Mt. Lemmon through montane fir forest and pine forest, pine–oak forest, pine–oak woodland, pygmy conifer–oak scrub, open oak wood-
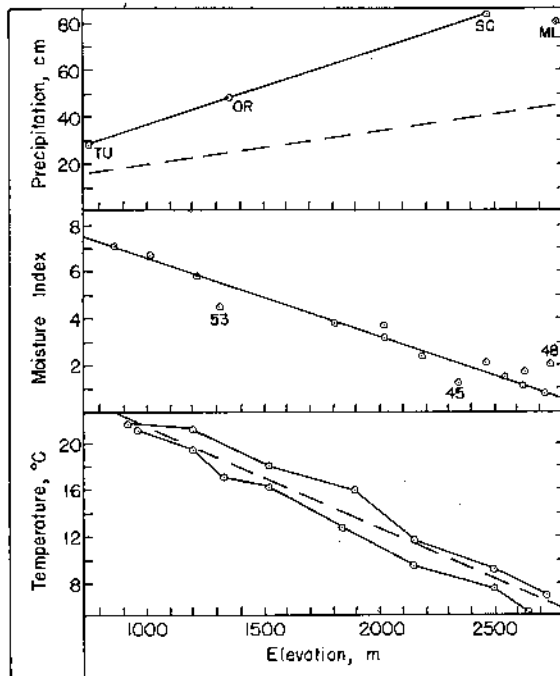
FIG. 1.   Elevation and climate, Santa Catalina Mountains.

Top: Mean annual precipitation in cm at four stations: Tucson (TU) and Oracle (OR) (Sellers 1960, McDonald 1956), Soldiers Camp (SC) (6-yr record, Mallery 1936), and Mt. Lemmon (ML) (3-yr record, Weather Bureau 1952–54). The solid line is a trend ($y = 3.0 + 34.2x$, with x in 1,000 m) for the first three points. The dashed line is the trend line for mean daily precipitation in mm/day times 100, from the network of rain gauges of Battan and Green (1971); these values times 1.8 approximate the slope for year-round precipitation.

Middle: Weighted-average moisture indices for the vegetation samples of this study. Three stations lie off the trend line ($y = 10 - 3.4x$, with x in 1,000 m) because of topographic position—48 (a summit SSW-slope), 45 (ravine), and 53 (a lower NNW-slope).

Bottom: Mean annual soil temperatures at 20-cm depth on south-facing slopes on the south side of the range (upper series) and north-facing slopes on the north side of the range (lower series), from Whittaker et al. (1968). The regression line is $y = 30.42 - 8.90x$, with x in 1,000 m. Short-term data of Shreve (1915) gave a mean decrease of 7.5°C per 1,000 m elevation.

land, and desert grassland to spinose–suffrutescent Sonoran semidesert on the mountain slopes, while on the desert plain or bajada below the mountains the desert gradation continues through the paloverde–bursage semidesert to the creosotebush desert of the lower bajada.

Changes in climate with elevation in the Santa Catalina Mountains were described by Shreve (1915), and available climatic data were summarized by Whittaker and Niering (1965). Changes in soils with elevation were described for the Catalinas by Whit-

taker et al. (1968) and for the nearby Pinaleno Mountains by Martin and Fletcher (1943). The top panel of Fig. 1 shows together the mean annual precipitation in four weather stations at different elevations, and a trend line for summer precipitation in a network of rain gauges. The data are not compelling, but suggest a linear increase in precipitation from 730 to 2,400 m elevation. Because the production samples were taken from different kinds of topographic positions, elevation is only a crude expression of their probable moisture relationships. A moisture index providing a better expression of these relationships was based on the intensive study of species distributions by Whittaker and Niering (1964, 1965). Plant species were classified by their relations to the moisture gradient in topographic transects for elevation belts from 0 (most mesic and highest elevation) to 8 (most xeric and lowest elevation). These species classes, or ecological groups, are applied as weights to the composition of vegetation samples to obtain weighted-average indices of the relative positions of samples along the gradient (Whittaker and Niering 1965). Index values for the production samples are given in Table 1-B and are plotted in relation to elevation in the middle panel of Fig. 1, where they show a linear trend.

The bottom panel of Fig. 1 gives the trend of mean annual soil temperatures at 20 cm depth, measured at 2-wk intervals from September 1962 to August 1963. At 10 of the stations, 5 pairs on each side of the range between 1,200 and 2,140 m, mean annual soil temperatures were obtained for both north-facing and south-facing slopes; the latter averaged 3.35°C warmer (Whittaker et al. 1968). Mean monthly temperatures for January and July, and mean annual temperatures, are 10.0°, 30.1°, and 19.6°C at Tucson, 7.7°, 26.5°, and 16.7°C at Oracle (1,370 m elevation) (Sellers 1960). Soil trends from high elevation to low included decreasing litter cover and organic content of soils, decreasing nitrogen content and carbon : nitrogen ratios, increasing pH, and increasing contents of Ca, Mg, and K (Whittaker et al. 1968). Although elevation is a complex-gradient of many climatic and edaphic factors, moisture conditions are considered the principal variable affecting vegetation structure and productivity along the gradient from fir forest to desert. Community characteristics are plotted in relation to both elevation and the moisture index in some of the figures that follow.

Communities sampled

Elevations, topographic positions, and other characteristics of the samples are summarized in Table 1. Samples 44–57 were taken to represent the major kinds of communities along the elevation gradient on the south slope of the mountains. Samples 44–55

TABLE 1. Summarized characteristics of productivity samples, Santa Catalina Mountains

Sample number and characteristic	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Forest/vegetation type	*Abies lasiocarpa* subalpine forest	*Abies concolor* ravine forest	*Pseudotsuga menziesii*–*Abies concolor* forest	*Pseudotsuga menziesii* forest	*Pinus ponderosa*–*Pinus strobiformis* forest	*Pinus ponderosa* forest	*Pinus ponderosa*–*Quercus hypoleucoides* forest	*Pinus chihuahuana*–*Quercus arizonica* woodland	Pygmy conifer–oak scrub	Open oak woodland	*Bouteloua curtipendula* desert grassland	Spinose-suffrutescent desert scrub	*Cercidium microphyllum*–*Franseria deltoidea* desert scrub	*Larrea divaricata* desert scrub	*Cercocarpus breviflorus* shrubland	*Populus tremuloides* successional forest
A. Sample number	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
B. Environment [a]																
Elevation (m)	2,720	2,340	2,640	2,650	2,740	2,470	2,180	2,040	2,040	1,310	1,220	1,020	870	760	1,810	2,550
Exposure	NNE	Rav.	NW	NNW	SSW	WSW	SW	SSE	W	NNW	SSW	SSE	SSE	W	ESE	E
Inclination (degrees)	25	27	27	29	11	8	15	17	13	26	27	22	3	4	33	27
Moisture index [b]	0.89	1.26	1.07	1.82	2.05	2.16	2.54	3.16	3.67	4.52	5.80	6.76	7.03	7.50	3.74	1.46
C. Cover and light																
Individual-point cover (%)																
Conifers	90	76	80	114	104	100	74	32	6	8						34
Broadleaf trees	10	44	2				42	54	4	34	6	20	19		33	74
Shrubs	8	18	8	6				6	52	32	30	16	15	13	42	14
Herbs	<1	4	6	<1	10	10	2	4		4 [d]	40	9	<1	<1		6
Thallophytes		4							4			18 [c]				
Rock		10								10	7	6	5			
Light penetration (%)																
Through trees	7.3	12.8	5.6	4.5	37.9	21.5	41.1	42.7	91.2	95	98	88.2	87.9	85.5	81.5	17.2
shrubs and seedlings [d]	7.2	12.6	5.1	4.3	34.4	20.6	36.8	34.2	25.5			76.7	62.4	85.5	49.7	15.8
herbs	7.2	9.7	4.7	4.3	32.1	19.9	36.3	34.0	25.4	32.4 [d]	32.8	73.5	62.4			15.5
Log light absorption	1.141	1.013	1.341	1.361	.693	.702	.441	.468	.430	.285	.484	.135	.205	.068	.293	.802
Leaf area index (m²/m²)	14.7	15.5	16.7	15.5	7.6	5.9	4.7	3.7	2.0	1.76	1.58	.94	.59	.60	1.40	6.4
Chlorophyll (g/m²)	5.8	6.2	7.0	6.1	2.0	1.7	1.8	1.8	1.0	.80	.75	.50	.34	.34	.85	3.0
D. Stand characteristics																
Stems/0.1 ha, [e] trees	59	151	40	34	270	110	128	278	57	19	2	387 [f]	146 [f]	4,950 [e]	393	235
shrubs	16		87	38				1	16		64					71
Basal area (m²/ha), [e] trees	57.8	58.6	118.1	70.5	39.4	46.3	34.9	26.0	4.32	4.01	.01	10.9	2.96	4.15 [e]	2.68	31.6
shrubs	.3		1.4	.26				.02	.58		.21					.38
Bark/stem basal area (%)	13.4	20.7	23.2	23.7	24.8	27.7	24.6	21.2	19.2	22.3						15.2
Weighted mean height (m)	33.5	25.5	27.9	27.6	12.8	18.4	15.2	7.5	2.7	5.3	2.5	3.4	3.1	1.7	3.7	16.1
Conic stem surface (m²/m²)	.78	.59	.72	.58	.36	.41	.30	.19	.02	.02	.0045			.09	.05	.51
Parabolic stem volume (m³/ha)	837	746	1666	980	253	425	265	98	6.6	10.7	.28	18.5	4.5	3.5	5.0	218
Mean radial increment (mm/yr)	.78	1.06	.95	.61	.59	.52	.38	.38	.28	.36						1.14
Basal area increment	.416	.530	.499	.243	.373	.275	.187	.238	.044	.026						.885
Estimated volume increment (cm³/m²·yr)	567	563	593	311	183	180	100	66	5.5	6.3						539
Weighted mean age (yr)	106	124	321	252	93	142	150	101	115	117						34

a Soils data are given in Whittaker et al. (1968, Tables I and II).
b Weighted-average index of Whittaker and Niering (1964, 1965); high values are xeric.
c *Selaginella*.
d Below stratum of shrubs and tree seedlings. In samples 53 and 54 the principal shrubs (*Agave schottii*, *Calliandra eriophylla*) are part of the herb stratum; penetration was consequently measured for the combined herb-shrub stratum.
e Stems over 1 cm at breast height (except sample 57, all stems at 10 cm above ground level).
f Arborescent shrubs and small trees together.

and sample 59 are all on the Catalina granite–gneiss soils; samples 56 and 57 are on coarse upper, and fine lower bajada deposits derived from the granite-gneiss slopes of the Catalinas. Data on soils of the samples are given by Whittaker et al. (1968); further information on species composition characteristic of the types of communities is given by Whittaker and Niering (1964, 1965). Probably all vegetation above the desert has been subject to ground-fires, at least, in the past. Two of the forest samples (44 and 48) may have less than climax biomass because of past crown fires, and one sample (59) was a successional stand of aspen *(Populus tremuloides)* resulting from a fire. The range has been subject also to grazing by cattle; but the south slope, where it is ascended by the Mt. Lemmon highway, has been protected against grazing since 1947. All the production samples are considered to represent climax or near-climax communities except for the aspen stand. In this statement "climax" does not refer to climatic climax in the sense of Clements (1936), but to steady-state natural communities that are self-maintaining in their particular climatic, topographic, and edaphic environments, and that are generally characterized by near-equality of gross primary productivity and total community respiration and by maximum bio-mass for successions in their particular environments (Whittaker 1953, 1974). Lightning-induced fires are part of the natural environment of all commu-nities between the deserts and the fir forests (Whit-taker and Niering 1965), and we believe that past grazing has not caused significant present departure from the climax condition in these communities. The samples were taken along the Mt. Lemmon highway or on the upper slopes of Mt. Lemmon, unless otherwise indicated.

