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ECOLOGICAL VARIATION IN THE LEAF ANATOMY OF
SELECTED SPECIES OF *CERCOCARPUS*

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This investigation stresses the analysis of leaf anatomy in relation to factors of ecology in selected species of the genus *Cercocarpus* HBK. of the family Rosaceae. Members of this genus are generally shrubs or small trees native to arid portions of the western United States, British Columbia and northern Mexico.

Species of *Cercocarpus* are ideally suited to comparative studies in ecological anatomy for the following reasons. First, comparisons of different species with respect to the adaptation problem is especially meaningful within a closely related group, e.g., a species or genus (Keller, 1925). Secondly, members of this genus occupy a broad range of habitats from xeric to more mesic ones, and possess anatomical modes that can be related to various ecological conditions. Thus, anatomical characteristics often serve as reliable indicators in the study and understanding of physiological processes and ecological adaptations of living organisms.

In some plant genera distinct phenotypic modifications exerted by environmental factors are evident, but there are none at all in others, and even in the former the degree of modification is different in different genera (Chowdhury, 1961). However, relationships between anatomical characteristics and environmental conditions have been experimentally established by statistical methods as well as by logical deduction. Contrary to Bonner's (1963) view that there is nothing more to be discovered in the morphological sciences, much still remains to be learned in this respect.

Since the leaf is the plant organ most exposed to atmospheric conditions, investigations in this study have been centered on leaf anatomy. Attention has been given to modifications in anatomical characteristics for the purpose of detecting structures which might be interpreted as adaptations to specific environments.

Many members of the genus *Cercocarpus* are montane xerophytes; therefore, the greatest concern in this study is with modifications of xeromorphic characteristics in the leaves.

The literature in ecological anatomy is surprisingly extensive despite the fact that the science of ecology is a relatively late arrival to the field of botany. Bonnier (1890) divided parts of plants which were growing at

intermediate elevations in mountains and transplanted one portion to low elevations and another to alpine elevations. Plants grown in the two habitats showed variation in appearance, habit, and structure. Boodle (1904), in his study on leaves of *Pteris aquilina* L., found that leaves of plants grown in dry and exposed situations had xerophytic structures while those of plants grown in more sheltered habitats were more mesophytic. The xerophytic leaves possessed hypoderm, the more mesophytic had none. And in the latter the palisade tissue was poorly developed or entirely missing. Chrysler (1904) compared the leaf anatomy of strand plants at Woods Hole, Massachusetts, with that of the same species growing on the shores of Lake Michigan near Chicago, Illinois. Leaves of maritime plants were less than once to more than twice as thick as the inland plants. The increase in thickness was due to increased palisade development. Greater compactness in tissue and increased thickness of the outer epidermal wall were found in certain of the maritime plants also. Cannon (1905) compared conductive tissue of desert plants after keeping some plants under irrigation and growing others of the same species without irrigation. Clements' (1905) detailed work shows the differences in structure of numerous hydrophytic, mesophytic and xerophytic leaves. Environmental factors were measured for most of the plant habitats. Clements also provided a good review of earlier papers on leaf structure. Harshberger (1908) investigated the leaf structure of strand plants in New Jersey and sand dune plants in Bermuda. Chermeson (1910) compared the anatomy of maritime vegetation with that of inland ecotypes. Adamson (1912) found the xerophytic leaves of certain species of *Veronica* to show reduction in leaf surfaces and intercellular spaces and an increase in cuticle thickness. Starr (1912) compared the structures of stems and leaves of plants on Indiana sand dunes with those of plants on the flood plains of the Desplaines River at Riverside and the Mississippi flood plain. She also discussed the ecological factors of the dunes. Hayden (1919) made a study of the foliar anatomy of some plants of a prairie province in central Iowa. Cooper (1922) studied the bearing of environmental factors on the internal structure of leaves of broad-sclerophyll trees and shrubs in the low-rainfall areas of California. Maximov's (1929) definitive review, *The Plant in Relation to Water*, contains references to more than 450 papers dealing with xeromorphy.

More recent knowledge concerning morphological and anatomical adaptations of xerophytes to their environment has been reviewed by Evenari (1938, 1962), Shields (1950, 1951), Killian and Lemée (1956), Stålfelt (1956), Oppenheimer (1960), Henckel (1964), Fahn (1964), and others.

All these investigators agree that anatomical structures have evolved with respect to environmental conditions.

MATERIALS AND METHODS

Vegetative material from one to four populations of each species studied was observed and collected in the field. Collection sites were chosen as much as possible for their ecological and climatological diversity. Sites are located in various counties of California and Nevada.

Special attention was given to the method of collection from each plant in a population so that uniformity was maintained. All plants sampled in a population were approximately uniform in size. Leaves were collected from five equidistant locations on the periphery and at approximately one-half the height of each plant.

Many anatomical characteristics of the leaves were studied and measured for each population or collection site. Leaf transections of five leaves from each of five plants per population were studied. The mean measurements given for each collection number in TABLE 1 are the averages of the averages obtained from the plants in a population. Therefore, each mean is the average of 25 leaves for each population of a species. Less extensive sampling was used for *Cercocarpus betuloides* var. *blancheae* (C. K. Schneid.) Little and *C. traskiae* Eastw., Santa Catalina Island, California, and also for *C. betuloides* var. *macrourus* (Rydb.) Jeps., Siskiyou County, California, because of the unavailability of sufficient habitat diversity in these species.

All specimens used for this study were collected by the writer and are cited in parentheses after each species name according to their collection numbers. Vouchers of pressed specimens have been prepared and deposited in the Rancho Santa Ana Botanic Garden Herbarium, Claremont, California. Specimens are not listed here because legends for the plates provide a virtually complete citation.

Specimens of mature leaves were preserved in 70% formalin-acetic acid-alcohol (Johansen, 1940). Preserved material was infiltrated and embedded according to the tertiary butyl alcohol series of Johansen (1940). Transections were cut 12–16 μ in thickness, stained with a safranin-fast green combination corresponding to Northern's modification of Foster's tannic acid-ferric chloride method (Johansen, 1940), and mounted in Permout. Fixed leaves were also transferred to water and then placed in 2.5% aqueous NaOH to remove as much of the cell contents as possible without overly softening the tissues by too prolonged immersion in NaOH. Chloral hydrate (250% solution) was used as a clearing agent following NaOH treatment. After the material was cleared it was washed and dehydrated in an ethyl alcohol series. Whole mounts were transferred from absolute ethyl alcohol to a 1% solution of safranin dissolved in equal parts of absolute ethyl alcohol and xylene. Destaining followed with changes of the alcohol-xylene mixture and transfer to pure xylene. Material was mounted on slides in Permout.

