

ECOLOGICAL WOOD ANATOMY OF THE WOODY SOUTHERN CALIFORNIAN FLORA

by

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Summary

Wood of 207 species, representing all 178 woody genera of the Munz flora of southern California, was studied by means of sections and macerations. Data were gathered on features relating to the conducting system: number of vessels per mm², diameter of vessels, length of vessel elements, number of bars per perforation plate, presence of true tracheids, vasicentric tracheids, vascular tracheids, helical sculpture, and growth rings. The occurrence of these features is analysed both with respect to each other and to ecological groupings and habit groupings. Statistically significant data permit ecological groupings to demonstrate degree of xeromorphy in wood features. Xeromorphy is indicated by more numerous vessels per mm², narrow vessels, shorter vessel elements, presence of vasicentric tracheids or vascular tracheids, presence of helical sculpture on vessel walls, and presence of well-marked growth rings (growth rings are common in moist habitats because in southern California these are also montane and therefore cold in winter). All of these appear to have developed in many phylads independently. Vessel element length appears to change less rapidly, at least in some phylads (those with true tracheids) than the other features. Presence of scalariform perforation plates and of true tracheids is interpreted as relictual; scalariform plates occur virtually only in mesic habitats and in a small number of species. True tracheids, although relictual in nature, have been preferentially preserved because of the value of their enormous safety. Groups without true tracheids have evolved vasicentric tracheids or vascular tracheids (the three types are mutually exclusive) to a high degree. By deducting the species with true and vascular tracheids, one finds that 100% of the alpine shrubs, 77% of the desert shrubs, and 75% of the chaparral shrubs which could possibly have evolved vasicentric tracheids actually have them. These are the three ecological groupings which have vasicentric tracheids not only in southern California, but other areas of the world as well. Tracheid presence (and to a lesser extent vasicentric tracheid presence) fore-

stalls vessel grouping, but in tracheid-free groups vessel grouping is a highly adaptive strategy for xeromorphy. One can rank xeromorphic connotation of qualitative features on the basis of data herein: growth rings are the most common numerically, followed by helical sculpture, vasicentric tracheids, and vascular tracheids. Vasicentric tracheids, like true tracheids, tend to occur in evergreen shrubs whereas vascular tracheids tend to be related to drought-deciduous shrubs. Among quantifiable features, number of vessels per mm² changes more rapidly than vessel diameter. Scalariform perforation plates, true tracheid presence, and long vessel elements are associated with each other statistically. By entering number of woody species for each genus in the flora and performing appropriate computations, a figure for each feature is projected on the basis of the 512 woody species of southern California. This pro-rated figure shows that phylads with any of the mechanisms cited as signifying xeromorphy speciate much more rapidly than do the phylads with mesomorphic wood features.

Key words: Ecological wood anatomy, southern Californian flora, wood anatomy, wood evolution.

Introduction

Analysis of wood anatomy on a floristic basis can be traced to such authors as Kanehira (1921a & b, 1924), Webber (1936), Versteegh (1968), Carlquist (1977a), and Baas et al. (1983). To be sure, our understanding of which features are significant in ecological analysis of wood anatomy on a floristic basis have also come from other sources: the works of Baas (1973) and Carlquist (1966a, 1975a, 1980) can be cited.

The reasons for analysis of the southern Californian flora at this time include the knowledge gained from the works mentioned above, for without an understanding of which characters possess ecological significance, such an analysis would be premature. To be sure, new understanding is yielded within the confines of each study, so that reliance on previous studies is not total. The southern Californian flora proves

exceptionally revelatory of the ecological value of wood features because of its size and ecological diversity. The genera studied here represent 178 genera (Table 1), which include all of the genera with woody species listed by Munz (1974), plus a few selected herbaceous groups to widen the comparison. There are 512 species which can be claimed to be woody in the Munz flora; study of all of these was impractical, and probably would not have increased understanding very greatly. Where habit and ecology varied, several species per genus were, in fact, studied (e.g., *Arctostaphylos*, *Haplopappus*). The results obtained from the 207 species studied were projected (Table 2, last line; see Materials and Methods) so as to produce a picture of what would have emerged had all 512 woody species been studied. The large number of woody species in the southern Californian flora does permit a clear picture of trends within the flora as a whole and within floristic and habitat fractions; a smaller floristic unit could not have yielded the large number of species (N values) available here. While southern California as defined by Munz is not itself a natural floristic province, it does contain large numbers of taxa for most of the ecological zones in this region.

The ecological zones of southern California are diverse because of the remarkable topography of this region. To be sure, it does not include high rainfall zones, but it does give an unusually clear picture of Mediterranean-type vegetation and desert vegetation because of the large numbers of genera and species in these zones. In the Mediterranean-type region, one can demonstrate wood features not merely for the chaparral, a sclerophyll scrub of the foothills and mountains, but also for coastal sage, a shrubby vegetation composed chiefly of representatives of families which are otherwise not strongly woody (e.g., Asteraceae, Lamiaceae) in which leaves are not sclerophyllous typically. In the desert region, one can analyse desert scrub, desert wash plants, and desert succulents separately. Additionally, other distinctive ecological zones are represented in the woody flora (Table 2). Riparian vegetation and alpine vegetation represent distinctive zones which contrast with the various kinds of dryland scrub, and further contrasts are provided by woodland trees, halophytes, and shrubs of moist areas (chiefly shady valleys).

The herbaceous flora of southern California is quite prominent; it grades into subshrubs, which form a category analysed separately here. The term 'herbs' in Table 2 refers to annuals, biennials, short-lived perennials, and two plants which are large but have a degree of succulence ordinarily associated with herbs (*Core-*

opsis gigantea, *Turricula parryi*). The herbs included in this study have been excluded from the habitat categories so as not to bias the data for chaparral (which thereby is strictly shrubby) or other zones. Herbs utilise soil differently from shrubs and either die at the end of the growing season or accommodate environmental extremes differently from the ways in which shrubs do. Therefore, their exclusion from habitat categories such as chaparral seems justified. Only a limited number of herbs have been admitted into this study. The reason for their inclusion is to permit a contrast between herbaceous and woody species growing in the same region, thereby permitting a better understanding of both. The number included (16) is small enough so that the categories of Table 2 other than habit and habitat (= the anatomical categories) are biased very little; one could recalculate non-herb versions of that portion of the table, and a few such figures are offered below. However, inclusion of herbs in the anatomical categories does have the merit of stressing the continuum between herbaceous and woody in the flora of southern California. Especially in the coastal sage, where frost is rare, brief, or mild, herbaceous phylads have evidently evolved (and are still evolving) into woodier growth forms.

The anatomical features covered in this survey are those which have been shown to bear a direct relationship to ecological conditions. Vessel wall thickness has been omitted, although it does appear to be correlated with ecology (Carlquist, 1975a, 1980; Baas et al., 1983). The other features omitted here can be said to bear only an indirect relationship to the hydrosystem: ray characteristics, axial parenchyma configurations, crystal presence. Fibre-tracheids are not considered here to be conductive in nature; the evidence for this comes from the effect that tracheids have in deterring vessel grouping (Carlquist, 1984a), an effect fibre-tracheids do not have, and the differentiation between vascentric tracheids and fibre-tracheids in woods which have those two cell types together (Carlquist, 1985). Tracheids are defined as having pits fully bordered, as large as those on lateral walls of vessels or nearly so, and with pit density approaching (but often not equalling) that on lateral walls of vessels. Fibre-tracheids are considered to show diminution in one or more of the pit features listed for tracheids. Libriform fibres are defined as having simple pits.

Although we think of tropical areas, frequently, as predominantly moist, ranges of ecology do occur within those zones and are related to ranges within anatomical features

(e.g., *Dillenia*, Dickison, 1979). However, there can be no doubt that the adaptive nature of the conductive system of dicotyledons is best studied in areas of more marked water stress. Although cool regions may provide physiological drought (e.g., water is unavailable when the ground freezes), regions which are both hot and dry offer the most clearly delineated examples of how water stress influences adaptations in secondary xylem.

Attention is called to details and concepts in the Materials and Methods section, since those factors influence the interpretation of data.

Wood versus other features in water relations

A central question of ecological wood anatomy is the extent to which wood anatomy is operative in comparison with other features of a plant as a way of dealing with water stress conditions. The evidence at hand, as well as that presented below, show clearly that indeed patterns of wood anatomy do follow ecology closely (Carlquist, 1959). However, as noted earlier (Carlquist, 1977a), one must take into account adaptations other than wood features, and such phenomena as succulence, C₄ photosynthesis, CAM, and deciduousness of foliage were cited.