Subalpine fir forest (sample 44).—*Abies lasiocarpa* is strongly dominant, making up 85% of stem volume in the sample, with *Pseudotsuga menziesii* as second species with 10% of volume. The undergrowth is very sparse; *Jamesia americana* was the principal shrub, *Pyrola virens* and *P. secunda* the principal herbs. The bulk of the trees were in size classes 25–50 cm dbh (and 100–130 yr of age), and there were few young trees. The stand occupies a limited area of convex, north-facing slope shortly below the summit of Mt. Lemmon.

Mesic ravine fir forest (sample 45).—This sample, in Marshall Gulch, is dominated by *Abies concolor* and *P. menziesii* (55% and 20% of volume), with several per-cent volume each for *Pinus strobiformis, Acer grandi-dentatum,* and *Alnus obtusa. Rubus neomexicanus* and *Symphoricarpus oreophilus* are the principal shrubs, *Glyceria elata, Pteridium aquilinum,* and *Bromus richard-sonii* the major species in a rich herb stratum. Ages of trees were mostly 50–145 yr at breast height; it is likely that the largest and oldest trees were cut from the stand some time in the past.

North-slope, montane fir forest (sample 46).—*Pseudo-tsuga menziesii* is dominant (79% of volume), with *A.*

concolor as second species (17%). The canopy trees were 90–150 cm dbh, 25–45 m tall, and 150–190 yr old at breast height. The undergrowth is sparse, though not so meager as in sample 44; *S. oreophilus* is the principal shrub, *Thalictrum fendleri* and *B. richardsonii* the prin-cipal herbs.

Drier montane fir forest (sample 47).—*Pseudotsuga menziesii* is dominant (88%) with *A. concolor* (7%) and *Pinus strobiformis* (5%); the canopy trees were 50–95 cm dbh, 25–37 m tall, and 200–250 yr old. *Jamesia americana* is the principal shrub, *B. richardsonii* and *Carex* sp. the principal species in the meager herb stratum.

High-elevation pine forest (sample 48).—*Pinus pon-derosa* makes up 68% and *P. strobiformis* 32% of stand volume; *P. menziesii* is present in the stand. There are few shrubs, but *Muhlenbergia virescens* and *Pteridium aquilinum* are the major species in an herb stratum of fair coverage (10%). Canopy stems were 25–50 cm dbh, 12–17 m tall, and 70–120 yr old; and in contrast to sample 44 the stand includes many younger trees. Maximum ages of trees suggest these may have replaced a forest destroyed by fire somewhat more than 130 yr ago.

Lower elevation pine forest (sample 49).—*Pinus pon-derosa* is strongly dominant (99% of volume vs. 1% for *P. strobiformis*); the canopy trees were 40–60 cm dbh, 15–25 m tall, and 100–180 yr old at breast height. Undergrowth composition resembled that of sample 48.

Pine–oak forest (sample 50).—*Pinus ponderosa* makes up 95% of stand volume, *Q. hypoleucoides* 4%, and *Arbutus arizonica* less than 1%. The canopy pines were 25–45 cm dbh, 15–20 m tall, and 120–170 yr old; a few larger pines are present. The oaks *(Quercus hypo-leucoides)* form a small-tree stratum beneath the pine canopy; the larger oaks were 10–25 cm dbh, 4.5–7.0 m tall, and 30–50 yr old. The undergrowth is sparse, with *Rhamnus californica* the principal shrub, *M. virescens* and *Commandra pallida* the principal herbs.

Pine–oak woodland (sample 51).—The stand is smaller and more open than the preceding, with dominance shared among two pine and two oak species—*Pinus chihuahuana* 45%, *P. ponderosa* 10%, *Q. hypoleucoides* 25%, *Q. arizonica* 18% of volume; *A. arizonica* and *Juniperus deppeana* are present. The rosette shrubs *Yucca schottii* and *Nolina microcarpa* and the sclerophyll *Arctostaphylos pungens* are the principal shrub species; *Muhlenbergia emersleyi* is strongly dominant in the herb stratum. The canopy pines were 25–40 cm dbh, 9–15 m tall, and 100–150 yr old; the oaks 10–20 cm dbh, 3–6 m tall, and 30–50 yr old.

Pygmy conifer–oak scrub (sample 52).—This physi-ognomically distinctive community has a very open stratum of *Pinus cembroides* (Mexican pinyon pine, 69% of volume), *Juniperus deppeana* (alligator juniper, 16%), and *Q. hypoleucoides* (silverleaf oak, 4%) above a denser but still open stratum of sclerophyll shrubs *(Arctostaphylos pringlei, A. pungens, Garrya wrightii)* and rosette shrubs *(Y. schottii, N. microcarpa, Agave palmeri,* and *Dasylirion wheeleri).* The trees are small; the "canopy" trees were mostly 12–20 cm dbh, 2–4 m tall, and 70–120 yr old (but some individual junipers were more than 200 yr old). Basal area and stem volume are in a range appropriate to a shrub community (cf. Whittaker 1963), and the radial wood increments of

the trees are lower than in any other forest or woodland sampled. Herb coverage is very low, with *M. emersleyi* the principal species.

Open oak woodland (sample 53).—Scattered evergreen oaks are of low coverage (8%) and small volume (56% in *Q. oblongifolia*, 44% in *Q. emoryi*), above shrub and herb strata of moderate coverage. The larger oaks were 25–35 cm dbh, and 5–7 m tall; their ages could not be read. The principal shrub species are *G. wrightii*, *Selloa glutinosa*, *Dalea pulchra*, *Baccharis thesioides*, and the rosette shrubs *N. microcarpa*, *Y. schottii*, and *Dasylirion wheeleri*; cacti (*Opuntia phaeacantha* and *O. spinosior*) first appear as a significant part of the shrub stratum in this sample. The herb stratum is strongly dominated by a low rosette shrub (*Agave schottii*) that from a distance appears to be part of the grass cover; the other principal species of the herb stratum are the grasses *M. emersleyi*, *Andropogon cirratus*, *Bouteloua curtipendula*, and *Aristida orcuttiana*, the xeric fern *Bommeria hispida*, and *Gnaphalium wrightii*.

Desert grassland (sample 54).—*Fouquieria splendens* contributed the small basal area and volume of the "tree" stratum; *Prosopis juliflora* and *Vauquelinia californica* were present on the slope. The principal shrubs were *Calliandra eriophylla*, *Carlowrightia arizonica*, *Haplopappus laricifolius*, and *Jatropha cardiophylla*. *Bouteloua curtipendula* was the dominant grass, with *B. filiformis*, *Aristida ternipes*, *Heteropogon contortus*, *Trichachne californica*, and *Muhlenbergia porteri* other principal herb species.

Spinose-suffrutescent Sonoran semidesert of the lower mountain slopes (sample 55).—In the complex physiognomy of this type the open "canopy" is formed by spinose trees and arborescent spinose shrubs—*Carnegiea gigantea* (giant cactus or saguaro), *Cercidium microphyllum* (paloverde), *Fouquieria splendens* (ocotillo), and *Prosopis juliflora* (mesquite). With these occur lower spinose shrubs (*Acacia greggii*, *Opuntia phaeacantha*, and other cacti), low shrubs of which *Encelia farinosa* (brittlebush) and *Calliandra eriophylla* are most important, perennial forbs (*Boerhaavia gracillima*, *Euphorbia melanadenia*, and *Allionia incarnata*), and grasses (*Muhlenbergia porteri* and *Aristida ternipes*). Annual herbs also are conspicuous during rainy seasons. Community structure and dynamics are further described by Niering et al. (1963).

Paloverde-bursage (Cercidium microphyllum–Franseria deltoidea) *semidesert of the upper bajada (sample 56), sampled near Campbell Avenue, Tucson.*—The two dominants form distinct strata, 2–4 m and about 0.3 m tall; other major species are *Fouquieria splendens*, *Opuntia phaeacantha* and *O. fulgida*, *Mammilaria microcarpa* and *Echinocereus fendleri*, *Jatropha cardiophylla* and *Janusia gracilis*, and *Calliandra eriophylla* and *Carlowrightia arizonica*. Herb coverage was very low, with *Bouteloua aristidoides* the principal species.

Creosotebush (Larrea divaricata) *desert of the lower bajada (sample 57), sampled near the Tanque Verde-Sabino Canyon Road near Tucson.*—*Larrea* was more strongly dominant than in many creosotebush deserts (cf. Rickard 1963, Lowe 1964, Shreve 1964); the stands below the Catalinas lack *Franseria dumosa*. Density of the *Larrea* shrubs (205/0.1 ha) was near the high extreme for creosotebush desert; for other stands (with *Larrea* in most cases mixed with other species) Woodell

et al. (1969) gave a *Larrea* density range of 6–54/0.1 ha and Barbour (1969) 3–187/0.1 ha. Small coverage was contributed by *Ephedra nevadensis* and the semishrubs *Psilostrophe cooperi* and *Zinnia pumila*. Herb coverage in this stand, which had probably been grazed in the past, was minute.

Mountain mahogany (Cercocarpus breviflorus) *scrub on limestone (sample 58), sampled on Marble Mountain above the Oracle Road on the north slope of the Santa Catalina Mountains.*—The shrubs form an open cover (33%), 1.5–2.5 m tall, above a well-developed grass and forb layer. The community thus resembles a woodland in miniature, and on limestone replaces the oak and pine–oak woodlands of corresponding elevations and topographic positions on acid rocks (Whittaker and Niering 1968*a*, *b*). Shrubs other than the dominant *Cercocarpus* include *N. microcarpa*, *A. palmeri*, *G. wrightii*, and *Sphaeralcea fendleri*. In the herb stratum *B. curtipendula* is dominant; other species are *Viguiera dentata*, *Hymenothrix wrightii*, and *Verbena neomexicanus*.