GENERAL HABITATS

CALIFORNIA

Field collections of *Cercocarpus* in California and Nevada are from various locations which lie in three plant communities. They are chaparral, pinyon-juniper woodland and yellow pine forest, as defined by Munz (1959), Plummer (1911) and this writer. Maps in Fig. 1 show approximate locations of collection sites.

Fig. 1. *Cercocarpus*. Collection sites of selected species in California and Nevada.

CHAPARRAL

Chaparral is characterized by rocky, gravelly, or sometimes heavy soils on dry slopes and ridges in the Coast Ranges from Shasta County south, and

TABLE 1. *Variation in yearly rainfall with relation to elevation and exposure in the chaparral areas of southern California.*

Elevation	Exposure	Yearly rainfall (in.)	
		Estimated	Average
Sea level		—	13
2,000 ft.	West and south slopes	25	17
	East and north slopes	9	
5,000 ft.	West and south slopes	43	35
	East and north slopes	27	
8,000 ft	West and south slopes	61	53
	East and north slopes	45	

below the yellow pine forests on the western slopes of the Sierra Nevada and more southern mountains. In some places chaparral extends down to sea level and in others reaches an altitude of 8,000 ft.

The plant composition of chaparral varies with slope exposure, soil, elevation, precipitation and temperature. Munz (1959) lists some of the indicator species for this community. Generally, chaparral consists of a broad-leaved sclerophyll type of vegetation, 3-6 or 10 ft high and is dense, often nearly impenetrable. Always subject to fire, many of the shrubs tend to crown-sprout following fires. This type of vegetation is known in the Mediterranean area as maquis, and in Australia and Chile as scrub.

Chaparral is found in Mediterranean climates. Over the chaparral regions of southern California moderate and scanty rains occur during the winter months, with little or no precipitation in summer. At San Luis Obispo, in the more northern portion of the chaparral, only 2.91% of the rainfall is in the summer; at Los Angeles, only 0.83%; and at San Diego, only 0.89%. Thus, the various species undergo greatest growth in the winter, rather than in the spring and summer growing seasons characteristic of other vegetation types.

Particular conditions create seeming reversals of the typical pattern described above. High mountains are usually barren and snow-covered at their summits; below this, typically, is the timber line (sub-alpine zone) with its stunted growth; farther down, forested slopes, with the trees increasing in size until, with the undergrowth, they form a heavy cover on the coastal plain. In southern California, however, the forests occur only at the higher elevations, and below is chaparral. Farther down is the coastal sage scrub, and vegetation is even sparser in the sandy belt bordering the ocean.

According to Plummer (1911), rainfall increases with altitude, at approximately the rate of Lippincott's formula, which is 0.6 in. for each 100 ft of rise. Over the chaparral area as a whole, conditions of precipitation and elevation estimated by Plummer (1911) are given in TABLE 1.

<i>Cercocarpus</i>	<i>ledifolius</i>				<i>betuloides</i> var. <i>betuloides</i>				<i>multiflorus</i>		<i>betu- loides</i> v. macro- urus	<i>intricatus</i>	<i>betu- loides</i> v. blan- cheae	<i>traskiae</i>	
Collection number	1509	1508	1512	1520	1531	1511	1524	1521	1516	1533	1526	1507	1527	1518	1517
Elevation	8450 ft	7500 ft	6500 ft	6000 ft	1250 ft	3500 ft	5000 ft	6500 ft	2500 ft	1250 ft	5900 ft	1250 ft	7500 ft	550 ft	550 ft
Mean annual precipitation	56 in	42 in	20 in	33 in	15.6 in	17.6 in	43 in	36 in	25 in	15.6 in	49 in	15.6 in	27.5 in	12.35 in	12.35 in
Mean annual temperature	35 F	40.5 F	60 F	47.5 F	62.6 F	55.5 F	50.3 F	45.1 F	60.2 F	62.6 F	47.5 F	62.6 F	40.5 F	60.9 F	60.9 F
LEAF CHARACTERISTICS															
1. Leaf length, mm	27.90	24.80	24.00	20.50	19.00	17.00	22.30	20.40	18.50	16.50	37.50	6.20	7.70	43.60	43.40
2. Leaf width, mm	8.20	6.90	6.60	5.90	10.50	8.80	12.90	11.70	8.65	7.50	20.50	1.40	1.90	22.90	24.80
3. Revolute leaf margins	×	×	×	×	Slightly				Slightly				×	×	×
4. Leaf thickness at major bundles, μ	792.00	858.00	792.00	990.00	390.50	616.00	352.00	440.00	330.00	407.00	363.00	654.50	561.00	484.00	902.00
5. Leaf thickness at minor bundles, μ	528.00	627.00	572.00	682.00	297.00	352.00	209.00	286.00	179.30	286.00	187.00	341.00	275.00	176.00	231.00
6. Cuticle thickness, μ	9.17	6.90	6.90	9.17	2.44	2.44	1.95	1.95	6.60	8.80	2.56	8.80	7.30	1.95	5.50
7. Outer epidermal wall thickness μ	.98	1.20	1.20	1.50	1.75	1.83	1.20	1.30	.98	1.46	1.90	4.40	2.20	2.19	3.30
8. Epidermal cells as seen in transection, height, μ	11.90	10.80	11.00	9.50	10.10	9.30	11.50	11.00	4.20	3.20	6.60	10.10	7.30	11.50	16.50
9. Epidermal cells as seen in transection, width, μ	17.90	15.80	16.40	14.30	17.25	16.70	18.25	17.90	8.50	6.20	16.50	18.20	14.56	14.56	22.00
10. Glandular trichomes, upper and lower epidermis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11. Nonglandular trichomes, lower epidermis	×	×	×	×	0	0	0	0	×	×	×	×	×	×	×
12. Stomatal crypts	×	×	×	×	0	×	0	0	0	0	0	×	×	0	×
13. Stomata—% of lower epidermal cells counted	12.10	10.50	9.70	7.70	7.40	8.10	6.00	6.60	6.50	8.11	6.50	13.60	10.10	9.57	12.20
14. Length of palisade cells, μ	30.00	25.80	26.40	24.00	22.50	20.90	29.40	26.10	24.20	25.80	25.50	18.30	25.50	15.50	22.00
15. Width of palisade cells, μ	6.10	4.90	5.30	4.50	8.00	4.50	8.30	3.60	7.00	6.70	6.88	5.10	5.30	5.60	4.40
16. Spongy mesophyll	Weakly developed				Weakly developed				Weakly developed				Weakly developed		
17. Intercellular spaces	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
18. Hypodermal cell layers—All average 2 tannin-filled layers, with multilayered tannin ribs transecting leaves	0	0	0	0	1-2	1-3	1.00	1-2	1.00	1.00	1.00	2-3	1-2	1.00	1.00
19. Mucilage cavities	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
20. Tannins	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
21. Frequency, bundles/ transection	64.00	61.00	55.00	64.00	50.00	56.00	42.00	46.00	41.00	47.00	48.00	18.00	15.00	51.00	41.00
22. Diameter of major bundles, μ	335.50	319.00	349.30	379.50	239.00	429.00	203.50	209.50	184.80	226.60	233.40	79.30	209.00	302.50	644.00
23. Bundle-sheath extensions	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

Obviously, precipitation varies with elevation and slope exposure. Since the mean annual precipitation and temperature data (U.S. Dept. of Commerce, 1956-1968) assembled for various areas in California is relatively precise only in nonmountainous areas, the precipitation data for collection sites at higher elevations are modified according to Plummer's (1911) estimates (TABLE 2).