Eriodictyon (Hydrophyllaceae) has wood features which are not strongly xeromorphic by most criteria currently cited (Table 1). One must first note that *Eriodictyon* does possess true tracheids, which certainly offer considerable safety. However, when one studies *Eriodictyon* in the field, water management mechanisms of a striking sort can be seen. Stems are innovated from roots which have succulent cortex and great longevity; the stems vary in size and longevity and thus can suit the severity of the growing season. More significantly, stems can experience various degrees of dieback without jeopardising the basic plant size as dictated by root system. The most widespread species of *Eriodictyon* (*E. trichocalyx*) has a heavy coating of resinous varnish on the leaves. Although observations indicate this varnish may function primarily as a device to deter predation by beetles, the varnish very likely also reduces transpiration.

During May 1984, the senior author examined shrubby vegetation above 3000 m on Mt. San Jacinto. The dominant shrub at these elevations is *Chrysolepis sempervirens*. Although the wood of this species qualifies as xeromorphic (Table 1), the extreme drought of the preceding year on Mt. San Jacinto evidently was supralimital for foliage or wood tolerances; nearly every shrub on the mountain experienced considerable dieback. Such dieback is not an

annual event, as examination of shrubs reveals. However, this species obviously has the capability of sacrificing branches and thereby surviving.

Obviously extensive dieback during most years is not a useful strategy for a tall shrub, much less a tree — the height of such plants could not be maintained and the canopy status would be lost. However, for non-canopy shrubs of open areas, degrees of dieback form important strategies for dealing with exceptionally bad seasons while remaining capable of taking advantage of favourable seasons. This kind of strategy is especially seen in coastal sage plants, such as *Artemisia*, *Eriogonum*, *Haplopappus*, and *Salvia*.

Another feature that must be appreciated in the southern Californian flora is the role of drought-deciduous foliage. This phenomenon takes various forms. *Aesculus californica* (Hippocastanaceae) characteristically sheds leaves in July. In *Toxicodendron* (Anacardiaceae), stems may lose leaves from June to October, depending on the nature and location of the plant; earlier deciduousness can be a response to drought, later deciduousness to cold. Genera such as *Eriophyllum* (Asteraceae) and *Keckiella* (Scrophulariaceae) tend to lose leaves gradually in proportion to progress of drought; some stems may also be lost as drought becomes more extreme. *Fremontodendron californicum* (Sterculiaceae) has broad leaves during the moist but frost-free months; with progressive dryness, larger leaves are lost, and the photosynthetic apparatus may consist of stems only, or stems plus small leaves during the dry season. *Isomeris arborea* (Capparaceae) tends to reduce foliage gradually, so that at least a few leaves are present at all times. Interestingly, all of the genera named here as drought-deciduous have vascular tracheids, whereas characteristically evergreen shrubs in the southern Californian flora typically have true tracheids or vasicentric tracheids.

In the evergreen sclerophyll shrubs, there may be transpiration-lowering mechanisms that can be demonstrated only by experimental means. Mooney et al. (1975) have shown mid-day stomatal closure for *Heteromeles arbutifolia*; similar reduction of transpiration has been demonstrated for macchia (maquis) species by Rouschal (1938) and Tenhunen et al. (1981). This phenomenon has also been reported in desert shrubs (Schulze et al., 1980).

Enough is known about patterns of roots in shrubs of this general region to suggest that root depth and extent may be important factors in water economy of plants. Cannon (1911), working in an area of Arizona comparable to

(text continued on page 328)

Table 1. Wood features related to conduction for species of all native woody genera in the Munz flora of southern California.

V/M = number of vessels per mm²; VD = mean vessel diameter, μ m; VL = mean vessel element length, μ m; V/G = mean number of vessels per group; BR = bars present on scalariform perforation plates, mean number; T = true tracheid presence; I = vascular tracheid presence; A = vascular tracheid presence; SC = helical sculpture presence (earlywood; latewood); G = growth ring presence; MESO = mesomorphy ratio (vessel diameter divided by vessels per mm² times vessel element length). In growth rings, + = ring-porous, - = semi-ring-porous, 0 = diffuse-porous. In other features, + = present, 0 = absent. Habitat column (HA) abbreviations: H = herbs; S = shrub; SS = subshrub; T = tree; V = vine. Habitat column (HI) abbreviations: AL = alpine; CH = chaparral shrub; CS = coastal sage, DS = desert scrub; DW = desert wash; HA = halophyte; MS = moist; PA = parasite; RI = riparian; SU = succulent; WO = woodland. For further information, see Material and Methods.

	V/M	VD	VL	V/G	BR	T	I	A	SC	G	MESO	HA	HI
Acanthaceae	146	49.8	245	1.96	0	0	+	0	--	-	83.6	S	DW
Aceraceae	83.9	43.5	407	2.04	0	0	0	0	++	-	211	T	RI
Adoxaceae	342	32.1	327	6.35	0	0	0	+	--	-	30.7	S	CH
	147	43.7	438	3.7	0	0	0	+	--	-	130	S	CH
Anacardiaceae	37.4	59.2	297	1.4	0	0	0	0	--	0	470	S	CS
	65.7	37.3	216	1.88	0	0	0	0	--	+	123	S	CS
Asclepiadaceae	196	20.9	224	2.85	0	0	+	0	--	-	23.9	SS	DS
Asteraceae	130	53	192	1.69	0	0	0	0	--	-	78.3	H	-
	199	29.9	167	10.6	0	0	0	+	--	+	25.1	SS	DS
	101	43.2	107	3.65	0	0	0	0	--	-	45.8	S	CS
	866	28.4	140	6.85	0	0	0	0	++	-	4.59	S	DS
	161	30.7	216	3.27	0	0	0	0	--	0	41.2	SS	DS
	269	32.2	184	29	0	0	0	0	++	+	22	S	MS
	155	37.8	135	6.1	0	0	0	0	++	-	32.9	S	CS
	127	55.6	163	1.52	0	0	0	0	--	-	71.4	S	DW
	128	53	183	1.94	0	0	0	0	--	+	75.8	S	CS
	302	25.5	126	16.6	0	0	+	0	--	+	10.6	S	DW
	662	13.9	128	13.1	0	0	+	0	--	+	2.69	S	AL
	300	38.2	124	4.9	0	0	+	0	--	+	15.8	S	DS
	51.2	36.7	210	2.24	0	0	0	0	--	-	151	H	-
	108	40.3	123	1.6	0	0	0	0	--	0	45.9	S	DS
	330	36.1	153	2.36	0	0	0	0	++	+	16.7	SS	CS
	344	27.6	182	2.7	0	0	+	0	--	+	14.6	SS	DS
	101	29.8	137	3.95	0	0	+	0	--	+	40.4	S	CS
	304	36.4	169	5.7	0	0	+	0	--	-	20.2	S	CS
	440	28.3	135	5.1	0	0	+	0	--	+	8.68	S	DS
	105	35.2	123	2.17	0	0	+	0	--	+	41.2	S	CS