Successional aspen (Populus tremuloides) *forest (sample 59).*—Trees other than *Populus* (which has 72% of stem volume) are *Robinia neomexicana* (7.5%), *Salix scouleri* (6.5%), and young *Pseudotsuga menziesii* (10%) and *A. concolor* (2.5%). The *Populus* were mostly 15–25 cm dbh, 12–18 m tall, and 36–65 yr old. *Jamesia americana* is the principal shrub species, *Pteridium aquilinum* and *Bromus richardsonii* the principal herb species. The stand is assumed to have replaced a fir forest following fire, and to be developing toward climax composition similar to that of sample 47.

Species subjected to dimension analysis

The Brookhaven system of dimension analysis (Whittaker and Woodwell 1968, 1971) was applied to eight of the major woody species of the woodlands, semideserts, and creosotebush desert.

Quercus hypoleucoides (silverleaf oak) is an evergreen oak with *Salix*-like leaves of upper-middle elevation woodlands. This, along with other evergreen oaks of the range, is a small tree species with relatively heavy branches; few of the stems exceed 15 cm dbh and 5–6 m, very few reach 30 cm dbh and 8–9 m height. Most twigs bear current and 1-yr-old leaves, and few 2-yr-old leaves; the estimate of older leaf growth of 10.4% of aboveground net production was based on increase in mean dry weight of 1-yr-old leaves compared with current (midsummer) leaves on the sample trees. Wood rings of the oaks are interpretable at higher elevations (the trees were from sample 50), but are increasingly difficult toward lower elevations.

Pinus cembroides (Mexican pinyon pine) is on the whole a smaller tree than the oak, growing in somewhat drier environments. The pinyons are irregular in form, with heavy branches; very few of them exceeded 15 cm dbh and 3–4 m height. Needles are persistent for 5–6 or rarely 7 yr; as in *Q. hypoleucoides*, older leaf growth was inferred from the curve of increased needle weight from current to 1- and 2-yr-old leaves. The wood rings are fairly clear, but light false rings alternating with darker true annual rings are frequent.

Cercocarpus breviflorus (mountain mahogany) is a deciduous, arborescent shrub that in this area occurs

primarily on limestone. The shrubs analyzed, taken from sample 58, ranged 1.6–5.2 cm dbh, up to 4.0 m in height.

Arctostaphylos pringlei and *A. pungens* are evergreen manzanitas with thick, sclerophyllous leaves; both contrast with the preceding three species in having very thin bark. *Arctostaphylos pringlei* is arborescent and similar to *Cercocarpus* in size; both *Arctostaphylos*, however, tend to have several stems from a common root crown, the *Cercocarpus* a single main stem per shrub. Basal diameters of the sample shoots of *A. pringlei* were 2.4–7.4 cm, heights 0.8–1.9 m; those for *A. pungens* were 1.3–3.1 cm, and 0.5–1.1 m. In both species many of the stems of older shoots are partly dead; in some only a strip of living bark and wood runs up one side of the stem. High dispersions from the regression equations for these species result from the variable fractions of living stem and branch wood supporting live foliage, in shoots of a given size.

Cercidium microphyllum (paloverde) is a many-stemmed, arborescent, leguminous desert shrub with compound leaves of minute leaflets; the leaves are produced in, and shed between, the rainy seasons. The bark is green, with stomata and a palisade-like chlorenchyma (Scott 1935); and the large area of bark was found to photosynthesize an amount comparable to that of the leaves in *Cercidium floridum* (Adams et al. 1967, Adams and Strain 1969). The seasonal timing of leaf production and radial stem growth are largely independent (Turner 1963). The twigs are tapered green spines, and branching occurs as new such spiny twigs are formed. In manner of growth the whole shrub is thus a multiply-branched and compounded spine. Because the shrub is branched to near ground level, branches cut near ground level were taken as "shoots" for dimension analysis, and the basal diameters of the short main stem and of the branches from it were measured instead of diameter at breast height. Mature shrubs in the spinose–suffrutescent desert (sample 55) from which the analysis plants were taken and the paloverde–bursage desert (56) had basal diameters of 10–25 cm, heights of 2.0–3.5 m. Wood rings of *Cercidium* and other desert shrubs are interpretable (Shreve 1911), but often not with assurance.

Larrea divaricata (creosotebush) is the most important plant species of the North American warm deserts. Numerous slender stems rise from the root crown; their branches end in green twigs bearing bifid, evergreen leaves that lack spongy tissue but are not otherwise evidently xeromorphic (Runyon 1934). As the twig elongates, several pairs of leaflets are produced in a year's growth. The ratio of fruit to current twig and leaf production in a Mojave desert was 0.154 (Soholt 1973). The plant is evergreen and has been shown to be continuously photosynthetic at a low rate during dry seasons (Strain and Chase 1966, Strain 1969, Oechel et al. 1972). During severe drought some, but not all, leaves are shed and some shoots die back to ground level. The stems in the sample ranged up to 2 cm, and a few to 3 cm in diameter at 10 cm above ground level; shrub heights were mostly 0.5–1.5 m, a few to 2.3 m. The wood rings were interpreted as annual; on the basis of them the shrubs in this sample add 7–10 leaf-nodes to the stem axis per year. Despite its remarkable adaptation to desert climates, creosotebush is unremarkable in its dry weight and growth distributions and other relationships in Table 2.

Fouquieria splendens (ocotillo) consists aboveground of numerous (usually 5–20) long, nearly cylindrical, spine-armed wands that extend in varied directions and angles to the horizontal from the root crown at the ground surface. The stems taper gradually from basal diameters and ages of 2.0–2.5 cm and 20–25 yr in older stems, to 0.5–0.7 cm in current twigs. The stems sampled from the spinose–suffrutescent desert (sample 55) were 0.6–3.6 m long; some longer and taller stems (over 4 m) occur in the desert grassland (sample 54). During the rains soft, ephemeral leaves 1–2 cm long are put out along much or the whole length of the stem; the leaves are lost when the rains end (Cannon 1905). Two or three sets of leaves may thus be produced in a year; the leaf production in Table 2 assumes annual leaf production twice that sampled in the summer rainy season. Annual segments are clearly defined in all but the oldest stems and can be clearly related to wood rings. The bark includes a thick chlorenchyma (Scott 1932), and bark dry weight and growth exceed wood dry weight and growth in all but the old stems. The bark chlorenchyma is photosynthetic during favorable periods, apparently not during drought (Mooney and Strain 1964). Assuming no branches (though a few stems of *F. splendens* are branched) and two leaf growths per year, then stem wood, stem bark, and leaves each include about one-third of aboveground growth with a smaller, unmeasured fraction in flowers and fruits.

Two of the desert low shrubs or semishrubs, *Encelia farinosa* (brittlebush) and *Franseria deltoidea* (bursage), were sampled on a less intensive basis. Fifteen individual shrubs were obtained with root crowns, and the aboveground shoots were treated as sample branches. Both species average about 0.3 m tall in the spinose–suffrutescent desert (sample 55) from which *Encelia* was taken, and the paloverde–bursage desert (56) from which *Franseria* was taken. Drought adaptation of *Encelia* is discussed by Shreve (1964), Strain and Chase (1966), Cunningham and Strain (1969a), and Strain (1969); the species is able to increase light utilization for photosynthesis up to the highest light intensities (Cunningham and Strain 1969b). The analyses of these shrubs suggest that the ratio of "branch" growth (of aboveground perennial wood and bark) to "clipping" growth (of current twigs with leaves) is about 25:75% in *Encelia* and 21:79% in *Franseria*.

Measurement and estimation techniques

The production samples were based on the 0.1-ha quadrats used also by Whittaker (1963, 1966) and Whittaker and Woodwell (1969). In each stand all trees were measured and recorded by diameter at breast height and species and all shrubs were tallied by species in a rectangle 10 m on each side of a 50-m tape. Heights were measured and increment borings taken from all trees or (in the denser forest stands) all trees above 30 cm dbh and some of the trees, as samples by size classes, below that diameter. Woody stems over 1.5 cm dbh including those of arborescent shrubs were tallied with the trees; those under 1.5 cm dbh were tallied and clipped as shrubs. The arborescent shrubs of the semideserts were treated as trees, and heights and diameters were measured for the larger cacti (*Carnegiea, Opuntia,*

Ferocactus). Undergrowth clippings were taken from twenty 0.5×2.0 m subquadrats, random numbers of meters out from points at 5-m intervals along the central tape. The aboveground growth of herbs, and current twigs with leaves of shrubs, were clipped in the subquadrats, bagged by species, and weighed fresh and ovendry. Minor herb and shrub species missed in the subquadrats were clipped in the full 0.1-ha quadrat. In the low-elevation stands clippings were taken of both summer herbs and shrub growth (1964) and spring herbs (1965). Light penetration through the tree, shrub, and herb strata was measured at 50 points along the central tape with a Weston sunlight illuminometer, and plant-individual point coverage was recorded for these sample points. In the nonforest samples light penetration and coverage were read also along the 50-m borders of the quadrats, hence for 150 points in all. We adapted the sample to the creosotebush desert by measuring diameters, heights, and numbers of stems for the shrubs in the 0.1 ha, and measuring stem diameters at 10 cm above ground level for all shoots of 20 random shrubs within the plot.

The eight woody species of the woodlands and deserts just described were subjected to intensive aboveground dimension analysis by the procedures of Whittaker (1961, 1962) and Whittaker and Woodwell (1968). Trees of two species (*Quercus hypoleucoides* and *Pinus cembroides*) were felled, and a tape was laid along the stem from apex to base. Branches were tallied from the tip downward by age and basal diameter, and five sample branches per tree were taken for more detailed measurement of length, current twig number, and fresh and dry weights of live wood and bark, deadwood and bark, current twigs with leaves, older leaves by ages, and fruits. The stems were cut into segments or logs, and for each of these length, diameters, bark thickness, and fresh weight were recorded, and a 10-cm basal disc was taken for measurement of fresh and dry weight of wood and of bark, wood mean diameter and bark mean thickness, age, and mean radial wood increment for the last 10 or the last 5 yr. The shoots of shrubs were treated in the same way, except that in the smaller shrubs stem segments were weighed fresh and dry and used for the measurements obtained from discs of the trees. Fruits were collected from all branches of a given plant, as well as the sample branches; and special twig samples were taken for measurement of leaf weights, areas, and chlorophyll content, and dry weight distribution between twigs, petioles, and leaf blades. The dimension analysis samples normally included 15 shoots of each species, but 10 each were taken from *Arctostaphylos pringlei* and *A. pungens*.