Mean temperature varies with changes in elevation, decreasing at a rate of about 3.3 F per 1,000 ft increase in altitude (Humphrey, 1962). Therefore, temperature data for collection sites at higher elevations are modified to approximate the formula stated by Humphrey (1962) (TABLE 2).

Habits, lateral stems and leaves of specimens from chaparral documenting this study are shown as follows: *Cercocarpus intricatus* Wats. (1527, Fig. 2c, d), *C. betuloides* var. *betuloides* Nutt. ex T. & G. (1521, Fig. 2a, b), and *C. minutiflorus* Abrams (1516, Fig. 3a; 1533, Fig. 3b). Included are *C. betuloides* var. *blancheae* (1518, Fig. 3c, d) and *C. traskiae* (1517, Fig. 4a, b), which are from Santa Catalina Island, California. Thorne (1967) has described the various ecological and climatological aspects of this island in his flora. It should be pointed out that *C. traskiae* is one of the relict island endemics. Only ten trees of this species are extant in the wild.

YELLOW PINE FOREST

Two species were collected in the yellow pine forest communities, at elevations ranging from 5,900 to 7,500 ft. They are as follows: *C. betuloides* var. *betuloides* (1521), *C. betuloides* var. *macrourus* (1526, Fig. 5a, b) and *C. ledifolius* Nutt. (1508, 1520).

Species associated with yellow pine forest communities are listed by Munz (1959). Generally, yellow pine forest communities lie above the chaparral and extend upward to 6,000 ft in the North Coast Ranges, to 6,500 or 7,000 ft in the Sierra Nevada, and to 8,000 ft in southern California.

Precipitation averages 25-80 in. per year. Temperatures range from a mean summer maximum of 86.5 F to a mean winter minimum of 28 F (Munz, 1959).

PINYON-JUNIPER WOODLAND

Specimens from pinyon-juniper woodland communities documenting this study are *C. ledifolius* (1504), and *C. intricatus* (1527). Munz (1959) lists the dominant indicator species for this community.

Precipitation in pinyon-juniper woodlands averages 12-20 in. annually, with some snow and summer showers. However, within the range of this community in the San Bernardino Mountains and in some areas of the White-Inyo Ranges, precipitation exceeds this level (U.S. Dept. of Commerce, 1956-1968).

Mean summer maximum temperatures are 88-95 F and mean winter minima, 20-30 F.

The pinyon-juniper woodlands occur at the east base of the Sierra Nevada, the White-Inyo Ranges southward through higher mountains of the Mohave Desert, mostly at elevations of 5,000-8,000 ft.

Fig. 2. *Cercocarpus*. Growth habits and lateral stems.—A—B. *C. betuloides* var. *betuloides* (Mortenson 1521).—A. Small tree ca. 4 m tall; hillside, Rt. 190 east of Springville, Tulare County, Calif.—B. Lateral stems and leaves. Leaves obovate to oval or broadly elliptical, 2–3 cm long, 1.5–2 cm wide, cuneate and entire below the middle, dark green and glabrous on upper surface, paler and somewhat pubescent below.—C—D.

NEVADA

Collections in Nevada are from the Charleston Mountains, which are located in west central Clark County, west and northwest of Las Vegas. According to Clokey (1951) this area, including Charleston Peak and the rugged shoulders surrounding it, contains approximately 656 square miles. Charleston Peak, with an elevation of 11,910 ft, is the only mountain in the southern Great Basin that rises above timber line. The small area above timber line is composed of talus slopes on the east side and of angular gravel produced by weathering on the other slopes. The mountains descend steeply from the summit to the foothills and alluvial fans at their base. The surrounding valleys are poorly drained and are, in some places, dry beds of old lakes. The east side of the range is characterized at middle elevations by steep slopes and by cliffs occasionally as much as 300 m high, alternating with ledges covered with talus. These cliffs are best shown in Kyle and Lee Canyons. Collections of *C. ledifolius* (1512, Fig. 5c, d) are from Kyle Canyon.

Frequently in the summer, local rains in the mountains produce flash flooding on the normally dry stream beds. Run-off is rapid on the steep slopes, and evaporation soon dries the surface of the thin soil. Winter snows vary in amount, and furnish the main supply of water for springs and seeps.

The climate on the alluvial fans and on the lower foothills is that of the Mohave Desert. Summer temperatures sometimes rise to 115–120 F, and freezing occurs in winter. With increase in elevation the climate becomes more moderate with lower temperatures and higher humidity. This is borne out by the climatological data assembled for the areas near each of the collection sites (U.S. Dept. of Commerce, 1956–1968; Toiyabe National Forest, District Office, Las Vegas, Nevada—personal communication). Mean annual precipitation for elevations of 3,500 ft, 5,000 ft, and 6,500 ft are 7.5 in., 13.5 in., and 19 in. respectively. Mean annual temperatures are 75.6 F at 3,500 ft, 70.1 F at 5,000 ft, and 63.3 F at 6,500 ft in Kyle Canyon where the collections were made.

Ponds and bogs are absent. Springs and seeps are limited in number and size. Streams are usually small and short, because water sinks into gravel beds or surface fractures. Thus the areas for hydrophytes are limited. Usually the ridges and steep slopes are dry, and at lower elevations the desert aridity is indicated by scattered trees and shrubs. Water, which may exist at higher elevations, disappears before it reaches the lower canyons.

Because of this markedly arid regime the perennials are characteristically xerophytes. During years with considerable precipitation annuals are abundant in spring and early summer; during dry years they are almost lacking except in very favorable locations.

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C. intricatus (Mortenson 1527).—C. Intricately branched, dark green shrub, ca. 3 m tall; Silver Canyon, between Bishop and Laws, Inyo County, Calif.—D. Lateral stems and leaves. Leaves to 1 cm long, 2–3 cm wide, linear, entire, marginally revolute almost to the middle, gray below.