(<i>Asteraceae</i> continued)	501	29	129	3.55	0	0	0	0	0	0	0	0	+	+	7.47	S	DS
<i>Hecastocleis shockleyi</i> Gray	131	33	133	1.6	0	0	0	0	0	0	0	0	---	---	33.5	SS	CH
<i>Hemizonia minthornii</i> Jepson	191	27.6	106	1.7	0	0	0	0	0	0	0	0	++	+	15.3	S	DS
<i>Hymenoclea salsola</i> T. & G.	93.9	44	104	2.25	0	0	0	0	0	0	0	0	---	+	48.7	SS	HA
<i>Iva axillaris</i> Pursh	203	49.9	164	17	0	0	0	0	0	0	0	0	---	0	40.3	S	CS
<i>Lepidospartum squamatum</i> (Gray) Gray	66.9	60	195	2.03	0	0	0	0	0	0	0	0	---	0	175	S	CS
<i>Malacothrix saxatilis</i> (Nutt.) T. & G.	49.4	44	172	2.6	0	0	0	0	0	0	0	0	---	+	153	S	CS
<i>Munrothamnus blairi</i> (M. & J.) Raven	89.8	20.6	161	3.5	0	0	0	0	0	0	0	0	---	0	36.9	S	DS
<i>Peucephyllum schottii</i> (Gray) Gray	72.3	36.7	239	2.4	0	0	0	0	0	0	0	0	---	0	121	S	MS
<i>Pluchea sericea</i> (Nutt.) Cov.	178	36.4	190	1.96	0	0	0	0	0	0	0	0	---	0	38.9	S	CS
<i>Senecio douglasii</i> DC.	164	44	266	3	0	0	0	0	0	0	0	0	---	0	71.4	H	-
<i>Stephanomeria exigua</i> Nutt.	664	17.2	199	7.52	0	0	0	0	0	0	0	0	---	+	5.15	S	DS
<i>Tetradymia glabrata</i> Gray	59	38.5	240	2.2	0	0	0	0	0	0	0	0	---	0	157	S	CS
<i>Venegasia carpesioides</i> DC.	94	35.7	102	1.84	0	0	0	0	0	0	0	0	---	0	38.7	SS	HA
<i>Batis maritima</i> L.	501	16.1	221	20	0	0	0	0	0	0	0	0	++	---	7.1	S	CH
<i>Berberis nevadensis</i> Gray	166	50	643	1.92	12	0	0	0	0	0	0	0	---	---	194	T	RI
<i>Alnus rhombifolia</i> Nutt.	154	27.1	426	2.4	18	0	0	0	0	0	0	0	---	---	75	S	MS
<i>Betula fontinalis</i> Sarg.	30.1	86.7	132	1.48	0	0	0	0	0	0	0	0	---	+	380	T	DW
<i>Chilopsis linearis</i> (Cav.) Sweet	218	24.7	167	1.92	0	0	0	0	0	0	0	0	---	+	18.9	S	DS
<i>Lepidium fremontii</i> Wats.	214	26.5	153	4.44	0	0	0	0	0	0	0	0	---	+	18.9	S	DW
<i>Stanleya pinnata</i> (Pursh) Britt.	303	27	156	1.76	0	0	0	0	0	0	0	0	++	---	13.9	S	DS
<i>Buddleja utahensis</i> Cov.	34.3	79.1	321	2.55	0	0	0	0	0	0	0	0	---	---	740	S	SU
<i>Bursera microphylla</i> Gray	38	53.5	330	1.6	0	0	0	0	0	0	0	0	---	+	465	S	SU
<i>Bergerocactus emoryi</i> (Engelm.) B. & R.	68.1	84.6	414	1.7	0	0	0	0	0	0	0	0	---	0	514	T	SU
<i>Carnegiea gigantea</i> (Engelm.) B. & R.	22.9	37.7	157	1.8	0	0	0	0	0	0	0	0	---	+	258	SS	SU
<i>Echinocactus polycephalus</i> E. & B.	72.3	26.2	261	2.95	0	0	0	0	0	0	0	0	---	+	94.6	SS	SU
<i>Echinocereus engelmannii</i> (Parry) Lem.	45.2	46.7	166	1.6	0	0	0	0	0	0	0	0	---	+	172	S	SU
<i>Ferocactus acanthodes</i> (Lem.) B. & R.	36.2	48	213	2.01	0	0	0	0	0	0	0	0	---	+	282	SS	SU
<i>Mammillaria dioica</i> K. Bge.	51.8	43	142	2.2	0	0	0	0	0	0	0	0	---	+	118	S	SU
<i>Opuntia acanthocarpa</i> E. & B.	36.8	62.6	189	1.65	0	0	0	0	0	0	0	0	---	---	322	S	SU
<i>O. bigelovii</i> Engelm.	320	21.5	111	5.1	0	0	0	0	0	0	0	0	---	0	7.46	S	CH
<i>Isomeris arborea</i> Nutt.	403	23.5	267	3.25	0	0	0	0	0	0	0	0	++	+	15.6	S	AL
<i>Symphoricarpos mollis</i> Nutt.	686	20	193	1.08	0	0	0	0	0	0	0	0	---	+	5.63	S	DS
<i>Mortonia urahensis</i> (Cov.) Nels.	183	16.3	80.1	5.2	0	0	0	0	0	0	0	0	---	+	7.13	S	HA
<i>Atriplex polycarpa</i> (Torr.) Wats.	247	18.2	61.9	2.24	0	0	0	0	0	0	0	0	---	+	4.56	S	DS
<i>Ceratoides lanata</i> (Pursh) J.T. Howell	232	23.2	76.4	5.4	0	0	0	0	0	0	0	0	++	+	7.64	S	DS
<i>Grayia spinosa</i> (Hook.) Moq.	341	21.5	192	1.33	0	0	0	0	0	0	0	0	---	+	12.1	SS	CH
<i>Helianthemum scoparium</i> Nutt.	47.6	85.7	334	1.08	35	+	0	0	0	0	0	0	---	---	601	S	RI
<i>Cornus nuttallii</i> Aud.						+	0	0	0	0	0	0	---	---			

Table 1 (continued)

	V/M	VD	VL	V/G	BR	T	I	A	SC	G	MESO	HA	HI
Crossosomataceae													
	185	21.2	365	1.24	0	+	0	0	---	---	41.8	S	CH
<i>Forselleia nevadensis</i> (Gray) Greene	453	13.7	296	1.11	0	+	0	0	---	+	8.95	S	DS
<i>Datisca glomerata</i> (Presl) Baill.	42.2	73.8	157	1.96	0	0	0	0	---	0	275	H	---
Elaeagnaceae													
<i>Shepherdia argentea</i> Nutt.	290	31	237	1.11	0	+	0	0	---	+	25.3	S	DW
<i>Arbutus menziesii</i> Pursh	259	23.4	413	2.1	0	0	+	0	++	---	37.3	T	MS
<i>Arctostaphylos glandulosa</i> Eastw.	288	22	291	1.65	0	0	+	0	++	---	22.2	S	CH
<i>A. glauca</i> Lindl.	449	18.1	312	1.64	0	0	+	0	++	+	12.6	S	CH
<i>A. patula</i> Greene	366	18.9	204	1.28	0	0	+	0	++	+	10.5	S	AL
<i>Comarostaphylos diversifolia</i> (Parry) Greene	65.1	30.2	324	1.08	0	0	+	0	++	+	169	S	CH
<i>Ornithostaphylos oppositifolia</i> Small	102	29.1	228	1.43	0	0	+	0	++	---	65	S	CH
<i>Phyllocoe breweri</i> (Gray) Heller	831	14.1	244	2.36	8	+	0	0	---	---	4.14	S	AL
<i>Rhododendron occidentale</i> (T. & G.) Gray	570	33.9	272	1.1	4	+	0	0	---	---	16.2	S	RI
<i>Vaccinium ovatum</i> Pursh	495	16.6	390	1.75	18	+	0	0	---	---	13.1	S	MS
<i>Xylococcus bicolor</i> Nutt.	337	20.1	206	1.8	0	0	+	0	++	---	12.3	S	CH
Euphorbiaceae													
<i>Acalypha californica</i> Benth.	207	29	363	3.8	0	0	0	0	---	---	50.9	S	CH
<i>Bernardia incana</i> Mort.	447	18.1	186	2.07	0	0	+	0	++	+	7.53	S	DS
<i>Tetracoccus dioicus</i> Parry	312	22	599	1.04	0	0	0	0	++	+	42.2	S	DS
<i>Acacia greggii</i> Gray	28.4	42.2	181	2.28	0	0	0	0	---	+	269	S	DW
<i>Amorpha fruticosa</i> L.	93	44.4	162	1.09	0	0	0	+	++	+	77.3	S	CS
<i>Calliandra eriophylla</i> Benth.	187	26.1	137	2.95	0	0	0	+	---	+	19.1	S	DW
<i>Cassia armata</i> Wats.	182	24.6	113	1.45	0	0	+	0	++	+	15.3	S	DW
<i>Cercidium floridum</i> Benth.	35.6	54.2	205	2.44	0	0	0	+	++	+	312	T	DW
<i>Cercis occidentalis</i> Torr. ex Gray	101	42.8	233	2.44	0	0	0	+	---	+	98.7	T	CH
<i>Dalea spinosa</i> Gray	90.4	35.9	159	7.1	0	0	0	0	---	0	63.1	T	DW
<i>Lotus scoparius</i> (Nutt.) Otlely	155	23.7	124	2.92	0	0	0	+	---	0	19	SS	CS
<i>Lupinus albitrions</i> Benth.	139	32.4	152	2.4	0	0	0	0	---	---	35.4	S	CS
<i>Oleia tesota</i> Gray	25.9	80	183	2.88	0	0	0	+	---	0	565	S	DW
<i>Pickeringia montana</i> Nutt.	283	22.4	140	3.48	0	0	+	0	++	+	11.1	S	CH
<i>Prosopis pubescens</i> Benth.	68.1	47.4	162	2.88	0	0	+	0	---	---	113	S	DW
<i>Chrysolepis sempervirens</i> (Keil.) Hjelm.	177	31.2	305	1.12	0	0	0	0	---	---	53.8	S	AL
<i>Lithocarpus densiflora</i> (H. & A.) Rehd.	17.5	53.6	641	1	0	0	+	0	---	---	1960	T	WO
<i>Quercus chrysolepis</i> Liebm.	10.8	84.5	336	1	0	0	+	0	---	---	2630	T	WO
<i>Q. dumosa</i> Nutt.	32.5	52.4	306	1	0	0	+	0	---	---	493	S	CH
<i>Fouquieria splendens</i> Engelm.	147	36.8	359	1.76	0	+	0	0	---	---	89.9	S	DS
Frankeniaceae													
<i>Frankenia grandifolia</i> C. & S.	263	19.9	115	1.12	0	0	+	0	---	0	8.7	SS	HA