The data from these sample plants were submitted to the computer program for dimension analysis developed at Brookhaven National Laboratory (Whittaker and Woodwell 1968, 1969, 1971). Regressions are calculated for the sample branches, relating the weights of branch fractions to branch basal diameter, and the weight of branch wood and bark to branch age. The regressions are used to calculate, from the tally of branch diameters and ages, the dry weights of wood and bark, current twigs with leaves, older leaves, and current annual growth of wood and bark (Whittaker 1965*a*) and older leaves (Whittaker and Garfine 1962), for all branches of each plant. The wood increment readings on discs or stem segments are used to calculate mean annual dry-weight growth of stem wood for the last 5 or 10 yr, and to estimate growth of stem bark from the ratio of current annual growth to mass for the wood, times the dry weight of the bark, for each stem segment. These and other calculations yield as results: (1) volume of stem wood and stem bark, (2) dry weight of stem wood, stem bark, branch wood and bark, current twigs and leaves, and older leaves, (3) annual dry-weight growth of stem wood, stem bark, branch wood and bark, current twigs and leaves, older leaves, and fruits, and (4) surface area of stem wood, stem bark, branch bark (Whittaker and Woodwell 1967), and leaves. The program then computes, for the 15 or 10 plant individuals, regressions of these as dependent variables on one or more of the independent variables: (1) dbh, or basal diameter, (2) parabolic volume estimate, one-half basal area times plant height, (3) conic surface estimate, one-half basal circumference times plant height, and (4) estimated volume increment, one-half wood area increment at breast height (or 10 cm) times plant height.

In the final stages of the program these regressions are used to compute the various dependent variables for the trees (or shrubs) recorded in the sample quadrats; and the results are summed by species in each quadrat. Each dependent variable is computed from two or more regressions, using different independent variables, and the more appropriate regression is used. In most cases regressions on parabolic volume have been used to estimate biomass values and growth of current twigs with leaves, whereas regressions on estimated volume increment have been used for other production estimates (cf. Whittaker and Woodwell 1969). Since only a few species were subjected to dimension analysis, regressions thought most appropriate have been applied to other species. (The regressions for *Quercus hypoleucoides* have been applied to other oaks, those for *Pinus cembroides* to *Juniperus deppeana*, those for *Arctostaphylos pringlei* to *Garrya wrightii*, etc.) For lack of regressions for the larger trees in the Catalinas, regressions from the southeastern forests

TABLE 2. Mean dimensions of trees and shrubs for dimension analysis, Santa Catalina Mountains, Arizona

Dimension	Quercus hypoleucoides	Pinus cembroides	Cercocarpus breviflorus	Arctostaphylos pringlei	Arctostaphylos pungens	Cercidium microphyllum	Larrea divaricata	Fouquieria splendens
A. Mean shoot dimensions								
Number of shoots measured	15	15	15	10	10	15	18	11
Diameter at breast height (cm)	7.65	8.43						1.49
Diameter at ground level (cm)			3.26	4.45	2.10	4.52	1.13	
Height (m)	4.81	3.65	2.58	1.32	.71	2.00	1.31	2.70
Age (yr)	52.3	107	18.9	54.8	27	25	12	21
Dry weight total (g)	24,645	26,932	1,482	1,406	205	2,054	148	383
Net production (dry g/yr)	1,844	1,482	269	153	51.4	422	45.8	78.8
Bark thickness (mm)	5.10	6.16	1.89	.38	.23	1.21	.56	2.99
Wood radial increment (mm/yr)	.69	.39	.64	.32	.32	.69	.33	.35
Biomass accumulation ratio	13.4	18.1	5.5	9.2	4.0	4.7	3.2	4.9
B. Volume (cm³)								
Parabolic volume estimate	21,444	19.356	1,641	1,246	139.4	2,242	114.6	312
True stem volume	24,014	25,424	1,305	1,049	87.6	1,280	95.5	653
Wood volume	17,854	19,247	980	1,014	83.4	1,120	79.6	328
Estimated volume increment	401	200	95.0	39.2	7.59	111	8.88	16.2
True volume increment	527	288	89.3	35.3	5.55	96	9.61	37.1
C. Surface (cm²)								
Conic surface estimate	7,037	5,764	1,510	972	243	1,583	286	707
Parabolic surface estimate	10,766	9,390	2,914	5,532	392	4,067	734	
Stem bark surface	9,231	8,811	1,643	1,032	186	1,418	313	1,415
Branch bark surface	71,960	122,322	33,467	3,252	1,507			
D. Shoot dry weight distribution, % in								
Stem wood	46.4	40.8	47.0	48.7	25.7	35.3	45.1	47.0
Stem bark	16.9	16.1	13.5	2.0	1.4	5.0	10.1	48.9
Branch wood and bark	24.3	30.7	29.4	30.5	30.6	56.9	28.4	
Current twigs and leaves	5.7	3.9	10.1	3.2	14.9	2.8	16.4	4.1
Older leaves	6.8	8.5		15.6	27.5			
E. Aboveground net production distribution, % in								
Stem wood	20.0	12.0	24.8	15.4	7.1	14.8	16.4	31.4
Stem bark	4.5	3.4	4.6	.5	.3	1.4	2.5	32.0
Branch wood and bark	27.9	25.1	30.3	22.7	16.5	48.7	21.2	
Current twigs and leaves	37.2	49.9	40.3	27.7	59.8	35.1	59.8	36.6
Older leaf growth	10.4	9.6		33.7	16.3			

were used: *Pinus echinata* (Whittaker et al. 1963) for pines, and *Picea rubens* biomass regressions (Shanks and Clebsch 1962) for the firs. Estimates of production and biomass are affected by high dispersions and by two sources of systematic error: a tendency to underestimation consequent on the logarithmic calculations (Crow 1971, Baskerville 1972, Beauchamp and Olson 1973) and a tendency to overestimate values for the largest individuals and consequently for samples (Ogawa et al. 1965, Whittaker and Woodwell 1968). Because these errors are of opposite direction, corrections for the logarithmic calculations have not been used here.

The production estimates for the forest trees were based primarily on calculations from estimated volume increments as described by Whittaker (1966). Production estimates for woodland trees and all arborescent shrubs were based on dimension analysis regressions. Estimates of production of smaller true shrubs used the clipping weights of current twigs with their leaves, times ratios of aboveground pro-

duction to clipping production from the dimension analyses. Estimates for suffrutescents or semishrubs used the clipping measurements times the ratios given for *Encelia farinosa* and *Franseria deltoidea*. Estimates for *Opuntia* were based on counts of new segments in the quadrats times mean dry weights per segment; production values for other cacti were based on volume and mass calculations, and division of the masses by age estimates. Production of herb species was based directly on quadrat clippings during the peak of summer growth and, in the woodlands and lower elevation communities, quadrat clippings taken also during winter or spring herb growth.

Many of the tree and shrub estimates are based on relationships for a different species, or the same species in a different sample. Leaf, twig, and chlorophyll data are limited to a few species. Annual wood rings are difficult to interpret in the woodland and desert samples, and very difficult or impossible in the open oak woodland; some of the growth rates

TABLE 3. Regressions for trees and shrubs of woodlands and desert, Santa Catalina Mountains. Regressions are in the forms: (linear) $y = a + bx$, and (logarithmic) $\log_{10} y = A + B \log_{10} x$. Coefficients of correlation are given as r; estimates of relative error in the forest e (SE of estimate divided by mean y) for linear regressions and E (antilog of SE of estimate) for logarithmic regressions. Stem diameter is measured at breast height (1.35 m) in the first two species, 10 cm above ground level in the remaining species.

Regression	Quercus hypoleucoides	Pinus cembroides	Cercocarpus breviflorus	Arctostaphylos spp.	Calcidium microphyllum	Larrea divaricata

A. Whole-shoot regressions on log basal diameter, x (cm) at breast height ... *at 10 cm above ground level*

(Sections A, B of Table 3 — dense numeric regression data, columns as above)

TABLE 3. Continued

Regression	Quercus hypoleucoides	Pinus cembroides	Cercocarpus breviflorus	Arctostaphylos spp.	Calcidium microphyllum	Larrea divaricata

C. Regressions on estimated volume increment, x (cm³/yr)

D. Regressions on conic surface estimate, x (cm²)

E. Branch regressions on branch basal diameter, x (cm)

F. Branch regressions on branch age, x (yrs)

[a] *A. pringlei.*

must be considered estimates, not measurements. It may be taken for granted that these growth rates, and clipping productions for herbs and low shrubs, vary significantly between years of drought and those of higher rainfall. The study should be considered a series of careful estimates of aboveground biomass and production from detailed information on the quadrats, but not systematic measurement such as applied at Brookhaven (Whittaker and Woodwell 1968, 1969) and Hubbard Brook, New Hampshire (Whittaker et al. 1974). No root data were obtained in this study. Estimates of likely root-shoot ratios from the literature (Whittaker 1962, 1966, Chew and Chew 1965, Rodin and Bazilevich 1967, Whittaker and Marks 1975) have been used to suggest

total, as well as aboveground, productivity and biomass in Table 4 and some of the figures.

RESULTS

Sample plant means and regressions

Table 2 summarizes mean dimensions, including dry weight mass and annual growth and the distribution of these in aboveground tissues, for the sets of sample plants. All values are arithmetic means, to permit comparisons with the similar summaries of Whittaker (1962), Whittaker and Woodwell (1968), Whittaker et al. (1974), and Andersson (1970, 1971).

Some of the regressions from the dimension analysis are summarized in Table 3. Because of their close similarity of form, the 10 sample shoots each of *Arctostaphylos pringlei* and *A. pungens* were combined to compute the *Arctostaphylos* regressions given. Dispersions from the regression lines are indicated both as *r* (coefficient of correlation) and *E* (estimate of relative error). *E* is the antilog of the standard error of estimate for a logarithmic regression (Whittaker and Woodwell 1968, cf. Furneval 1961, Attiwill 1966, Bunce 1968). It consequently expresses the expected range of values for *y* (to include 68% of individuals, assuming lognormal distribution) for a given value of *x* as a factor by which *y* is to be multiplied and divided. An *E* of 1.10 thus implies an expected range of values of 1.10*y* to *y*/1.10, for a given value of the independent variable.

The regressions are generally similar to those given for shrubs and small trees in the Brookhaven forest (Whittaker and Woodwell 1968) and in the studies of Andersson (1970, 1971) and Reiners (1972). *Quercus hypoleucoides* and *Pinus cembroides* in the Catalinas are stockier and heavier-branched than *Q. alba* and *P. rigida* at Brookhaven and the *Quercus* studied by Andersson (1970, 1971) and Reiners (1972). Correspondingly the slope constants (*B*) for stem surface, volume, and weight and other variables with a height component are lower in the Catalina trees. Slope constants for growth of stem wood and bark, branches, and twigs with leaves also are lower, reflecting the slower growth of the trees in the more arid climate of the Catalina woodland. The slope constants for the shrubs are generally higher and more consistent with those for the Brookhaven shrubs and trees.