Fig. 3. *Cercocarpus*. Growth habits and lateral stems.—A-B. *C. minutiflorus* (Mortenson 1516).—A. Small shrub, ca. 2.5 m tall; hillside, back of Tenaja Ranger Station near Murietta, Riverside County, Calif.—B. Lateral stem with obovate leaves ca. 1–2 cm long.—C-D. *C. betuloides* var. *blancheae* (Mortenson 1518).—C. Small tree, ca. 5 m tall; Wild Boar Gully (*Cercocarpus* Arroyo), Salta Verde, Santa Catalina Island, Calif.—D. Lateral stems showing leaves broadly ovate to obovate, ca. 3–4 cm long, 2.5–3 cm wide.

Below 4,500 ft the dominant shrub which forms a characteristic belt on the alluvial fans and lowest foothills is *Larrea divaricata* Cav. The dominant species found at approximately 5,000 ft elevation in Kyle Canyon was *Juniperus osteosperma* (Torr.) Little. This large shrub or sometimes small tree was quite abundant, actually forming a belt above the *Larrea* zone. This juniper occurs on dry ridges and slopes from the lower foothills to an average elevation of approximately 7,000 ft. Single individuals occasionally reach an elevation of 8,000–8,500 ft where they were observed growing with *Cercocarpus ledifolius*, *Pinus monophylla* Torr. & Frem. and *Pinus ponderosa* Dougl. ex P. & C. Lawson. The presence of yellow pine is indicative of more subsoil moisture than is present at lower elevations. The size of the trees and density of growth also provide good protection from evaporation and thus furnish a more mesic environment.

TABLE 1 provides data on elevation, precipitation and temperature. All data in this table reflect mean values of information accumulated from various sources for the years up to and including the year I collected the species. The habit and leaf description (Figs. 2–5) are based on the taxonomic treatments of Rydberg (1913, 1914), Munz (1959), and Thorne (1967). Some consideration is also given to Martin's (1950) revision of the genus *Cercocarpus*.

ANATOMICAL COMPARISONS

Species of *Cercocarpus* selected for this study are largely montane xerophytes. Leaf characteristics associated with xeromorphy have been described from leaves of different populations of the same species. Each population selected occupies a relatively small geographical area. Each area possesses its own specific set of ecological conditions such as elevation, precipitation and temperature.

At present, one cannot establish precise links between particular climatic conditions and particular modes of anatomical structure in angiosperms at large. Many authorities point out that there are no exactly defined anatomical or physiological characteristics common to the entire group of xerophytes. Each species has solved its adaptational problems within the scope of its own genetically fixed possibilities of variation. A plant possessing certain

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Fig. 4. *Cercocarpus traskiae*. Growth habit and leaves (Mortenson 1517).—A. Leaves ca. 4–5 cm long, 3–4 cm wide, coriaceous, nearly entire, upper surface with deeply impressed veins, lower surface gray, densely tomentose.—B. Small tree, ca 6 m tall; bark rough, grayish brown; branches downy-tomentose; Wild Boar Gully (*Cercocarpus Arroyo*), Salta Verde, Santa Catalina Island, Calif.

Fig. 5. *Cercocarpus*. Growth habits and lateral stems.—A–B. *C. betuloides* var. *macrourus* (Mortenson 1526).—A. Small tree, ca. 2 m tall; Humbug Mountain, below Gunsight Peak, west of Yreka, Siskiyou County, Calif.—B. Lateral stems showing broadly obovate leaves with coarse ovate teeth above the middle, ca. 3–4 cm long.—C–D. *C. ledifolius* (Mortenson 1512).—C. Small tree, ca. 6 m tall; Kyle Canyon, ca. 6,500 ft, Charleston Mountains near Las Vegas, Nevada.—D. Lateral stems showing lance-elliptic, lanceolate to oblanceolate leaves, entire with revolute margins, thick-coriaceous, glabrous above, tomentose below, ca. 3 cm long, 0.5–1 cm wide.

structural features usually seems to have become adapted to a dry habitat just as successfully as other species growing nearby that have completely different adaptational features. This is why a comparison of different species with respect to the adaptation problem is meaningful only within the confines of a particular taxonomic group such as a species or genus.

In this investigation I should like to draw attention to some factors which perhaps throw additional light on the problem of xeromorphy in general, and in which the correlation between anatomical features and the environmental factors of elevation, precipitation and temperature is, in my opinion, obvious.

The following widely accepted characteristics are used as criteria for progressive xeromorphy in the genera studied here.

- A. *External morphology*.—1. Reduction of the surfaces. 2. Revolute margins. 3. Increased thickness of the leaf.
- B. *Epidermis*.—1. Thicker cuticle. 2. Increased thickness of the outer epidermal cell walls. 3. Decreased epidermal cell size. 4. Types, density, and distribution of trichomes. 5. Increased stomatal frequency on lower epidermis. 6. Presence of stomatal crypts.
- C. *Mesophyll*.—1. Strongly developed palisade parenchyma at the expense of spongy parenchyma. 2. Greater compactness of mesophyll cells. 3. Decreased size of cells. 4. Presence of tannins and mucilage. 5. Smaller intercellular spaces. 6. Presence of hypodermis.
- D. *Vascular system*.—1. Increased size of major vascular bundles. 2. Increased frequency of vascular bundles. 3. Low frequency of bundle-sheath extensions.

Variations in leaf characteristics of each species studied are shown in TABLE 1. All figures in each table represent mean measurements. Measurements are given in micra, except for leaf length and leaf width, which are given in millimeters. Presence or absence of a characteristic is stated as "x" and "0," respectively. Percentages are shown where applicable. Environmental factors of elevation, mean annual precipitation and mean annual temperature are also provided for each species location to facilitate ease in comparison of individuals across xeric-mesic gradients.

DISCUSSION

External Leaf Morphology.—Xerophytes are dry habitat plants with transpiration decreased to a minimum under conditions of water deficiency (Maximov, 1931). The most obvious characteristic of xeromorphic leaves is the low ratio of surface to volume (McDougall and Penfound, 1928; Weaver and Clements, 1929). Reduced external area is generally accompanied by certain modifications in internal leaf structure. A discussion of these internal variations follows later.

Transeau (1904) points out that when *Rumex acetosella* L. was grown on dry sand, the leaves became thicker, smaller in size and revolute margined. Starr (1912) found that all leaves with the exception of *Populus balsamifera* L. were thicker in the dune (xerophytic) form than in the mesophytic. Philpott (1956) discovered that leaves of Carolinian shrub-

bog plants are smaller in blade area and thicker than their mesic montane vicariants. According to Shields (1951), decreased external surface of xeromorphic leaves apparently results from the greater development of palisade.