Garryaceae	<i>Garrya veatchii</i> Kell.	145	22.4	573	1.08	5	+	0	0	---	---	88.5	S	CH	
Grossulariaceae	<i>Ribes cereum</i> Dougl.	391	19.6	313	1.56	0	+	0	0	---	---	15.7	S	AL	
Hippocastanaceae	<i>Aesculus californica</i> (Spach) Nutt.	294	29.4	329	3.12	0	0	0	0	++	+	32.9	T	CH	
Hydrophyllaceae	<i>Eriodictyon angustifolium</i> Nutt.	137	60	360	1.32	0	+	0	0	---	+	158	S	DS	
	<i>E. trichocalyx</i> Heller	20.1	45	240	1.25	0	+	0	0	---	+	537	S	CS	
	<i>Phacelia floribunda</i> Greene	56	50	240	3.28	0	0	0	0	---	---	214	H	---	
Juglandaceae	<i>P. ramosissima</i> Dougl.	205	53	101	1.55	0	0	0	0	---	---	26.1	H	---	
	<i>Turricula parryi</i> (Gray) Macbr.	127	53	343	1.2	0	+	0	0	---	---	143	H	---	
	<i>Juglans californica</i> Wats.	29.5	95.4	385	1.45	0	0	0	0	---	---	1250	T	WO	
	<i>Koerberlinia spinosa</i> Zucc.	245	18.1	229	1.04	0	+	0	0	++	+	16.9	S	DS	
	<i>Krameria parviflora</i> Benth.	409	23.9	186	1.25	0	+	0	0	---	+	10.9	S	DS	
	<i>Hyptis emoryi</i> Torr.	48.8	63.8	254	1.6	0	0	0	0	---	---	332	S	DW	
Lamiaceae	<i>Lepechinia calycina</i> (Benth.) Epling	533	21.4	209	8.1	0	0	0	0	---	---	8.39	SS	CH	
	<i>Monardella linoides</i> Gray	303	19.7	177	2.16	0	0	0	0	++	+	11.5	SS	CH	
	<i>Salazaria mexicana</i> Torr.	268	24.5	142	2	0	0	0	0	++	+	13	S	DW	
	<i>Salvia dorrii</i> (Kell.) Abrams	697	19.3	162	3.2	0	0	0	0	++	+	4.49	S	DS	
	<i>S. mellifera</i> Greene	241	21.6	166	3.6	0	0	0	0	++	+	14.9	S	CH	
	<i>Trichostema lanatum</i> Benth.	328	18.2	182	1.34	0	0	0	0	++	+	10.1	S	CH	
	<i>Umbellularia californica</i> (H. & A.) Nutt.	34.9	57.2	333	2.32	0	0	0	0	---	---	546	T	RI	
	<i>Eucnide urens</i> Parry	29	86	269	1.6	0	0	0	0	---	---	0	798	SS	SU
	<i>Mentzelia laevicaulis</i> (Dougl.) T. & G.	46	61	490	1.9	0	0	0	0	---	---	0	650	H	---
	<i>Petalonyx linearis</i> Greene	36	63	258	1.17	0	0	0	0	---	---	0	452	SS	SU
Malvaceae	<i>P. nitidus</i> Wats.	65	59	220	1.23	0	0	0	0	---	---	0	200	SS	SU
	<i>Lavatera assurgentiflora</i> Kell.	69.9	34.2	219	3.2	0	0	0	0	---	---	0	107	S	CS
Myricaceae	<i>Malacothamnus fasciculatum</i> (Nutt.) Greene	198	23.3	230	6.2	0	0	0	0	---	---	0	27.1	S	CH
	<i>Sphaeralcea emoryi</i> Torr.	322	21.5	128	8.8	0	0	0	0	---	---	0	8.55	SS	DS
	<i>Myrica californica</i> C. & S.	136	23.4	490	1.56	5	+	0	0	---	---	0	84.3	S	MS
	<i>Forestiera neomexicana</i> Gray	66.9	29.9	245	1.96	0	0	0	0	---	---	0	109	S	CH
	<i>Fraxinus dipetala</i> H. & A.	59	35	227	1.8	0	0	0	0	---	---	0	135	T	CH
	<i>Menodora scoparia</i> Engelm.	699	18.6	169	1.32	0	0	0	0	++	+	4.5	SS	DS	
Onagraceae	<i>Camissonia californica</i> (Nutt.) Raven	78	59	308	2.1	0	0	0	0	---	---	0	233	H	---
	<i>Clarkia xantiana</i> Gray	130	46	341	2.7	0	0	0	0	---	---	0	121	H	---
	<i>Epilobium paniculatum</i> Nutt.	104	54	235	2.1	0	0	0	0	---	---	0	122	H	---
	<i>Gaura parviflora</i> Dougl.	70	79	236	2.4	0	0	0	0	---	---	0	266	H	---
	<i>G. sinuata</i> Nutt.	320	46	106	1.6	0	0	0	0	---	---	0	15.2	SS	CS
	<i>Heterogaura heterandra</i> (Torr.) Cov.	77	53	286	2.4	0	0	0	0	---	---	0	197	H	---
Zauschneriaceae	<i>Oenothera deltoides</i> T. & P.	72	58	292	2.9	0	0	0	0	---	---	0	235	H	---
	<i>Zauschneria cana</i> Greene	360	41	151	1.6	0	0	0	0	---	---	0	17.2	SS	CS

Table 1 (continued)

	V/M	VD	VL	V/G	BR	T	I	A	SC	G	MESO	HA	HI
Papaveraceae	561	13.8	298	11.7	0	0	+	0	++	-	7.33	S	CH
<i>Dendromecon rigida</i> Benth.	1350	18	223	150	0	0	+	0	++	+	2.97	S	CS
<i>Romneya coulteri</i> Harv.	137	44	529	1.56	3	+	0	0	--	-	170	T	RI
Platanaceae	552	31	260	1.92	0	+	0	0	--	-	14.6	SS	DS
<i>Platanus racemosa</i> Nutt.	444	38	146	1.92	0	+	0	0	++	-	12.5	H	-
Polemoniaceae	462	28	229	1.24	0	+	0	0	---	-	13.9	H	-
<i>Eriastrum densifolium</i> (Benth.) Mason	482	32	250	1.4	0	+	0	0	++	-	16.6	SS	CH
<i>Ipomopsis aggregata</i> (Pursh) Grant	751	23	116	1.67	0	+	0	0	++	-	3.55	SS	AL
<i>I. tenuifolia</i> (Gray) Grant	718	19	172	1.26	0	+	0	0	++	-	4.55	SS	AL
<i>Leptodactylon californicum</i> H. & A.	483	26.8	95.2	1.6	0	+	0	0	--	+	5.28	S	DS
<i>L. purgens</i> (Torr.) Rydb.	272	14.4	151	6.2	0	0	0	+	---	-	7.99	S	CS
Polygalaceae	269	25.5	126	2.8	0	0	0	+	---	+	11.9	S	CS
<i>Phlox diffusa</i> Benth.	425	20.6	198	18.3	0	0	+	0	++	-	9.6	V	CH
<i>Polygala acanthoclada</i> Gray	345	21.4	266	2.32	0	0	+	0	++	-	16.5	S	DS
<i>Eriogonum fasciculatum</i> Benth.	308	18.4	307	6.03	0	0	+	0	++	-	18.3	S	CH
<i>E. giganteum</i> Wats.	219	17.8	323	3.73	0	0	+	0	++	-	26.3	S	CH
Ranunculaceae	202	32.2	217	1.85	0	0	+	0	++	+	34.6	S	DS
<i>Clematis lasiantha</i> Nutt.	377	20.6	212	1.36	0	0	+	0	---	-	11.6	S	DS
Rhamnaceae	207	34.3	287	2.95	0	0	+	0	++	+	47.6	S	CS
<i>Ceanothus arboreus</i> Greene	563	17.1	185	2.55	0	0	+	0	++	+	5.62	S	CS
<i>C. leucodermis</i> Greene	210	30.9	196	2.55	0	0	+	0	++	+	28.8	S	DS
<i>Colubrina californica</i> Jtn.	233	19.9	198	1	0	0	+	0	---	0	16.9	S	CH
<i>Condalia globosa</i> Jtn.	414	18.3	210	1.04	0	+	0	0	++	-	9.28	S	CH
Rosaceae	831	14.1	377	1.24	0	+	0	0	++	-	6.4	S	CH
<i>Rhamnus californica</i> Esch.	183	15.5	291	1.2	0	+	0	0	++	+	24.6	S	DS
<i>R. crocea</i> Nutt.	334	22.2	268	1.2	0	+	0	0	++	+	17.8	S	CH
<i>Zizyphus parryi</i> Torr.	525	20.7	214	1.04	0	+	0	0	---	+	8.44	S	DS
<i>Adenostoma fasciculatum</i> H. & A.	616	17.4	127	1.12	0	+	0	0	++	+	3.59	S	DS
<i>A. sparsifolium</i> Torr.	328	37.9	214	1.08	0	+	0	0	---	-	24.7	S	DS
<i>Amelanchier pallida</i> Greene	444	20.6	208	1.95	0	+	0	0	++	-	9.65	S	DS
<i>Cercocarpus intricatus</i> Wats.	193	28.5	470	1.08	0	+	0	0	++	-	69.4	S	CH
<i>Chamaebatia australis</i> (Bdg.) Abrams	83	26.5	315	1.64	0	0	+	0	---	-	101	S	CH
<i>Chamaebatia millefolium</i> (Torr.) Maxim.	65.7	28.8	243	1.44	0	0	+	0	---	-	107	S	AL
<i>Chamaebatia millefolium</i> (Torr.) Maxim.	122	19.7	451	1.18	0	+	0	0	++	+	72.8	T	CS
<i>Coloogyne ramosissima</i> Torr.	460	18.2	294	1.14	0	+	0	0	---	-	11.6	S	AL
<i>Cowania stansburiana</i> Torr.													
<i>Fallugia paradoxa</i> (D. Don) Endl.													
<i>Heteromeles arbutifolia</i> Roem.													
<i>Holodiscus discolor</i> (Pursh) Maxim.													
<i>H. microphyllus</i> Rydb.													
<i>Lyonothamnus floribundus</i> Gray													
<i>Peraphyllum ramosissimum</i> Nutt.													