Biomass

Table 4-B summarizes the community biomass estimates by plant fractions and strata. The total aboveground biomass values for fir forest samples 44, 45, and 47, 360–440 t/ha (dry metric tons per hectare, equals 36–44 kg/m²), are in the range of
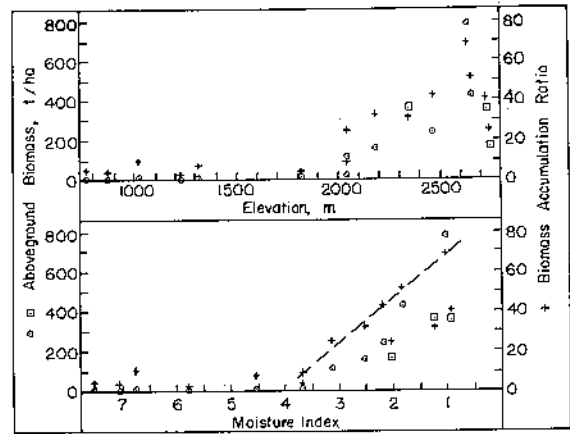
FIG. 2. Aboveground biomass (circles and squares, left ordinate) and biomass accumulation ratios (crosses and right ordinate) in relation to elevation and moisture index in the Santa Catalina Mountains. Biomass accumulation ratio (Table 4-B) is biomass/net annual production of vegetation, both in dry weights aboveground; moisture index (Table 1-B) is a weighted-average expression of position along the moisture gradient from subalpine fir forest (< 1.0) to desert (> 6.0). The three samples represented by squares are probably immature in biomass because of a fire about 130–150 yr ago (samples 44 and 48) or past selective cutting (45). A visual trend line has been fitted to the biomass accumulation ratios of the fully mature stands in the lower panel.

some of the climax forests of favorable environments in the Smokies (Whittaker 1966). Sample 46, in contrast, exceeds in biomass any of the southern Appalachian forests; with allowance for roots its aboveground value of 790 t/ha should become approximately 920 t/ha. The sample was taken from a particularly good stand of large trees by Santa Catalina standards; but it is not a large forest compared with those of the Pacific Northwest and the California coastal redwoods. The four pine forests and woodlands (samples 48–51) have total aboveground biomasses of 114–250 t/ha and compare with the pine forests and high-elevation fir forests (130–210 t/ha) in the Smokies. The low biomass of the aspen sample 59 (and a biomass accumulation ratio of 11.8) reflects its youth; these values are comparable with those for other young deciduous forests (Whittaker and Woodwell 1969, Andersson 1970, 1971, Duvigneaud et al. 1971, Reiners 1972, Reichle 1973).

The remaining woodland, grassland, and desert samples (52–58) have biomasses between 3 and 19 t/ha. The higher values compare with some of those for shrub communities in the southern Appalachians (heath balds, with biomasses of 11–110 t/ha, Whittaker 1963) and the lower values with those for other grasslands and deserts; comparable aboveground

TABLE 4. Summary of biomass and production estimates and diversity measurements for samples, Santa Catalina Mountains

Sample number and characteristic	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
(species)	Abies lasiocarpa subalpine forest	Abies concolor ravine forest	Pseudotsuga menziesii–Abies concolor forest	Pseudotsuga menziesii forest	Pinus ponderosa–Pinus strobiformis forest	Pinus ponderosa forest	Pinus ponderosa–Quercus hypoleucoides forest	Pinus chihuahuana–Quercus arizonica woodland	Pygmy conifer–oak scrub	Open oak woodland	Bouteloua curtipendula desert grassland	Spinose-suffrutescent desert scrub	Cercidium microphyllum–Franseria deltoidea desert scrub	Larrea divaricata desert scrub	Cercocarpus breviflorus shrubland	Populus tremuloides successional forest
A. Sample number	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
B. Biomass (dry t/ha)																
Trees[a] — Stems	290	270	681	363	126	213	134	79	9.06	6.13	0.56	7.90	2.35	2.54[a]	4.89[a]	103
Branches	50	74	82	57	28	30	23	27.9	4.81	2.87	0.04	4.00	1.35	1.33	1.84	16
Foliage	16.2	16.7	20	17	7.3	6.8	5.4	6.6	1.43	.40	0.04	.18	.08	.42	.47	5.2
Total	356.2	360.7	783	437	161.3	249.8	162.4	113.5	15.30	9.40	0.64	12.08	3.78	4.29	7.20	124.6
Shrubs[b] — Stems	.4	.012	4.0	.34	.05	.014	.20	.04	1.02	.04	.22	.64	.16	.0004	.03	.24
Branches	.2	.007	2.3	.22	.03	.005	.12	.01	.94	.09	.87	.07	.87	.0001	.05	.04
Foliage	.04	.002	.46	.03	.02	.006	.04	.12	1.45	1.45	.42	.14	.11	.0025	.34	.70
Total	.64	.021	6.76	.59	.10	.025	.36	.17	3.41	1.61	1.51	.85	1.14	tr.	.397	.98
Herbs	tr.	.108	.006	.002	.039	.045	.004	.034	.031	.188	.483	.112	.004	tr.	.42	.030
Lichen and moss		.036	.045	.007	.028			.002	.044	.020		.053				tr.
Selaginella											tr.		tr.			
Total, above ground	357	361	790	438	161	250	163	114	18.8	11.22	2.63	13.10	3.92	4.29	8.02	126
Total, above and below[c]	420	420	920	520	190	300	200	150	30	17	6	21	6	6	14	200
Biomass accumulation ratio[d]	41.1	32.1	69.0	52.2	26.0	43.1	32.8	25.6	10.1	7.5	1.90	10.2	3.72	4.7	4.33	12.0
C. Net productivity (g/m²/yr)																
Trees[a] — Stem wood	275	395	340	227	138	136	129	75	6.6	13.9	4.1	24.7	12.0	16.7[a]	32.3[a]	325
Stem bark	48	85	113	67	35	27	17	20	1.7	3.2	4.3	3.7	3.6	2.4	6.1	68
Branch wood and bark	130	164	177	139	100	97	72	90	12.5	22.1	1.4	29.9	20.0	18.7	37.1	217
Foliage	365	412	395	360	309	290	255	235	40.1	27.5	6.0	23.0	13.6	53.7	45.5	375
Fruit, flower, etc.	42	54	50	40	30	25	20	15	4.0	5.0	0.5	2.0	2.0	.2	4.0	45
Total	860	1,110	1,075	833	612	575	491	435	64.9	71.7	16.3	83.3	51.2	91.7	125.0	1,030
Shrubs[b] — Stems	2.1	.08	21	1.7	.4	.08	.6	2.0	11.8	.9	25.0	13.0	26.6	.01	.5	5.8
Branch wood and bark	2.2	.06	23	1.8	.3	.10	.7	.1	20.0	2.0	33.4	17.0	22.4	.02	1.0	5.9
Foliage	4.0	.16	46	3.4	1.1	.20	3.1	4.0	80.2	32.8	4.0	3.3	4.5	.03	9.5	6.6
Fruit, flower, etc.	0.2	.01	3	.2				.6	5.0	11.6					3.2	.5
Total	8.5	.31	93	7.1	1.8	.38	4.4	6.7	117.0	47.3	62.4	33.3	53.6	.06	14.2	17.8
Herbs	.01	12.0	.6	.17	4.2	5.0	.45	4.0	3.6	29.6	59.8	12.0	.4	.003	46.0	3.3
Total, above ground	869	1,123	1,146	840	618	580	496	446	186	149	139	129	105	92	185	1,051
Total, above and below[c]	1,020	1,300	1,340	1,000	740	700	620	580	350	300	280	210	170	140	330	1,220
Aboveground prod./leaf area (g/m²)	59.0	72.5	68.6	54.2	81.3	98.4	105.4	120.1	93.0	84.7	87.6	137	178	153	132	165
Aboveground prod./chlorophyll (g/g)	150	181	164	138	309	341	275	248	186	186	185	257	310	270	218	351
D. Diversity																
Species numbers[e] — Trees	6	9	6	3	4	5	5	8	4	3						7
Shrubs	3	5	2	1	1		4	6	10	23	26	30	27	4	15	3
Herbs (20 m²)	6	30	8	6	8	3	3	4	6	32	20	11	6	2	22	8
Winter annuals									2	18	20	24	23	8	4	2
Other herbs	1	10	4	4	4	8	7	6	20	58	4	41	33	6	37	18
Sample total	15	44	16	10	13	8	12	18	20	58	46					18
Indices — Simpson C	.71	.27	.54	.83	.48	.86	.55	.35	.23	.21	.14	.26	.39	.99	.53	.36
Shannon-Wiener H'	.262	.667	.411	.168	.354	.143	.321	.553	.738	.856	1.066	.924	.543	.003	.478	.605
Equitability E'c	2.29	7.98	3.04	2.28	2.61	2.23	2.81	4.43	4.53	9.84	11.46	9.19	6.17	1.21	7.66	3.12
Equitability E'c	1.62	8.59	2.56	1.93	2.06	1.74	2.55	3.85	4.21	11.76	11.90	9.54	7.75	.92	9.32	2.79

[a] "Trees" includes small trees and arborescent shrubs (Cercidium, Prosopis, Fouquieria, Carnegiea) in desert samples 55 and 56, and the canopy shrubs in desert samples 57 and 58.

[b] "Shrubs" include subordinate true shrubs and all semishrubs in samples dominated by shrubs (55–58). Rosette-shrubs and succulents (Opuntia, etc.) are responsible for some of the differences in distribution of biomass and production by tissues.

[c] No root data available; belowground estimates are based on plausible root/shoot ratios for different growth-forms.

[d] Biomass/net annual production, both as aboveground dry weight for all vascular plants.