As seen in Table 1 results of this study show that decreased leaf size characterizes all species of more xeric environments.

Although revolute leaf margins are common in leaves of xeromorphic plants and occur in some species included in this investigation, this feature did not appear to be significantly intensified in any species across a mesic-xeric gradient.

Thickness of the outer walls of the epidermal cells and of the cuticle.—As can be seen from TABLE 1, *Cercocarpus ledifolius* (1508, 1509, 1512, 1520, Fig. 6), *C. minutiflorus* (1516, 1533), *C. intricatus* (1507, 1527), and *C. traskiae* (1517) have a thick outer epidermal cell wall and cuticle (more than $7\ \mu$), at least on one surface of the leaf.

Epidermal cell outer walls and cuticle of medium thickness ($4\text{--}7\ \mu$) are found only in *C. betuloides* var. *betuloides* (1511, 1531), *C. betuloides* var. *macrourus* (1526, Fig. 8e, f) and *C. betuloides* var. *blancheae* (1518).

Thin outer walls of the epidermis and a thin cuticle ($1\text{--}4\ \mu$) are characteristic of *C. betuloides* var. *betuloides* (1521, 1524).

A thick cuticle is considered to be a distinct xeromorphic characteristic because it is very common in plants of dry sunny habitats. In some of the leaves I examined, the outer wall of the epidermal cells was even thicker than the cuticle. Each is thought to have a distinct functional significance, but both act efficiently in reducing cuticular transpiration from the leaf (Linsbauer, 1930; Stålfelt, 1956; Frey-Wyseling and Muhlethaler, 1965).

The correlation between the thickness of the cuticle and outer epidermal wall and the habitat of plants cannot be considered fully clarified (Linsbauer, 1930). A thick cuticle is typical of plants in dry habitats, on the one hand, and of those in sunny habitats, on the other. However, as a rule dry habitats are sunny; the vegetation is sparse and there is little or no shading effect. A thick cuticle might conceivably afford protection against the effect of excessive light as well as excessive transpiration. Indeed, it has been found that leaves possessing a shiny cuticle may reflect a considerable proportion of the incident light; the cell tissues in the leaf will then be subjected to less heating and the chloroplasts protected against excessive radiation (Linsbauer, 1930). Schanderl and Kaempfert (1933) showed that the epidermis of shade plants was permeable to light rays (up to 98%), whereas that of mountain and desert plants having thick, cutinized outer walls of the epidermal cells, and a thick cuticle transmitted much less light (15–25%).

It has also been suggested that a thick cuticle and cuticular layer protect the inner parts of a leaf from ultraviolet radiation (Ursprung and Blum, 1917). However, closer study has shown that in numerous instances this is not true. But if the cuticular layer contains flavone pigments, as is true of numerous xerophytes, it is remarkably impermeable to ultraviolet radiation (Frey-Wyseling and Muhlethaler, 1965).

Possibly a thick cuticle and thickened outer walls of the epidermal cells

Fig. 6. *Cercocarpus ledifolius*. Anatomical features of leaf transections.—A. Midrib region. Bundle sheath and bundle-sheath extensions mostly filled with tannins; large intercellular spaces with scanty parenchyma. Tannins also fill hypodermal cells. Cuticle present. (Mortenson 1512).—B. Midrib region with numerous tannins at phloem pole,

also act to protect against the mechanical action of the wind (Weaver and Clements, 1929). It is certainly true that resistance of the leaves to bending increases with increased epidermal wall thickness.

Perhaps the thick cuticle and thick outer epidermal walls have many different functions, but I suggest that they are correlated with aridity of the habitat and low temperatures. According to Stålfelt (1956), cold temperatures may induce a stronger expression of xeromorphy more often than lack of moisture. Among the species examined, the cuticle and outer walls of the epidermal cells were thinnest in individuals from more mesic environments; thick in the majority of the types from environments intermediate between mesic and xeric; and thickest in plants from the most xeric habitats, including those plants from habitats having more than ample moisture but possessing low annual temperatures.

The specimens of *C. ledifolius* are from habitats with fairly high rainfall, but nearly all of them have a thick cuticle and outer epidermal wall. Ecologically, this type corresponds to the coriaceous-leaved evergreen trees of the Mediterranean countries which transpire copiously during the rainy season but are able to regulate water loss efficiently during the dry period by means of their stomata. No doubt a thick cuticle also helps to prevent the leaf from collapsing when it has lost water (Pisek, 1960).

The cells of the epidermis in all species studied comparatively (TABLE 2) show a decrease in size in those individuals from rather xeric environments compared to those from more mesic habitats.

Trichomes, stomatal frequency, and stomatal crypts.—Plant hairs are a most characteristic feature of plants of arid regions. Many investigators have noted that hairiness of plants varies according to their habitat. For example, hair cover is usually much more common in species of dry and sunny habitats than in those of shady and wet habitats (Vesque and Viet, 1881; Eberhardt, 1903). Where a single plant species exists in both mesic and xeric habitats, the latter is usually more hairy (Coulter, Barnes and Cowles, 1931). In the present study this is true of *Cercocarpus betuloides* var. *betuloides*, (Fig. 7) and *C. intricatus* (Fig. 9).

It has been shown that trichomes and a waxy covering have little value in reducing transpiration as long as stomata are open, but when stomata close, these modifications appear to fulfill an important protective function (Weaver and Clements, 1929).

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in bundle sheath, and bundle-sheath extension; sclereids present in xylem; mesophyll compact. (Mortenson 1520).—C. Lateral to the midrib region. More weakly developed palisade mesophyll with large intercellular spaces and scanty spongy mesophyll. Stomatal crypts present and an average of two tannin-filled hypodermal layers. Tannins present in bundle-sheath extensions. (Mortenson 1509).—D. Lateral to the midrib region. Palisade mesophyll more abundant than in 1509, thick cuticle, thicker leaves, bundle sheaths with few tannins. (Mortenson 1508).—E. Lateral to the midrib region. Tannins heavily developed in epidermis, hypodermis, bundle sheaths and their extensions. Palisade mesophyll very compact with very little spongy mesophyll. Intercellular spaces almost nonexistent. (Mortenson 1520).—(Scale: each vertical line = 10 μ .)

Fig. 7. *Cercocarpus betuloides* var. *betuloides*. Anatomical features of leaf transections.—A. Lateral to midrib region, with bundle sheaths and bundle-sheath extensions for most lateral minor veins, tannin-filled hypodermis, compact palisade, and little spongy mesophyll. (Mortenson 1531).—B. Midrib region showing central vascular bundle enclosed with tannin-filled bundle sheath. Palisade less dense in these leaves; intercellular space volume greater. Tannins present in hypodermis. (Mortenson 1424).—C. Central and lateral vascular bundles enclosed by tannin-filled sheaths and extensions. Tannins present in hypodermal cells and mucilage accumulations appear in some intercellular

If insolation is strong, the interior parts of some leaves may warm up more than those of hair-covered leaves. Baumert (1909) observed that leaves of *Centaurea candidissima* Lam. from which the hair cover had been removed could warm up as much as 37.5% more than normal leaves protected by hairs.