some parts of California, showed, for example, the extensive and deep root system of *Prosopis* (Fabaceae), a desert wash shrub. Simpson and Solbrig (1977) contrast *Prosopis* with *Larrea* (Zygophyllaceae), which grows in non-wash situations and has shallower roots.

One can only conclude that evolution does not work on one or several fronts in producing adjustment of a phylad to water stress situations, but on all fronts, and in any given species a combination of features may be expected. Where wood anatomy does not seem to conform to degree of xeromorphy expected on the basis of habitat, one should look for other kinds of adaptations, and indeed, wood anatomy can be said to be predictive in this respect.

Materials and Methods

Features are discussed in the order in which they appear in Table 1. Taxa recognised are in accordance with Munz (1974) with certain exceptions. *Forsellesia* is included in Crossosomataceae, in accord with recent practice. *Sambucus* is excluded from Caprifoliaceae; *Sambucus* shares a curious roster of characters with *Adoxa*, and consequently should be included in Adoxaceae (Thorne, 1983). *Ribes* is recognised under Grossulariaceae rather than Saxifragaceae. *Simmondsia* is excluded from Buxaceae as Simmondsiaceae. Subspecies are not given in Table 1. These and collection data are specified on the wood section and maceration slides used for this study; those slides can be consulted at the Rancho Santa Ana Botanic Garden. The majority of wood samples were collected in the wild. Samples from the herbarium (8% of the collections studied), wood collection, and living collection of the Rancho Santa Ana Botanic Garden provided the balance. Cultivated materials may show somewhat more mesomorphic wood features than wild-collected specimens (Bissing, 1982), but the differences are not believed to alter the quantitative image presented to an appreciable degree. Wood taken from herbarium specimens potentially has the disadvantage of showing narrower vessels or other differences as compared to wood from fully grown specimens. Wood was taken from herbarium specimens only if a relatively large wood sample was furnished by the specimen, and if the plant was a relatively small shrub in any case. Materials collected from the Botanic Garden were preserved in 50% ethyl alcohol; the others were available dried. Standard microtechnical methods were utilised for preparation of sections and macerations. Following the suggestion of Van den Oever et al. (1981), 20 measurements per quantitative feature were taken for obtaining means.

Data on vessels per mm² were obtained by viewing transection fields under a $\times 40$ objective; no attempt was made to select ray-free fields or, in the species with successive cambia, to avoid parenchyma between xylem bands. Each vessel seen was counted, contrary to the method of some workers who count grouped vessels as one.

Vessel diameter was measured on the basis of lumen, rather than on the basis of lumen plus wall as is usually done; the lumen alone is more significant in terms of physiology of conduction. Vessel diameter was taken at the widest point. Vessel element length was obtained from macerations, and includes tails of the elements.

Number of vessels per group represents a mean base upon groupings in which a solitary vessel = 1.0, a pair of vessels 2.0, etc. Vessels must be in actual contact to qualify as grouped. The mean was based on at least 20 (often more) measurements; observation was made with a $\times 40$ ocular. Ring-porous woods were scanned radially so as to avoid bias toward any growth ring portion. The value of vessels per group as opposed to the percentage solitary or grouped lies in the ability of the vessels per group figure to demonstrate degrees of grouping over the entire range, especially large groupings. Thus, vessels reported as, say, 90% grouped might actually have 4.5 vessels per group or 8.8 vessels per group, and that difference is significant in terms of ecology. Degree of grouping can change within a growth ring in some instances: in *Salix goodingii* latewood vessel groups are larger than those in earlywood.

The number of bars per perforation plate was obtained from macerations for species in which bar number was appreciable, and from sections in those species in which bars were few or none in earlywood, but several per plate in latewood. Instances in which the number of bars is greater in latewood, with the mean latewood number given in parentheses, are as follows: *Arbutus menziesii* (2.5); *Arctostaphylos patula* (3); *Comarostaphylos diversifolia* (2); *Rhododendron occidentale* (7); *Myrica californica* (8; bars present on 75% of plates, others simple); *Platanus racemosa* (7; bars present on 50% of plates, others simple); *Styrax officinalis* (3).

The term 'tracheid' is defined as in Bailey (1936) and Carlquist (1984a), and connotes imperforate tracheary elements in which pits are fully bordered, and approach vessel walls for any particular species in pit diameter and density. A distinction is made between true tracheids, as listed in the column labelled T, and vasicentric and vascular tracheids, in the following two columns of the tables. Vasicentric

tracheids are defined as in Carlquist (1985). If a wood has libriform fibres or fibre-tracheids, and tracheids are present only in the last layers of a growth ring, vascular tracheids are said to be present. If fibre-tracheids or libriform fibres are present in a wood but tracheids are present intermixed with vessels in some way – in other words, in a distribution other than merely as the last layers of a growth ring – then vasicentric tracheids are said to be present. This distinction seems related to functional differences, as mentioned earlier, and also comes very close, in its actual application, to agreement with the way Metcalfe and Chalk (1950) used the term (see Carlquist, 1985). All of the families recognised by Metcalfe and Chalk as having vasicentric tracheids are so recognised by me, except for Staphyleaceae in which I could not find any such tracheids. One must remember that vasicentric tracheids are not a unitary phenomenon, and the condition seen in *Quercus* is quite different from that in *Ribes*, which in turn is different from that in *Salvia*. There are some borderline instances of vasicentric tracheid presence; they are scarce in *Toxicodendron diversilobum* and *Betula fontinalis*, where they are reported, but they are slightly scarcer in *Acer macrophyllum* and *Zauschneria cana*, where they are not reported. In the present paper, woods in which both vascular tracheids and vasicentric tracheids are present are cited as having vasicentric tracheids only. This convention was followed so that the categories would not overlap and thus quantification of species with these features would be less confused.

Presence of helical sculpturing patterns in vessels is reported in the tables for earlywood and latewood separately in the columns (in a horizontal line, cited merely as present or absent). The term ‘helical sculpturing’ is used here because in some instances, sculpturing does not take the form of thickenings, but of grooves interconnecting pit apertures. This phenomenon can be seen most easily in Asteraceae, as in *Hymenoclea salsola* (Carlquist, 1960a). Helical sculpture of this sort is present outside Asteraceae in such southern Californian species as *Bernardia incana*, *Amorpha fruticosa*, and *Solanum xantii*. In these, there are commonly not merely grooves between adjacent pit apertures, but also raised ridges beside the grooves. Because all degrees of intermediacy between grooves and helical thickenings can occur, the more inclusive term ‘helical sculpture’ has been employed.

Growth rings are denoted in Table 1 in degrees: diffuse-porous (0), weakly ring-porous (–), and ring-porous (+). For computation pur-

poses (Tables 2 & 3), diffuse-porous is assigned the value of 0.0, weakly ring-porous (= semi-ring-porous) 50%, and ring-porous 100%. The reader should keep this in mind because a group of species may all have growth rings yet have an average value below 100%, as in the woodland trees, most of which are semi-ring-porous, yet which average 50% (Table 2).