[e] Trees, shrubs, and winter annual species in 0.1 ha. Perennial herbs and summer annuals are given both for the twenty 1-m²-subquadrats, and (as "other herbs") for the remainder of the 0.1-ha quadrat. Sample total includes trees and shrubs in 0.1 ha and perennial herbs and shrubs in 20 m².
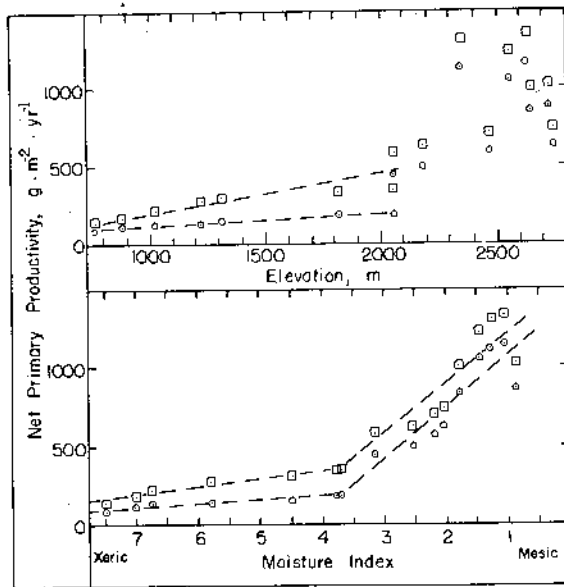
FIG. 3. Net primary productivity vs. elevation and moisture index in the Santa Catalina Mountains. Circles are aboveground productivity, squares estimates for aboveground and belowground productivity of the same samples. The moisture index (Table 1-B) is a weighted average of community composition, based on ecological groups for species responses to topographic moisture gradients and elevation.
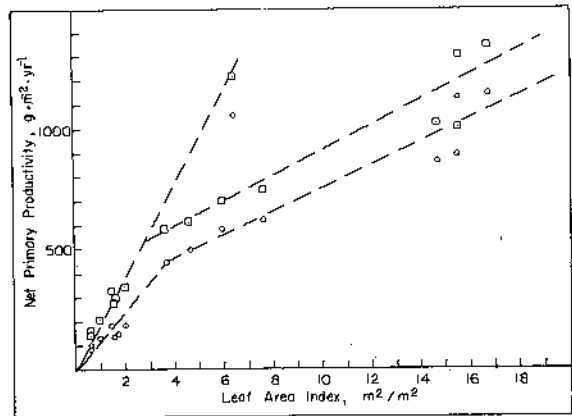

FIG. 4. Net primary productivity vs. leaf area index for communities in the Santa Catalina Mountains. Circles are aboveground productivity, squares estimates for aboveground and belowground productivity for the same samples. Visual trend lines suggest different slopes for deserts and desert grassland, with leaf area indices less than 3, and evergreen woodlands and forests, with leaf area indices of 4–16. The sample with a leaf area index of 6.5 is a high-elevation deciduous, successional forest (*Populus tremuloides*).

values from Eurasia (Rodin and Bazilevich 1967) are as follows: arid steppes 0.3–3.0, *Artemisia* deserts 0.53–2.6, and shrub tundra 4.9 t/ha.

Figure 2 shows the trends of biomass and biomass accumulation ratios in relation to elevation and moisture index. The trend of biomass decrease toward lower elevations and increasing drought is evident, though the samples are scattered. The study in the Smokies (Whittaker 1966) gave a mean decrease in biomass of 230 t/ha with each gain of 1,000 m elevation. The increasing aridity toward lower elevations in the Catalinas produces a reverse biomass trend of about 590 t/ha increase per 1,000 m elevation gain within the forest and woodland zones (samples 44–52 only). No trend is evident for the lower elevation samples.

Biomass accumulation ratios (BAR, the biomass present/net annual production) express the delayed decomposition and accumulation of persistent, and particularly woody, tissues in terrestrial communities. In forests the ratios correlate with age of the dominants. BAR ranges in the Great Smoky Mountains were 2.5–11 for shrublands (heath balds), 10–20 in young forests, 20–30 in forests of intermediate stature, and 41–52 in mature cove forests (Whittaker 1966). The ratios in the Catalinas are consistent with these, except for the BAR of 69 in sample 46, exceeding that of any eastern forest sampled. In

the forest and woodland zones the trend of decrease of BAR toward lower elevations generally parallels the trend for biomass. Apart from the desert grassland (sample 54, BAR = 1.9), the BAR values of lower elevation samples 52–58 are in the range of expected values for shrublands and show no elevation trend. Both biomass and BAR are less scattered in relation to moisture index, in the lower part of Fig. 2, than in relation to elevation.

Production

Three of the forest samples (45, 46, 59, Table 4-C) have net primary productivities in the range suggested as normal for climax temperate forests of favorable environments (Whittaker 1966): 1,000–1,200 g/m² · yr aboveground, 1,200–1,500 g/m² · yr aboveground and belowground. The two samples at highest elevations, a fir and pine forest (44 and 48), are less productive. It is not evident what aspects of their environments (on opposite sides of the summit of Mt. Lemmon) may make these stands less productive than the other fir forests, or the spruce forests in the Great Smoky Mountains. Productivities of the pine forests and woodlands (48–51) range downward from 446–618 g/m² · yr, aboveground. Pine and oak heaths in the Smokies have similar values (419–578 g/m² · yr), but the low-elevation pine forests there were more productive (875–983 g/m² · yr).

The remaining open woodland, grassland, and desert productivities in the Catalinas, 92–186 g/m² · yr aboveground, are conspicuously low
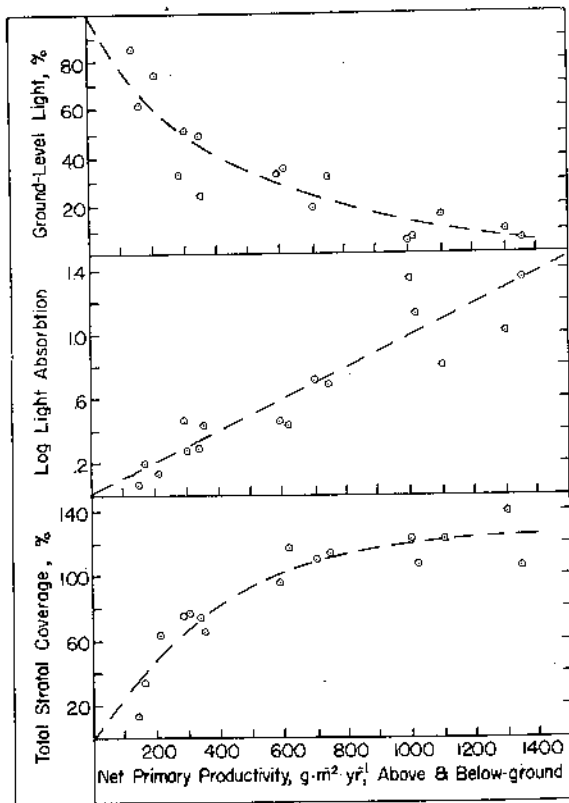
FIG. 5. Light and cover relationships to primary productivity in the Santa Catalina Mountains. Top: ground-level light intensity in per cent of incident sunlight; middle: $\log_{10}$ light absorption (logarithm of incident sunlight, minus mean of logarithm of light intensity at ground level); bottom: total individual-point coverage (number of plant individuals of all strata with foliage above 100 points in the community).
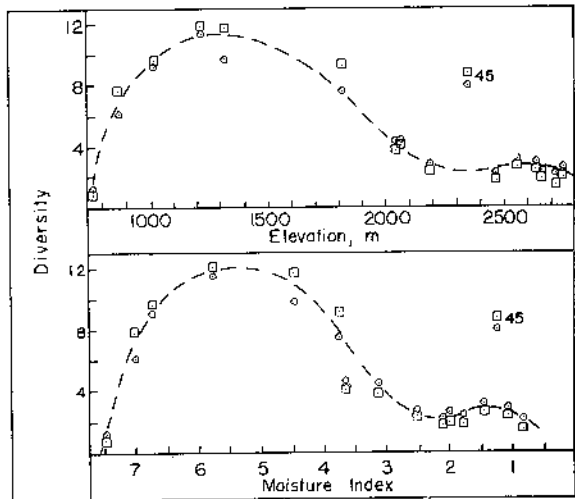

FIG. 6. Vascular plant diversity in relation to elevation and moisture index in the Santa Catalina Mountains. Equitability indices, mean number of species per logarithmic cycle (Whittaker 1972), are plotted $E_c = S/\log p_1 - \log p_s$), circles, and $E'_c = S/4 \sqrt{\Sigma(\log p_i - \log \bar{p})^2/S}$, squares. S = number of species in samples, and p_i aboveground net primary productivities—p_1 of the most productive and p_s of the least productive species in the sample, $\bar{p}$ the geometric mean for the sample; logarithms are to base 10. The curve for species diversity or richness, S, has the same form. Peak diversity occurs in the desert grassland and open oak woodland 1,220 and 1,310 m elevation, a lower secondary peak in fir forests at 2,500–2,700 m. Sample 45 is a ravine forest with diversity departing from the elevation trend.

compared with both forests and the closed heath balds (380–590 g/m²·yr) of the Smokies. The productivities of the open woodlands (samples 52, 53, and 58) are low compared with some other woodlands for which data are available (Whittaker and Woodwell 1969). Productivity of the desert grassland (54) is close to that of the spinose-suffrutescent semidesert (55). Sample 54 seems near the arid limit for grasslands; it may be compared with the dry steppes of Rodin and Bazilevich (1967), the short grass plains of Weaver (1924, 160 g/m²·yr), and African dry grasslands producing 90–170 g/m²·yr aboveground (Walter 1939, 1964). Chew and Chew (1965) estimated 130 g/m²·yr aboveground for a *Larrea* desert in Arizona. Their stand was in a somewhat less arid area and may have replaced desert grassland in consequence of grazing. Soholt (1973) measured aboveground production in a Mojave creosotebush desert, California, as 23.6 g/m²·yr in annual herbs and 7.0 g/m²·yr in leaves, twigs, and fruits of shrubs. The above-

ground total (estimating shrub stem and branch production as 4.1 g/m²·yr on the basis of the ratio of these to twig and leaf production in Table 2-E) would be 37.7 g/m²·yr. The four Arizona desert samples (Chew and Chew's and our samples 55–57) with net productivities of 92–130 g/m²·yr aboveground represent the mesophytic margin of southwestern desert environments, and much lower productivities occur in more arid areas (Lavrenko et al. 1955, Rodin and Bazilevich 1967).