Haberlandt (1914) compared the normal leaf of *Stachys lanata* Crantz. with a leaf from which the hair cover on the upper side had been removed; the lower surface in both had been coated with cocoa butter. In direct sunshine, the transpiration of the leaf with the hairs removed was twice that of the normal leaf. A dense cover of woolly hair is thus seen to be an efficient protection against transpiration in direct sunshine.

Many species studied in this investigation (TABLE 2) had stomata sunken in grooves or crypts on the lower leaf surfaces. These crypts or grooves are covered with small, nonglandular trichomes. Wiegand (1910) states that these hairs do not act against the effect of excessive light. Obviously, they act as a windbreak and thus as a deterrent to excessive water loss.

Shields (1950) suggests that possibly trichome development is a response to water loss rather than a deterrent. Transpiration apparently can act as a stimulus to trichome development. There are no hairs in the vegetative bud of *Spiraea ulmaria* (Tourn.) Hill., but pubescence develops and increases as buds unfold, appearing first along the larger veins of the young leaves (Yapp, 1912). Shields (1950) also states that living trichomes do not protect the plant from excessive transpiration as do dead trichomes which form protective layers. However, leaves of *Cowania mexicana* var. *stansburiana* (Torr.) Jeps. and *Purshia glandulosa* Curran (Mortenson, 1970) possess glandular trichomes that secrete a sticky, resinous material which helps varnish the surfaces of the leaves. This material provides a protective coat impervious to water and obviously provides the leaf with an additional agent against desiccation.

Whether leaf hair cover consists of glandular or nonglandular trichomes, or both, this investigation suggests that the occurrence of hair cover may effectively reduce transpiration by providing insulation against excessive solar radiation and the desiccating effect of arid winds which prevail in the habitats of these taxa. It should also be remembered that of all anatomical features, trichomes are perhaps most often enlisted for systematic comparisons because of their variety, their almost universal presence in angiosperms, their ease of preparation and study, and the close relation of their variation patterns to the taxonomic system (Carlquist, 1961).

Increase in stomatal frequency is correlated with decrease in soil moisture.

spaces. (Mortenson 1531).—D. Midrib region showing tannin-filled hypodermis, bundle sheath, and phloem pole of central bundle. Palisade very compact with few intercellular spaces. Bundle-sheath extensions mostly without tannins. (Mortenson 1511).—E. Midrib region with tannins in hypodermis, phloem pole of central bundle, bundle sheath and its extension. Palisade less compact than in 1511 and 1531. Little spongy mesophyll, and intercellular space volume greater than in 1511 and 1531. (Mortenson 1521).—F. Lateral to the midrib region showing tannin-filled hypodermis, bundle sheaths and their extensions where they occur. Nonglandular trichomes on lower surface. (Mortenson 1521).—(Scale: each vertical line = 10 μ .)

The experiments of Penfound (1931) showed that the number of stomata per unit area was greater by 50% in dry-soil plants and by 33% in moist-soil plants when compared to that in wet-soil plants. Philpott (1956) compared the smaller, thicker leaves of some Carolina shrub-bog plants with the leaves of their mountain mesic vicariants. Higher stomatal frequencies occurred in the shrub-bog plant leaves than in their mesic mountain vicariants.

Higher stomatal frequencies were also found in xerophytes by Maximov (1929), Weaver and Clements (1929), and others.

In the present study, greater stomatal frequency was found in species from xeric habitats than in those growing in more mesic environments (TABLE 1, *Cercocarpus betuloides* var. *betuloides* and *C. ledifolius*), *C. minutiflorus* (Fig. 8d), and *C. intricatus*.

Mesophyll.—A higher ratio of palisade to spongy chlorenchyma layers has been considered, in dicotyledons, to be a xeromorphic feature (e.g., Yapp, 1912; Shields, 1950; Fahn, 1964; Esau, 1965). An early investigator, Dufour (1887), and more recently Wylie (1951), as well as numerous others have come to the conclusion that differences in palisade development in sun and shade leaves are exclusively a response to differences in light intensity. In the opinion of others, light intensity in conjunction with sufficient soil moisture is the causative factor. The studies of Boodle (1904) with *Pteris aquilina* L. and Groom (1893) with *Renanthera albescent* Lour., an epiphyte, among others, support this idea. Penfound's (1931) experiments with *Helianthus annuus* L. revealed that the leaves of sun plants which received water in adequate amount were larger than those of shade plants, but the leaves of sun plants that had suffered from drought were smaller than those of shade plants. The palisade tissue was invariably better developed in the sun leaves than in the shade leaves, although this was only evident as a lengthening of the cells, not as an increase in the number of cell layers. According to Burström (1961), conditions permitting absorption of water are an indispensable prerequisite for elongation.

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Fig. 8. *Cercocarpus*. Anatomical features of leaf transections.—A–D. *C. minutiflorus*.—A. Midrib region with tannins at phloem pole and filling the bundle sheath and its extension. (Mortenson 1533).—B. Lateral to the midrib region. Tannin-filled hypodermis, sheaths on all veins, and bundle-sheath extensions on some. Palisade mesophyll very compact. (Mortenson 1533).—C. Leaf margin, somewhat revolute with unicellular trichomes on lower surface. (Mortenson 1516).—D. Lateral portion showing much less development of palisade mesophyll, large intercellular space volume, and leaf thickness much less than 1533 (Fig. 8B). Also shown are the tannin-filled cells of the hypodermis and bundle sheaths and bundle-sheath extensions of the lateral veins. (Mortenson 1516).—E–H. *C. betuloides* var. *macrourus*. (Mortenson 1526).—E. Leaf margin showing lateral veins with tannin-filled bundle sheaths; tannins also present in the hypodermal layer underlying the epidermis. The palisade mesophyll cells are interrupted near the lower surface by numerous intercellular spaces.—F. Midrib region showing large central vascular bundle with a few tannins at the phloem pole, in the bundle sheath, often in the bundle-sheath extension and in the hypodermis.—G, H. Lateral to the midrib region and marginal transections, respectively, showing lateral veins with tannin-filled sheaths; bundle-sheath extensions present only near margin. Numerous intercellular spaces near lower surface. Small, nonglandular trichomes are scantily produced on lower surface.—(Scale: each verticle line = 10 μ .)