The Mesomorphy value, given in all three tables, is based upon a ratio offered earlier (Carlquist, 1977b). This ratio is not identical to Conductivity, a figure equivalent to the fourth power of the vessel diameter (Zimmermann, 1983). However, the Hagen-Poiseuille equation for Conductivity consistently overpredicts hydraulic conductance (K_H) for various dicotyledons, ranging from factors of 1.5–3.0 (Tyree & Zimmermann, 1971; Gibson et al., 1984) to 100 (Giordano et al., 1978), and only in one instance (Dimond, 1966) has equivalence been found. Thus the fact that the Mesomorphy ratio usually computes to somewhat less than Conductivity may place it in the range of actual rather than theoretical conductivity values. More importantly, however, do narrow vessels equate to poor conduction if wide vessels equate to good conduction? Not necessarily, for as Martin Zimmermann (personal communication) has stated, there is no single value based on equations like the Hagen-Poiseuille formula which expresses safety. Safety is not always the opposite of high conductivity; it may reside either in narrowness of vessels, high density of vessels, or both, or even perhaps in shortness of vessels or shortness of vessel elements. Therefore low values for the ratios Vulnerability and Mesomorphy (Carlquist, 1977b) seem expressive of safety, and do seem to correlate more closely with drought or physiological drought induced by cold than any other scheme devised thus far. These ratios can be computed easily for any vessel-bearing dicotyledon. Vulnerability is vessel diameter divided by vessels per mm^2 ; Mesomorphy is Vulnerability multiplied by vessel element length. Where the computed ratios deviate from values expected on the basis of, say, rainfall in an area, they are predictive of some kind of modification, e.g., succulence. Presence of growth rings, helical sculpture, or grouped vessels are all indicative of xeromorphy, but they do not occur in all vessel-bearing woods and so they cannot be incorporated in a simple Vulnerability or Mesomorphy ratio.

The habit categories (Table 1) are relatively obvious. Herb is used for an annual, biennial, or short-lived perennial (plus *Coreopsis gigantea* and *Turricula parryi*). Cacti are placed in tree, shrub, and subshrub categories according to

their respective height, despite the fact that concepts based upon nonsucculents are dubiously applicable to cacti.

The ecological categories represent considerable modification of the plant communities utilised by Munz (1974); these modifications are aimed toward unifying groups of similar plants. Island scrub has been merged into coastal sage because both represent shrubby vegetation of areas near coasts where summer heat and winter cold are moderated. Some elements of the coastal sage (*Rhus laurina*, *Lyonothamnus floribundus*) may be indicators of underground water presence. The concept of chaparral is broadened here so as to include shrubs of dry montane areas (e.g., in the Yellow Pine forest), since shrubs of the Yellow Pine forest (e.g., *Fremontodendron californicum*, *Garrya veitchii*) are subject to essentially the same summer and winter stress as chaparral shrubs and are mostly shrubs of open forest areas rather than understory elements. Riparian species occur along semipermanent or permanent streams. The species grouped as 'moist' are chiefly from shady valley situations (*Myrica californica*) but may occur in seeps (*Rosa woodsii*). Alpine species are all found at elevations above 3000 m in the area. The category labelled succulents consists essentially of desert succulents. In addition to cacti, the tree *Bursera*, which is a stem succulent, and certain perennial Loasaceae which tend to have succulent roots (and, to a lesser extent, stems) are included. The halophytes represented here are from coastal salt marshes, alkaline seeps, alkaline sinks, and alkaline flats, and thus are not a uniform grouping, but the number is so small that further subdivision would simply have highlighted individual species. The three trees grouped as woodland (*Lithocarpus densiflora*, *Quercus chrysolepis*, and *Juglans californica*) are more similar to each other than to any of the other vegetation categories. They are all broad-leaved non-riparian species which very likely tap underground water sources characteristically.

Collection of anatomical data and computer transformation of data represent the work of the junior author. Collection of woods, preparation of slides, and construction of text represent the work of the senior author. Some of the data come from papers representing groups already surveyed: Carlquist (1957, 1958, 1959, 1960a, 1960b, 1961, 1962, 1965, 1966b, 1975b, 1984b), Carlquist and Eckhart (1984), Carlquist et al. (1983, 1984), Gibson (1973, 1977).

If one takes the number of species per genus for each genus with woody species in the southern Californian flora, one can project (Flora pro-rated, Tables 2 & 3) figures which approxi-

mate what might have been obtained had all 512 woody species of the region been studied (e.g., mean number of vessels per group in *Ribes*, based upon vessel diameter of all species of *Ribes* studied and averaged, is multiplied by the number of species in *Ribes* in the area, etc.). Admittedly this is an approximation, but it is probably more accurate than one might guess, since most speciation of larger genera does not involve wide ranges ecologically; where wide ranges are involved, as in *Quercus*, more than one species was sampled. Among the larger genera of the flora are the following, listed in alphabetical sequence of families to which they belong (number of woody species in parentheses): *Brickellia* (12); *Haplopappus* (18); *Opuntia* (21); *Arctostaphylos* (13); *Quercus* (12); *Ribes* (18); *Phacelia* (12); *Salvia* (12); *Ceanothus* (17); *Salix* (13); and *Lycium* (10). The statistical tests used were: chi-square (qualitative features); Mann-Whitney (quantitative features). Pomona College kindly permitted use of its computer facilities.

Results and Discussion

Indicators. -- From Table 2, we can see that certain features are indicators of xeromorphy or mesomorphy. Table 3 represents a transformation of data of Table 2, expressed as percentages of the total flora species studied, with values interpretable as indicative of xeromorphy (italics) or mesomorphy (bold face) stressed; features related to tracheids are not so indicated. The following may be regarded (but to varying degrees) as indicators of mesomorphy: small number of vessels per mm², wide vessel diameter, long vessel elements, small number of vessels per group, absence of vasicentric tracheids, absence of helical sculpture on vessels, and absence of growth rings. Scalariform perforation plates are present in only a small portion of the plants one could call mesomorphic, but these plates are associated with mesomorphy. Perhaps the only surprising feature is the citation of absence of growth rings (= diffuseporosity), 7 lines from bottom of Table 2; if one remembers that onset of dryness causes cessation of growth far more than onset of cold in southern California, the correlation between growth ring absence with mesomorphy becomes more obvious.

Phylads that have retained true tracheids show patterns different from those of phylads without true tracheids: in tracheid-bearing groups, vessel grouping is depressed and vessel elements tend to be somewhat longer than they are in plants without tracheids in a given habitat. True tracheids are probably primitively present in mesophytic groups, such as Corna-

Table 2. Wood features related to conduction for species of all native woody genera in southern California. Data transformed from Table 1 for ecological, habitat, and anatomical categories.

Columns 2–6 are means; columns 7–12 are percentages based on means; column 13 is a mean. Conventions as in Table 1 except BAR = bars number on scalariform perforation plates; VASI = vasicentric tracheids; VASC = vascular tracheids; SE = helical sculpture in earlywood; SL = helical sculpture in latewood; and GR = growth rings. Last line is a projection for the entirety of the woody flora. For further explanations, see Materials and Methods.

	N	V/M	VD	VL	V/G	BAR	T	VASI	VASC	SE	SL	GR	MESO
Riparian	8	163	50.7	418	1.77	6.75	37.5	0	0	12.5	12.5	56.3	253
Moist	10	198	36.6	338	4.62	4.1	30	20	10	20	20	75	106
Chaparral	41	299	29.2	261	4.76	0.122	24.4	43.9	17.1	53.7	56.1	62.2	66.7
Coastal sage	33	212	34.5	188	7.55	0	6.06	33.3	24.2	36.4	48.5	65.2	80.7
Alpine	12	442	20.9	266	2.53	4.75	58.3	41.7	0	25	33.3	75	27.1
Desert scrub	50	361	25.9	190	2.62	0	40	40	8	30	58	80	20.9
Desert wash	17	148	42.2	185	3.61	0	11.8	29.4	41.2	23.5	29.4	70.6	139
Succulent	12	44.6	57.5	245	1.84	0	0	33.3	0	0	0	66.7	368
Halophyte	4	158	29	100	2.6	0	0	50	0	0	25	50	25.8
Parasite	1	72.3	33.9	53.1	1.8	0	0	0	0	0	0	50	24.9
Woodland	3	19.3	77.8	454	1.15	0	0	66.7	0	0	0	50	1950
Tree	19	99	53.9	365	2.16	0.789	10.5	21.1	15.8	21.1	26.3	52.6	486
Shrub	138	277	30	228	4.48	1.03	27.5	39.1	14.5	34.8	47.8	72.8	71.8
Subshrub	32	285	33.7	173	2.63	0	21.9	31.3	9.38	18.8	28.1	64.1	80.6
Vine	2	225	103	156	10.4	0	0	50	50	50	50	50	441
Herb	16	141	52.5	255	2.16	0	12.5	0	0	6.25	6.25	40.6	176
Simple	196	249	35.3	222	3.99	0	20.4	35.2	13.3	30.6	41.3	67.6	123
Bars	11	287	32.6	437	1.55	14.3	81.8	0	9.09	0	9.09	54.5	122
T absent	158	216	37.9	218	4.65	0.19	0	43.7	17.1	29.1	39.2	65.8	144
T present	49	365	26.4	281	1.33	2.59	100	0	0	28.6	40.8	70.4	54.9
VASI absent	138	234	38.7	244	2.58	1.14	35.5	0	19.6	19.6	29.7	62	128
VASI present	69	286	28.2	212	6.42	0	0	100	0	47.8	59.4	76.8	113
VASC absent	180	259	34.1	239	3.82	0.772	27.2	38.3	0	30.6	40.6	65.8	120
VASC present	27	201	42.7	198	4.15	0.667	0	0	100	18.5	33.3	74.1	143
No helices	125	175	42.3	246	2.55	1.18	23.2	22.4	14.4	0	0	60	186
Helices	82	368	24.4	213	5.87	0.122	24.4	50	11	73.2	100	77.4	26.8
GR absent	21	129	44	211	3.46	0	14.3	19	9.52	9.52	9.52	0	191
GR weak	95	225	39.4	269	2.69	1.46	24.2	25.3	10.5	29.5	34.7	50	170
GR strong	91	307	28.8	201	5.18	0.198	25.3	45.1	16.5	33	51.6	100	57.3
Grouped	178	249	35.7	225	4.32	0.36	16.3	34.3	14.6	29.2	40.4	67.7	106
Solitary	29	260	31.8	284	1.07	3.21	69	27.6	3.45	27.6	34.5	62.1	226
Flora total	207	251	35.2	233	3.86	0.758	23.7	33.3	13	29	39.6	66.9	123
Pro-rated	512	257	34.4	225	3.9	0.342	15.3	37.8	11.7	31.3	43.9	69.1	120