The *Cercocarpus* shrubland on limestone (sample 58) is in a class with the pygmy conifer–oak scrub (52) and open oak woodland (53) in productivity. Sample 58, however, is at a higher elevation than the open oak woodland, and the pygmy conifer–oak scrub does not occur on the north side of the range where *Cercocarpus* scrub appears on limestone. The vegetation patterns of limestone and granite on the north slope (Whittaker and Niering 1968b) would predict a denser, mesic phase of the oak woodland or a pine–oak woodland for the *Cercocarpus* site if it were on granite. The limestone soil thus implies reduction of productivity, as well as a more xeric moisture index, compared with a corresponding site
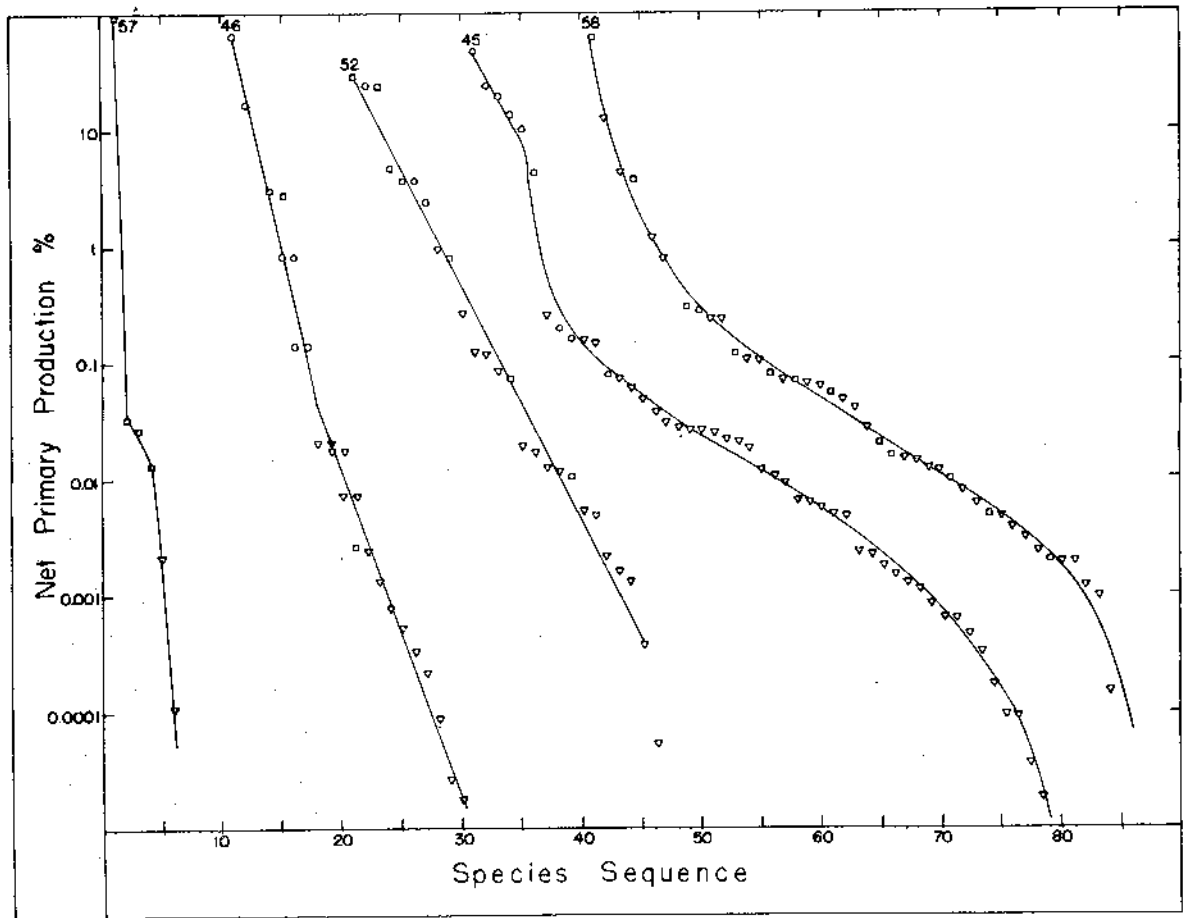
FIG. 7. Dominance-diversity curves for five samples from the Santa Catalina Mountains. The ordinate is the logarithm of aboveground net primary production for species, expressed as per cent of the totals for each sample. Species are arranged in sequence from the most to the least productive, by the scale on the abscissa. Four of the curves are displaced to the right to avoid overlap, and their first species are consequently at positions 11, 21, 31, and 41 on the abscissa. Circles are tree species, squares shrub species, and triangles herb species. Communities sampled: 57 a creosotebush (*Larrea divaricata*) desert; 46 a montane fir forest of *Pseudotsuga menziesii* and *Abies concolor*; 52 a pygmy conifer–oak scrub with *Pinus cembroides, Juniperus deppeana, Quercus hypoleucoides,* and *Arctostaphylos* spp.; 45 a ravine forest dominated by *Abies concolor*; and 58 a middle-elevation shrubland dominated by *Cercocarpus breviflorus* on limestone.

on an acid soil. The limestone is fissured and may permit rapid drainage of rainwater.

Figure 3 shows a trend of productivity increase with elevation up to 2,000 m, but at higher elevations the values are scattered. The moisture indices so transpose the samples as to produce a recognizable, though irregular, trend at higher elevations. Different slopes of production increase with elevation are suggested for more arid and more humid environments in Fig. 3. The visual trend lines give increases of about 25 g/m² · yr aboveground per moisture index unit for the more arid, and 320 g/m² · yr for the more humid series. Figure 1 suggests that a moisture index unit may correspond to about 10 cm precipitation difference. On this basis net aboveground production would increase by about 2.5 g/m² · yr

per cm of precipitation in the more arid, 32 g/m² · yr per cm in the more humid series. For dry grasslands Walter (1939, 1964) obtained a linear increase of aboveground productivity with rainfall of about 10 g/m² · yr per cm of precipitation between 10 and 55 cm.

Leaf area and chlorophyll

Estimates of leaf area index and chlorophyll per unit ground area are given in Table 1-C, ratios of aboveground productivity to these in Table 4-C. The surface area and chlorophyll estimates for fir forests, with evergreen needles persistent over 5 yr, are high in comparison with most literature values (Art and Marks 1971). The surface area and chlorophyll values for the lower elevation commu-

nities are underestimates in that photosynthetic surface and chlorophyll in stems and branches were estimated only for the cacti. In the lower elevation communities photosynthesis occurs in stems and branches of some shrub species during the dry season, when the leaves have been lost. The chlorophyll and photosynthetic surface estimates for leaves (and cacti) only are thus low for the rainy, but high for the dry season. The ratios of aboveground net productivity to leaf area and chlorophyll are low in the fir forests (54–72 g/m², 138–181 g/g), and consistently higher in the open woodland, grassland, and desert communities (85–165 g/m², 185–350 g/g).

The relationship is shown in another form in Fig. 4. Two slopes of total net primary productivity in relation to leaf area index are suggested: a steeper slope (of about 190 g/m² · yr increase per LAI unit) for the lower elevation communities, and a less steep slope (of about 50 g/m² · yr increase per LAI unit) for the higher elevation forests. A similar relation applies to production/chlorophyll ratios. The only deciduous community of a humid environment sampled, the aspen stand (59), falls on the line for the lower elevation communities.

Three other production relations—to ground-level light, log light absorption, and total stratal coverage —are shown in Fig. 5. Ground-level light percent (the geometric mean of light intensity at ground level, as a percent of incident sunlight) decreases as productivity and, in correlation with this, biomass and coverage, increase. Productivity in relation to log light absorption ($\log_{10}$ of incident sunlight minus $\log_{10}$ of ground-level sunlight) is complementary to the preceding, but is linear. In both cases the points are scattered in relation to the trend, and light penetration or absorption seems not effective as an index of production (Whittaker 1966). The curve of total stratal coverage on production relates to Fig. 4, though based on a different expression of community coverage. Total stratal coverage is the sum of individual-point coverages (number of plant individuals with foliage above 100 points) for the tree, shrub, and herb strata.

Growth-forms and diversity

Relations of vascular plant species diversity to elevation are shown in Table 4-D as several indices: S = number of tree and shrub species in 0.1-ha plus herb species in 25-m² quadrats (additional herb species in the 0.1 ha are indicated separately); the Simpson index, $C = \sum_s p_i^2$; the Shannon-Wiener index, $H' = -\sum_s p_i \log_{10} p_i$; and mean species per log cycle, E_c and E'_c (Fig. 6). In these p_i is relative productivity (percent in a given species of the total aboveground net productivity for a sample). The Simpson (1949) index expresses relative concentra-
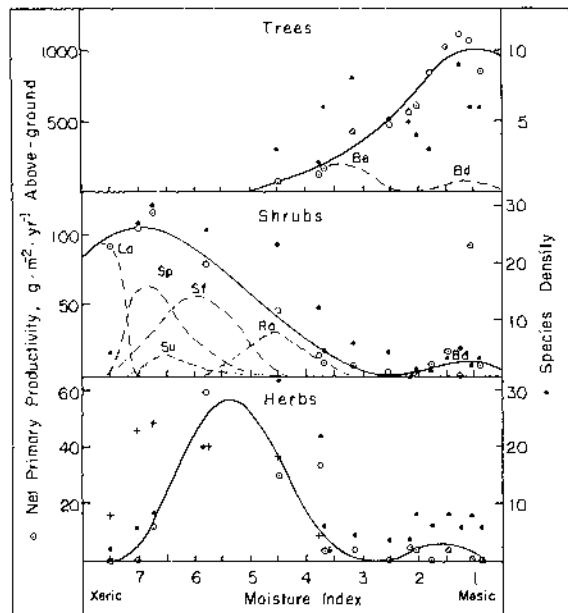

FIG. 8. Net primary productivity and species diversity of strata in relation to the moisture index, Santa Catalina Mountains. The circles are net primary productivity aboveground in g/m²/yr, left ordinate; the solid points are numbers of species per 0.1 ha (or, for herbs, 25 m²), right ordinate. Smoothed curves for productivities of fractions of strata are indicated by dashed lines, without datum points. Top: Bd is broadleaf deciduous and Be broadleaf evergreen trees; the remaining trees are needle-leaf evergreen. (*Cercidium* and other small trees of the desert are here treated as shrubs.) Middle: Bd is broadleaf deciduous, Ro rosette shrubs, Sf suffrutescent semi-shrubs, Su succulents, and Sp spinose shrubs; La is *Larrea divaricata*. Bottom: the solid points are numbers of perennial and summer annual species in 25 m², the crosses numbers of winter annual species in 0.1 ha.

tion of dominance, H' primarily expresses equitability (Auclair and Goff 1971, Whittaker 1972), and E_c is an equitability measure (Whittaker 1972). The alternative form E'_c gives results paralleling E_c.

The fir forest sample 45 has a rich streamside flora that makes it diverse beyond the other high-elevation forests. Apart from this sample, the pattern of species diversity as represented by E_c and S is an increase from the high-elevation fir forests to the open oak woodland and desert grassland of lower elevations, followed by a decrease through the three deserts to a minimum in *Larrea* sample 57 (Fig. 6). If the samples are arranged by moisture index, the pattern is further complicated by a decrease from mesic fir (45, 46, 59) to more xeric pine (47–49) high-elevation forests, followed by the more conspicuous increase from the latter into the woodlands (51–53). The Shannon-Wiener index and the one complement of the Simpson index largely parallel the pattern for S and E_c; exception to this parallelism involve contrasts in relative dominance.