Amer and Williams (1958) demonstrated that thickness of the palisade tissue in leaves of *Pelargonium zonale* L'Hérit. depend on moisture conditions. The thickest palisade developed was produced in the leaves of a plant grown in dry conditions, the next thickest in one first kept in arid conditions and then watered. The leaves of a normally watered plant acquired only one palisade cell layer.

Cooper (1922), in his study on the coriaceous-leaved plants of California, noted that increased development of palisade tissue and decreased spongy parenchyma coincided with decrease in humidity and increase of light. He was conservative in his conclusions and did not want to extend them any further, but in his opinion it was natural to assume that humidity rather than light is the decisive factor.

My investigation reveals that the palisade parenchyma is maximized if the plant receives water in adequate quantity, yet not in abundance. Generally, the palisade cells are longer and occasionally thinner in ecotypes from areas of higher moisture availability, and actually are shorter in ecotypes from increasingly drier areas (TABLE 2). The inference to be drawn from this is that in leaves of xerophytes receiving abundant light a well-developed palisade parenchyma occurs only if these plants are able to transpire sufficiently (which is possible for them even in comparatively dry habitats if their root systems are extensive enough). But when the plants are forced to reduce their transpiration to a minimum, the palisade cells formed in the leaves are shorter, sometimes more narrow, or even cuboid or spherical. This opinion is supported by Bergen (1904), Haas and Halma (1932) and Turrell (1936), according to which, as a rule, leaves having a well-developed palisade parenchyma transpire more water per unit area of the epidermis than those having a less completely developed palisade tissue and less compact mesophyll. It is also consistent with the observations of Watson (1942) to the effect that in adequate light the leaves of *Hedera helix* Mitch. become thicker and their palisade parenchyma acquire a greater number of layers, provided the plant receives water in sufficient quantities.

In the foregoing it has been mentioned that extreme xerophytes have a highly compact mesophyll composed of small cells. Reduction in cell size is a concomitant of reduction in external surface area. Thus, small cell size is thought to possess significance chiefly with regard to desiccation resistance. TABLE 2 clearly shows smaller mesophyll cell size in leaves from more xeric habitats.

According to Shields (1950), compactness of spongy mesophyll varies directly with xerophily of the habitat. None of the species studied herein possess more than scattered groups of spongy cells or a short, interrupted layer of spongy mesophyll. Spongy parenchyma is almost nonexistent in many or very weakly developed. Even in habitats which could be considered more mesic, development of spongy mesophyll is minimal. Greater development of this tissue may depend on environmental factors other than mesic habitats, or it may be that the genetic potential of the species studied does not allow for much plasticity in spongy mesophyll development.

The compact quality of the mesophyll is significant in relation to the

presence and size of intercellular spaces. The presence of intercellular spaces between the palisade cells limits water transport in the plane parallel to the leaf surface (Wylie, 1943). The volume of intercellular spaces in xeromorphic leaves is smaller than that in mesomorphic leaves. However, according to Turrell (1936) the ratio between the internal free surface area of the leaf and its external surface is small in shade leaves (6:8-9:9) and large (17:2-31:3) in xeromorphic leaves. Similar results were obtained by Fahn (1964) from plants belonging to various ecological types—e.g., *Styrax officinale* L.: 8:91; *Olea europaea* L.: 17:95; *Quercus calliprinos* Webb: 18:59. Fahn (1964) further states that the increase in the free internal surface area is due to the increased development of palisade tissue. This is probably one of the reasons, besides raised photosynthetic activity, that the rate of transpiration of the xerophytes is high under conditions of a favorable water supply.

No attempt was made in this study to measure intercellular space volume or to obtain ratios as discussed above. However, it was noted from leaf transections of *Purshia tridentata* (Pursh) DC. and *Purshia glandulosa* (Mortenson, 1970), *Cercocarpus betuloides* var. *betuloides* (Fig. 7), *C. minutiflorus* (Fig. 8d), and *C. intricatus* (Fig. 9), that intercellular space volume generally increased in leaves from more mesic habitats, as did also the number of intercellular spaces per transection.

Tannins occur in all species considered in this investigation and appear to be common in xerophytes. Chemically they are water-soluble secretions that occur in cell sap, especially of parenchyma cells, of a large number of plants. They are derivatives of phenol and phenol acids, and give either dark blue or green precipitates with solutions of ferric chloride, and red or brown precipitates with safranin stain.

Very often considerable quantities of tannin are present in epidermal cells, especially in the case of leaves which persist through the winter. Some anatomists believe that compounds of this nature serve to diminish desiccation, a danger by which arctic and alpine plants in particular are often threatened, especially in the absence of snow. Tannin might also conceivably assist in preventing parasitic fungi from gaining access to the epidermal cells, and because of its strongly astringent taste and irritating properties on the digestive tract it may also protect against the assaults of animals. Some authors consider tannin in particular instances to be a reserve material capable of further utilization, but in other instances it may be purely an excretory product.

Because tannin occurs in large amounts in plants of temperate habitat—in the bark and in the epidermis of leaves which persist through the winter—one might infer that tannin can serve as a protection against frost. Since many tropical plants also contain large quantities of tannin, the substance would also seem to have some other function, perhaps protection against animals and fungi.

It seems that tannins found at a greater depth in the cellular tissues of the leaf are formed as secondary or end products of metabolism. They are not excreted externally and therefore continue to be accumulated in quantity.

Tannin-containing cells are often arranged in groups or rows in the leaves and can serve to protect against the effect of light. The accumulation of tannins in epidermal and subepidermal cells appears indeed to support this assumption, but this does not explain their occurrence in the sheath surrounding the vascular bundles, where they are, after all, very common. Tannins may lower the transpiration rate and the temperature of the plants. Because the occurrence of secretion-containing cells in the material studied was so distinctly concentrated among the plants of the arid regions, the phenomenon must be causally related to the particular thermal or light conditions of these regions.

Mucilaginous accumulations also appear in some of the intercellular spaces of *Cercocarpus betuloides* var. *betuloides* and *C. minutiflorus*. The idea that large cells containing dilute and/or mucilaginous cell sap function as water-storage tissue is discussed by Fahn (1964). Their occurrence in plants considered in this study indicates that they may be functioning in water storage because many of the species in which they appear are xerophytic. However, there is not significant variation in number or size of these cavities in plants from xeric or more mesic environments. Carlquist (1961) suggests that the size, distribution, etc., of these cavities may be useful in systematics.