Table 3. Values from Table 2 expressed as percentages of mean values for the flora (207 species).

Figures in boldface represent statistically significant deviation ($t = < .05$) from flora mean in a mesomorphic direction; those in italics are for xeromorphic direction. Values are deleted where they represent reciprocals of each other wholly or partly.

	N	V/M	VD	VL	V/G	BAR	T	VASI	VASC	SE	SL	GR	MESO
Riparian	4	65	144	179	46	891	158	0	0	43	32	84	206
Moist	5	79	104	145	120	541	127	60	77	69	51	112	86
Chaparral	20	<i>119</i>	<i>83</i>	<i>112</i>	<i>123</i>	<i>16</i>	103	<i>132</i>	<i>132</i>	<i>185</i>	<i>142</i>	<i>93</i>	<i>54</i>
Coastal sage	16	84	98	<i>81</i>	<i>196</i>	0	26	100	<i>186</i>	<i>126</i>	<i>122</i>	<i>97</i>	<i>66</i>
Alpine	6	<i>176</i>	<i>59</i>	<i>114</i>	66	627	246	<i>125</i>	0	86	<i>84</i>	<i>112</i>	<i>22</i>
Desert scrub	24	<i>144</i>	<i>74</i>	<i>82</i>	68	0	169	<i>120</i>	62	103	<i>146</i>	<i>120</i>	<i>17</i>
Desert wash	8	59	120	<i>79</i>	<i>94</i>	<i>0</i>	50	88	<i>317</i>	<i>81</i>	<i>74</i>	<i>106</i>	<i>113</i>
Succulent	6	18	163	<i>105</i>	48	<i>0</i>	0	100	0	0	0	100	299
Halophyte	2	63	<i>82</i>	<i>43</i>	67	<i>0</i>	0	<i>150</i>	0	0	63	<i>75</i>	<i>21</i>
Parasite	0	<i>29</i>	<i>96</i>	<i>23</i>	<i>47</i>	<i>0</i>	0	0	0	0	0	<i>75</i>	<i>20</i>
Woodland	1	8	221	195	30	<i>0</i>	0	<i>200</i>	0	0	0	<i>75</i>	1585
Tree	9	39	153	157	56	104	44	63	<i>122</i>	73	66	79	395
Shrub	67	110	<i>85</i>	<i>98</i>	<i>116</i>	136	116	<i>117</i>	<i>112</i>	<i>120</i>	<i>121</i>	<i>109</i>	<i>58</i>
Subshrub	15	114	<i>96</i>	<i>74</i>	68	<i>0</i>	92	<i>94</i>	72	65	71	<i>96</i>	<i>66</i>
Vine	1	90	293	<i>67</i>	<i>269</i>	<i>0</i>	0	<i>150</i>	<i>385</i>	<i>172</i>	<i>126</i>	<i>75</i>	359
Herb	8	56	149	<i>109</i>	56	<i>0</i>	53	0	0	22	16	61	143
Simple	95	99	100	95	103	---	86	106	102	106	104	101	100
Bars	5	114	93	188	40	---	345	0	70	0	23	81	99
T absent	76	86	108	94	120	25	---	131	132	100	99	98	117
T present	24	145	75	121	34	342	---	0	0	99	103	105	45
VASI absent	67	93	110	105	67	150	150	---	<i>151</i>	68	75	93	104
VASI present	33	114	<i>80</i>	<i>91</i>	<i>166</i>	<i>0</i>	0	---	0	<i>165</i>	<i>150</i>	<i>115</i>	<i>92</i>
VASC absent	87	103	97	103	99	102	115	115	---	106	103	98	98
VASC present	13	80	121	<i>85</i>	<i>108</i>	<i>88</i>	<i>0</i>	0	---	64	<i>84</i>	<i>111</i>	<i>116</i>
No helices	60	70	120	<i>106</i>	66	156	98	67	111	---	---	90	151
Helices	40	<i>147</i>	<i>69</i>	<i>91</i>	<i>152</i>	<i>16</i>	103	<i>150</i>	85	---	---	<i>116</i>	<i>22</i>
GR absent	10	51	125	<i>91</i>	<i>90</i>	<i>0</i>	60	57	73	33	24	---	155
GR weak	46	90	112	115	70	193	102	76	81	102	88	---	138
GR strong	44	<i>122</i>	<i>82</i>	<i>86</i>	<i>134</i>	<i>26</i>	107	<i>135</i>	<i>127</i>	<i>114</i>	<i>130</i>	---	<i>47</i>
Grouped	86	99	101	97	112	47	69	103	112	101	102	101	86
Solitary	14	104	90	122	28	423	291	83	27	95	87	93	184
Flora total	100	100	100	100	100	100	100	100	100	100	100	100	100
Pro-rated	247	102	98	97	101	45	65	114	90	108	111	103	98

ceae, but they have presumably been retained because of the great safety they confer on the conductive system in groups of desert plants, such as *Fouquieria* or *Krameria*. Obviously one cannot under these circumstances interpret tracheid presence as a xerophytic or mesophytic indicator; it has relictual aspects. Presence of bars on scalariform perforation plates is characteristic of certain primitive dicotyledons, usual-

ly in mesophytic circumstances, but bars are readily lost as a phylad enters habitats with more seasonal water availability (by which occurrence of a marked dry season is meant in this context), whereas true tracheids are retained more often because of their selective value, so here we have two primitive features which are preserved differentially as a group evolves into drier areas. Once lost in the course of evo-

lution, neither bars on perforation plates nor true tracheids are re-evolved, although vascular tracheids and vasicentric tracheids appear to represent ways in which the safety of the true tracheid can be conferred on woods in which true tracheids are not present because fibre-tracheids or libriform fibres have supplanted them. Aside from presence of bars on scalariform perforation plates and presence of true tracheids, features which are cited as indicators of xeromorphy can evolve polyphyletically, which is why they can show statistical correlations with xeromorphy or mesomorphy. However, helical sculpture may not be able to evolve in all groups in xeric habitats, and there is more than one kind of helical sculpture in any case.

Thus, we can say that for phylads in southern California in which true tracheids have been retained, xeromorphy can be achieved in terms of loss of bars (where present) on perforation plates, increase in number of vessels per mm^2 , decrease in vessel diameter, increase in vessel wall thickness, decrease in vessel-element length (to a limited extent), development of helical sculpture on vessels, and development of growth rings. For phylads in which the basic imperforate tracheary element type is the fibre-tracheid or the libriform fibre, adaptation to xeromorphy includes the above (with more marked shortening of vessel elements) plus grouping of vessels and introduction of either vasicentric or vascular tracheids. In either type of phylad, not all features related to xeromorphy may be evolved, and the features are not synchronous in their progress.

Ecological categories. – Riparian trees and shrubs have wood more mesomorphic than that of other categories with the exception of woodland trees according to the criteria given above. Riparian shrubs may have lower transpiration than the woodland trees because of their understorey status; shadiness and coolness of riparian habitats (which are not on flatlands but in valleys, canyons, and gorges in southern California) may explain why riparian trees have wood suited to a lower conductive capacity (and therefore less mesomorphic) than wood of the woodland trees according to the criteria just cited.