Dominance-diversity curves, using aboveground net productivity as the importance value, are shown for five communities in Fig. 7. Sample 57, the *Larrea* desert, has extreme dominance by one species and low species diversity. Three subordinate shrubs and semishrubs (*Ephedra nevadensis, Psilostrophe cooperi,* and *Zinnia pumila*) make up the hump in the middle of the curve, and two herbs with trivial productivities (*Tridens pulchellus* and *Pectis papposa*) the bottom points. In sample 46, as in all other forest samples of this study, the trees suggest a straight line approaching a geometric series (Whittaker 1965*b*, 1972). In sample 46 the herb stratum also suggests a geometric slope; in sample 45, in contrast, the rich herb stratum is sigmoid and suggestive of a lognormal distribution. Sample 52, a community of intermediate species diversity, suggests a geometric slope and resembles the curve for a pine forest in the Great Smoky Mountains (Whittaker 1965*b*, sample 10). Sample 58 represents a pattern more typical of woodlands, combining strong dominance with moderately high species diversity and sigmoid form. The remaining samples range from approximately geometric slopes (44, 47, 48, 49, 59) to sigmoid curves suggesting sparse lognormal distributions (50, 51, 53, 54, 55).

Correlation of diversity with productivity has been suggested (Connell and Orias 1964, MacArthur 1969). Figures 3 and 6 do not support such a correlation. The vegetation gradient from high to low elevation in the Catalinas is a physiognomic continuum, within which the various growth-forms have their peak importances in this sequence: needle-leaf evergreen trees, broadleaf-evergreen trees, rosette shrubs, grasses, semishrubs, and spinose shrubs (Whittaker and Niering 1965). Relations of diversity and productivity can be examined for these growth-forms as components of plant communities, but these relations are complex (Fig. 8). Consideration of growth-forms suggests these observations: (1) Within the tree stratum, no correlation of species number with productivity is in evidence. (2) Among perennial herbs both diversity and productivity are bimodal (with minima in the pine forests), and the two measures appear loosely correlated. Annual herbs are concentrated in the open and xeric communities, increasing in diversity and productivity from woodlands through desert grassland to less extreme deserts, but decreasing from these to the more extreme *Larrea* desert. (3) A loose correlation of diversity and productivity is suggested for the shrub stratum, when all shrub growth-forms are grouped together. (Certain arborescent shrubs forming part of the community canopy have been grouped with the tree stratum in Fig. 8—*Arctostaphylos* in sample 52, *Cercocarpus* in sample 58. Arborescent, spinose

plants of the desert—*Carnegiea, Cercidium, Fouquieria*—have, in contrast, been grouped with other spinose shrubs.) Within the shrub stratum the different growth-forms have separate centers of maximum diversity and productivity. (4) For the strata of dominants—whether trees, shrubs, or grasses—there is no correlation of diversity and productivity where these strata are dominant. For subordinate strata and growth-forms diversity and productivity are in general loosely correlated. (5) In temperate vegetation the tree stratum is in general less rich in species than are the herb and shrub strata, and the herb and shrub strata are on the average less rich beneath a closed forest canopy than in open woodland and grassland communities.

DISCUSSION

The relations of diversity to productivity do not encourage sweeping generalizations (cf. Whittaker 1965*b*, 1969, 1972). This study is in accord with others in indicating, however, that the highest temperate vascular plant species diversities are not in the most productive, closed forests but in less productive, open communities of intermediate environments—certain woodlands, grasslands, and shrublands. For the elevation gradient in the Catalinas the relation of diversity to moisture is combined with the relation to temperature, from which increasing diversity toward lower elevations would be expected. The high diversity of the spinose–suffrutescent semidesert may reflect the fact that this is a warm-temperate, near-subtropical community.

The results on productivity and biomass are generally in accord with those from the Great Smoky Mountains (Whittaker 1966) in suggesting characteristic ranges of these for most climax temperate forests and woodlands: for forests net productivity of 600–1,200 $g/m^2 \cdot yr$ aboveground and 700–1,500 $g/m^2 \cdot yr$ total, and biomass of 200–500 t/ha aboveground and 250–600 t/ha total; for woodlands net productivity of 150–600 $g/m^2 \cdot yr$ aboveground and 250–700 $g/m^2 \cdot yr$ total, and biomass of 20–200 t/ha aboveground and 30–250 t/ha total. Biomass of a mature Douglas-fir forest was higher, and that of an open oak woodland lower, than the ranges given. The transition from semidesert to one of the intermediate communities (grassland or woodland) appears to occur at about 150 $g/m^2 \cdot yr$ aboveground, probably 250 $g/m^2 \cdot yr$ total net primary productivity. Aboveground semidesert biomasses (4–13 t/ha in this study) exceeded those of desert grassland (2.6 t/ha in one sample of this study). Mountain-slope limestones in this area support vegetation that is Chihuahuan in floristic affinities and is more xeric in composition and structure than that on granite (Whittaker and Niering 1968*b*).

Many sites (as defined by elevation and topographic position) that support *Cercocarpus* shrubland on limestone support pine–oak woodland on granite. The contrast of these two types in biomass and production is represented by samples 58 and 51, which are roughly, though not closely, comparable in site: 8 t/ha and 185 g/m^2·yr aboveground for *Cercocarpus* shrubland, 114 t/ha and 446 g/m^2·yr for pine–oak woodland.

The most interesting result from the study may be the evidence of change in the character of productive relationships along the moisture gradient. In Fig. 2–4 different slopes for these relationships apply to the forest communities of more humid, and the woodland, grassland, and desert communities of more arid environments. The data are not adequate to assure that this is an abrupt change of slope, as distinguished from a curve of changing relationships toward higher elevations. To the extent a change of slope can be located, however, it is not at the desert border but at the transition from open to denser woodland, hence at the point along the gradient where trees become the primary basis of community productivity. As shown in Fig. 1, the limited climatic data suggest a linear relation of precipitation to elevation. One should be cautious in relating the productivities of this study to probable climate as implied by elevation. Accepting the evidence as it stands, however, the dual slopes in Fig. 2–4 suggest as an hypothesis different patterns of community response to the moisture gradient:

1) The communities of arid environments are surface-limiting, with transpiring surfaces minimized but with high productive efficiency of those surfaces made possible by their exposure to relatively full sunlight (and, in some species, such special photosynthetic adaptations as C$_4$ and crassulacean acid metabolism).

2) The evergreen forests of more humid environments are surface-abundant; with sufficient moisture they have much higher leaf area indices, but the productive efficiency per unit leaf surface is lower. The possibility of supporting high leaf surface areas permits, however, more rapid increase in productivity per unit of available moisture from woodlands into forests than in the surface-limiting communities.

3) With still greater moisture availability in humid forests, factors other than moisture (nutrient turnover, balance of respiring and photosynthetic tissue, light absorption) may become limiting, producing the 1,200–1,500 g/m^2·yr range for mesophytic climax temperate forests. (Some young and floodplain temperate forests exceed this range.)

The two slopes of the Catalina productivity measurements (Fig. 3) in relation to probable precipitation values, and the assumption of a plateau
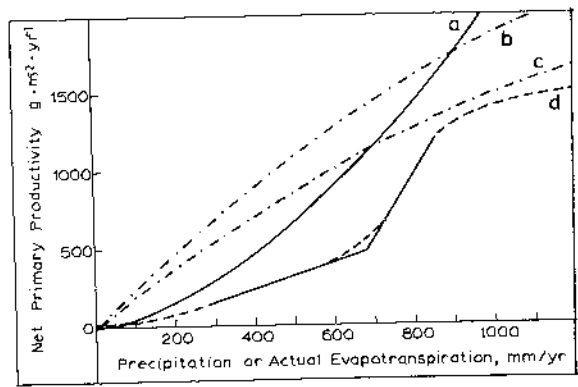

FIG. 9. Four interpretations of the relation of net primary productivity (dry g/m^2/yr) to precipitation and actual evapotranspiration. *a*: The curve fitted by Rosenzweig (1968) for aboveground net primary productivity of forests and shrublands in relation to actual evapotranspiration (mm/yr), with the form NPP $= 1.66$ log$_{10}$ AE $- 1.66$. *b*: The curve fitted by Lieth (1974) for total net primary productivity of diverse kinds of communities in relation to actual evapotranspiration, with the form NPP $= 3,000 \, (1 - e^{-0.0009695 \, (AE - 20)})$. *c*: The curve fitted by Lieth (1973, 1974) for total net primary productivity in relation to mean annual precipitation (mm/yr), with the form NPP $= 3,000/(1 + e^{1.315 - 0.119 \, MAP})$. The nearly linear lower part of this curve is the ratio obtained by Walter (1939, 1964) for dry grasslands: NPP $=$ MAP (g/m^2/yr aboveground, mm/yr), hence total NPP is about 2× MAP for the same units. *d*: A hand-drawn curve relating the two slopes of the Santa Catalina total net primary productivity estimates (Fig. 3) to probable mean annual precipitation, and adding to these a third, upper slope for limitation of climax temperate forest productivity at around 1,500 g/m^2/yr.

of productivity at precipitations higher than those reached in the Catalinas, have been combined in curve *d* of Fig. 9. The hollow lower part of the curve resembles the logarithmic fit of net productivity to evapotranspiration by Rosenzweig (1968), rather than the convex curves fitted to mean productivity in relation to precipitation and evapotranspiration by Lieth (1973, 1974). The curve may fall below Rosenzweig's (for primarily cooler temperate communities) because in a hot, dry climate the net production efficiency of a given amount of precipitation and evapotranspiration may be less (as a result of increased respiration and evaporative stress) than in a cooler climate. The response of productivity to combinations of moisture and temperature may be complex: for surface-abundant communities of humid environments higher net productivity for a given amount of precipitation should occur at higher temperatures; for surface-limiting communities of arid environments lower net productivity for a given amount of precipitation should occur at higher temperatures. (The latter statement excludes arctic-alpine communities in which productivity is limited by temperature and growing season.)

The available data for evapotranspiration in Southwestern mountains indicate that actual evapotranspiration should be the same as precipitation at lower elevations in the Catalinas, up to the woodlands and precipitation values of 400–500 mm. For the cooler climates toward higher elevations evapotranspiration should remain roughly constant at values between 400 and 500 mm (Thornthwaite and Mather 1957, Buol 1964, Mather 1964). It is in this range of higher elevations with relatively constant actual evapotranspiration indices that the steep increase in productivity with increasing precipitation shown in Fig. 3 and 9 occurs. In this area the Thornthwaite actual evapotranspiration values seem not more useful than precipitation itself as a variable to which productivity may be related. Figure 9 suggests that the response of community productivity to climate is complex and nonlinear (comparing related communities in a given area, rather than Lieth's world averages), and therefore more interesting than has been recognized.

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