Hypodermal tissue from one to several layers thick occurs beneath the leaf epidermis in all species studied. In his study of the leaf structure of *Abies* (Tourn.) L., Fulling (1934) states that physiologically the hypodermis provides partial protection against injury and extreme desiccation, with the epidermis sharing in this function. The implication made is that both hypodermis and epidermis provide mechanical strength and prevent water loss from the leaf. In his work on *Atriplex* (Tourn.) L., Black (1954) refers to hypodermal cells as functional in water storage. He reasons that since this tissue is inside the epidermis and in direct contact with palisade assimilating cells, a transfer of water conceivably could take place from the large hypodermal cells back to the much smaller palisade cells, even under the conditions of active transpiration because of the difference between their respective surface/volume ratios.

Individuals of *Cowania mexicana* var. *stansburiana* and *Purshia tridentata* (Mortenson, 1970) that occur in more xeric habitats possess greater amounts

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Fig 9. *Cercocarpus intricatus*. Anatomical features of leaf transections.—A. Shows revolute margin, thick palisade, and dense lateral venation. Below the cuticle and epidermis lie 2–3 layers of tannin-filled hypodermal cells. Nests of tannin cells extend deeply into the mesophyll in places. Lateral veins housed by parenchymatous bundle sheaths; the major vein is enclosed by tannin-filled bundle sheath. Tannins are present in the bundle-sheath extension. Intercellular space volume is much less than in 1527. Stomatal crypts are lined with small, nonglandular trichomes. (Mortenson 1507).—B. Shows epidermis, tannins in hypodermis, bundle sheaths and their extensions of major and minor veins. Palisade development is less and intercellular space volume greater than in 1507. Stomatal crypts are lined with small, nonglandular trichomes, and are almost completely enclosed by revolute leaf margins. (Mortenson 1527).—(Scale: each verticle line = 10 μ .)

Fig. 10. *Cercocarpus*.—A. *C. traskiae*. Cleared leaf showing huge central bundle with smaller lateral veins, $\times 2$. (Mortenson 1517).—B–E. Anatomical features of leaf transections.—B–C. *C. betuloides* var. *blancheae*. (Mortenson 1518).—B. Midrib region showing tannins in hypodermis, phloem pole of bundle, and bundle sheath. Large, thin-walled parenchyma cells occupy the region outside the bundle sheath.—C. Lateral to midrib showing epidermis, tannin-filled hypodermal layer, compact mesophyll with numerous lateral veins (most of which are enclosed by parenchymatous bundle sheaths), bundle-sheath extensions, and intercellular spaces.—D–E. *C. traskiae*.

of hypodermis than those from more mesic environments. Thus, hypodermis in these xeric ecotypes may function as water-storage tissue and may even provide added mechanical strength to leaves.

The presence of large amounts of tannins in the hypodermis of *Cercocarpus betuloides* var. *betuloides* (Fig. 7), *C. ledifolius* (Fig. 6), *C. minutiflorus* (Fig. 8a-d), *C. betuloides* var. *blancheae* (Fig. 10b, c) and *C. traskiae* (Fig. 10d, e) suggests additional protection against desiccation if tannins indeed provide a shading effect against insolation.

Vascular system.—According to Philpott (1956) and Wylie (1952), dense venation, characteristic of many xerophytes, is associated with a low frequency of bundle-sheath extensions, although Wylie (1952) admits the incompleteness of his study. As can be seen in TABLE 1, venation is more dense in leaves from more xeric habitats, yet bundle-sheath extensions are present. In *C. betuloides* var. *betuloides* (Fig. 7), *C. ledifolius* (Fig. 6), *C. intricatus* (Fig. 9), and *C. traskiae* (Fig. 10d, e) these bundle-sheath extensions possess tannins, which conceivably could be providing additional shading from insolation.

The size and frequency of vascular bundles in xerophytes studied in this investigation is of significance. On the whole, the increase in quantity of vascular tissue and size of the major bundles is associated with drier conditions in the regions from which material for this study was collected. This increase seems to occur in direct proportion to increased xerophily of habitats, but only mildly so with *C. ledifolius* (TABLE 2). This is consistent with other observations, according to which more conductive and mechanical tissue is generally formed in sun leaves and leaves of dry habitats (succulents excluded) than in those of shade plants, plants of mesic sites, or aquatic plants (Starr, 1912; Maximov, 1929).

Vascular tissue helps sustain the leaf by preventing the wind from bending it, by which action air containing water vapor could be pumped out of the intercellular spaces. Maximov (1929) and especially Stålfelt (1956) recognized the significance of this reinforcing tissue in connection with the occasional wilting of leaves. In a wilted leaf the risk of mechanical damage to the cell contents was thought to increase when the wind had a chance to bend and batter the leaf.

Additionally, the abundance and increased size of vascular tissue in many plants of this study could be because these plants possess rather coriaceous leaves that are exposed to very arid conditions during part of the year. Well-developed vascular tissue would produce a very strong structural framework, and its cells would probably be safe from wilting even in the case of complete water loss.

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(Mortenson 1517).—D. Large central vascular bundle showing great concentration of tannins.—E. Lateral to midrib showing large tannin-filled hypodermal layer and bundle sheaths. Bundle-sheath extensions may not have tannins within. Intercellular spaces present. Numerous nonglandular trichomes line the stomatal crypts.—(Scales: upper right, B; lower left, D; lower right, C, E. Each verticle line on the scales = 10 μ .)

In ensuing investigations, I shall attempt to determine whether or not cotyledon, seedling leaf, and wood anatomy of the same species employed in this study possess patterns with parallel ecological significance.

SUMMARY

This investigation stresses analysis of leaf anatomy in relation to ecological factors in selected species of *Cercocarpus* (Rosaceae). One to four collection sites for each species were chosen in California and Nevada. Each site possessed ecological factors of elevation, mean annual precipitation and temperature distinct from the others. The purpose was to establish an ecological xeric-mesic gradient for those species in which variations in leaf characteristics could be compared. Mean measurements of widely accepted xeromorphic leaf characteristics were calculated for each species.

Mesoxeromorphs, those growing in more mesic environments, when found also in xeric habitats, show the following modifications of the leaf: decrease in overall leaf size; increase in leaf thickness at major and minor vascular bundles; sometimes an increase in outer epidermal cell wall and cuticle thickness; a decrease in epidermal cell height; increase in stomatal frequency, trichome cover, and stomatal crypts; decrease in length of palisade parenchyma cells and an increase in width of same; decrease in the number of intercellular spaces; sometimes an increase in the number of hypodermal cell layers (never a decrease); increase in frequency of vascular bundles; and an increase in diameter of major vascular bundles for a majority of the species.

Other features considered xeromorphic were present, yet appeared not to vary significantly with the ecological factors considered in this investigation. They are: revolute leaf margins; tannins; mucilage cavities and accumulations. Low frequency of bundle-sheath extensions has been considered to be associated with the xeromorphic feature of dense venation, however, bundle-sheath extensions were present in most species.

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