The plants from moist habitats represent a range of habitats such as flood plains, walls of shady canyons, wet ditches, and seeps. If one reviews the data for the species of this category, one finds a wide range of values represented. Evidently plants of such habitats will, in part, encounter dry conditions from time to time, much more so than for the riparian species. Interestingly, the figures for plants of desert

washes (Table 2) are in the same range as those for the moist habitat plants. The fact that desert wash species rank that high in mesomorphy suggests that they have roots which tap reliable water sources for longer periods of time than do desert shrubs. This is validated by the data of Cannon (1911), although he studied only a small number of desert wash (phreatophyte) and desert flat plants, as well as by the comparison by Simpson and Solbrig (1977: 17). However, desert phreatophytes probably have not had an unbroken history of occupancy of moist sites, which would account for the relatively small number of them with true tracheids and the small number with scalariform perforation plates. Desert wash plants are essentially opportunistic in their ability to develop deep roots, and wood adaptations to drought are relatively few (Tables 2 & 3): their vessel density, vessel element length, and presence of vascular tracheids suggest xeromorphy, but in other features they deviate from the flora mean in the direction of slight mesomorphy (Table 3).

The woodland trees can be called mesomorphic in all features as compared with the flora as a whole; the fact that two of the three species in this category belong to Fagaceae and are characterised by vasicentric tracheids, so common in Fagaceae, accounts for the high percentage in that feature. The three woodland trees are not unlike tropical lowland trees in having conductive systems adapted to coping with transpiration of large volumes of water.

Succulents would be expected to have mesomorphic wood features (Carlquist, 1975a: 206), and those of the present study do. The features expressed in Tables 2 and 3 show only mesomorphic wood features except for the high percentage of vasicentric tracheids. These are the cells of cacti, formerly reported as vascular tracheids (see Carlquist, 1984a), which are of a rather special sort, not comparable to vasicentric tracheids in other groups. One may think of succulents as both moderate in conductive ability and low in safety (note the low number of vessels per mm^2). Succulents show that, as noted above, the opposite of high conductivity is not necessarily high safety.

Ecological groupings with Mesomorphy ratios below 100 (Table 2, far right column) may be considered as xeromorphic by any standard. The least xeromorphic of these is, predictably, coastal sage. There is a wide range of adaptations in this community. The highest Mesomorphy values reported are for *Rhus laurina*, a large shrub which is a reliable indicator of subsurface water availability, and for *Eriodictyon trichocalyx*, the remarkable adaptations of which are noted above as well as elsewhere. Notably xero-

morphic wood can be reported for the coastal sage subshrubs *Eriophyllum confertiflorum* and *Eriogonum fasciculatum* and the shrub *Romneya coulteri*. In most of the features cited as indicative of xeromorphy (Tables 2 & 3), coastal sage exceeds the flora mean, notably so in number of vessels per group and percentage of species with vascular tracheids. The tendency of stems to die back, the nonsclerophyllous leaves, and the tendency for taxa in coastal sage to be woody representatives of predominantly nonwoody families (e.g., Asteraceae, *Lotus*, *Eriogonum*, *Salvia*, Scrophulariaceae) are noteworthy; these features are probably interrelated to each other. Reasons for this syndrome of features are discussed in connection with the distinction drawn between vascular and vascentric tracheids (Carlquist, 1985).

Like coastal sage, chaparral qualifies as xeromorphic on most indicators (Tables 2 & 3). How does chaparral differ from coastal sage on the basis of these indicators? It is appreciably higher in vessels per mm², appreciably narrower in vessel diameter, and higher in proportion of species with helical sculpture in vessels. There is a lower proportion of species with vascular tracheids in chaparral, but a higher proportion of species with vascentric tracheids or true tracheids. The percentage of species with true tracheids is about the same as that in the flora at large, but the proportion of species with vascentric tracheids is high, particularly in view of the fact that a large number of chaparral species is represented in this study. This suggests that there is indeed a selective value for vascentric tracheids in the evergreen chaparral shrubs, as contended earlier (Carlquist, 1985). Chaparral equals desert scrub in its high proportion of species with helical sculpture in vessels, validating Webber's stress on this feature in these two communities of the southern Californian flora. Helical sculpture is also common in vessels of macchia shrubs (Baas et al., 1983).

Desert scrub shows notably xeromorphy expressions in the figures for vessels per mm², a good indicator of high safety. The vessel elements are short, as suggested by Webber, but not excessively short; the high proportion of species with true tracheids may explain this, since presence of true tracheids tends to deter or delay shortening of vessel elements somewhat. The high proportion of desert species with true tracheids was signalled earlier (Carlquist, 1980). The comparatively low (for a highly xeromorphic community) number of vessels per group is a byproduct of presence of true tracheids, since that tends to depress vessel grouping strongly (Carlquist, 1984a). The occurrence of true tracheids in such a number

of desert shrubs may be surprising to those who think of this feature as characteristic of primitive, and therefore perhaps mesomorphic dicotyledons, but the safety value of tracheids explains why they are been selected for in desert scrub, concomitantly with xeromorphic vegetative apparatus modification (e.g., microphyllly). True tracheids in riparian species may have a relictual rather than a selective significance. The percentage of desert scrub species with vascentric tracheids is above the flora average. The low Mesomorphy figure for desert scrub as compared to coastal sage is noteworthy. Desert Loasaceae are regarded here as succulents, a concept validated by their quantitative characteristics (Table 1).

The alpine flora ranks very close to desert scrub in xeromorphic features, both quantitative and qualitative. Had *Holodiscus microphyllus*, a shrub of alpine seeps, not been included, the Mesomorphy figure for alpine shrubs would have dropped below that for desert scrub. It has the highest figure for vessels per mm² of any of the ecological groupings, and also a conspicuously low mean vessel diameter. The low number of vessels per group and the moderately low vessel element length are related to true tracheid presence, as noted above. The reader will note that the percentage of true tracheids plus that for vascentric tracheids totals 100 in alpine shrubs; either is presumably equally effective in conferring safety. The alpine flora of southern California seems to represent mostly a boreal group of phylads with primitive wood, very likely with origin from moist but cold (in winter) temperate areas (e.g., Ericaceae, Rosaceae, Saxifragaceae). For these, presence of tracheids preadapts to the alpine zone, which is much like high latitude habitats but with the addition of greater drying, especially in late summer, because of low humidity. A few presumably 'newer' elements, such as *Chrysothamnus parryi* (Asteraceae) have adapted to alpine conditions by mimicking the 'primitive' pattern in true tracheid presence, but with vascentric tracheids. The percentage of species with helical sculpture is not exceptionally high, but with other vessel features so markedly xeromorphic, perhaps that is not of prime significance, since the percentage is not significantly below the flora average. Those who believe length of imperforate tracheary elements is related to habit will be mystified by the fact that the alpine shrubs have relatively long vessel elements considering their stature; likewise, those who might be tempted to think vessel element length ought to be roughly proportional to diameter would not find support for that idea in alpine shrubs. The explanation appears

to lie in the preponderance of primitive features in the wood of most of the alpine species, perhaps especially in true tracheid presence, which seems to correlate with longer vessel elements (see horizontal line for true tracheid presence and absence in Table 2). The representatives of families with specialised wood features among alpine shrubs, Asteraceae and Polemoniaceae, do not conform to this pattern, and they have short vessel elements.

The remaining ecological categories are represented by too few species each to permit conclusions about interrelationships of particular zones. We are, in fact, dealing with the characteristics of particular taxa when we deal with such limited numbers. Halophytes as defined here include both those of wet saline habitats (*Batis*) and dry salty places (*Atriplex*, *Frankenia*). The wood of *Iva* in the present study is from cultivation; otherwise its wood might be more xeromorphic. However, even if one neglects these distinctions, the halophytes considered here have remarkably xeromorphic wood. The wood of the single parasite (*Phoradendron tomentosum*) is noteworthy for its very short vessel elements, which are not proportionate to their diameter. The number of vessels per mm² is also low, suggesting low safety at the same time as only moderate conductivity.

Growth forms. — One sees that trees qualify as mesomorphic on a larger number of features than do other growth forms. Herbs, however, are very nearly as mesomorphic, differing notably only in having a lower proportion of helical sculpture in vessels. This is understandable in terms of lack of perennation of some of the herbs. Helical sculpture possibly aids maintenance of integrity of the hydrosystem during dry or cold (or both) periods; annuals and succulent herbs do not experience these extremes, or else do not persist through them. In terms of persisting through seasons, annuals might be said not to have annual rings, although in the present study annuals which show marked diminution of vessel diameter were counted as having annual rings.

In the shrubs studied, wood features indicative of ecology are all in xeromorphic ranges compared to the flora as a whole (except for bars per perforation plate). The values would be dramatically xeromorphic in comparison to the world flora or any forest flora, but one should note (Tables 2 & 3) that the shrubs studied constitute 2/3 of the southern Californian flora, so one can hardly expect shrubs to deviate very much from the total flora which they define to such a large degree. Especially

noteworthy, then, is the fact that the Mesomorphy value is only 58% of that for the flora as a whole (Table 3). Notable in shrubs is the presence of either true, vasicentric, or vascular tracheids.

Subshrubs qualify as less xeromorphic than shrubs in some wood features, about the same in others. The fact that subshrubs have a lower number of vessels per group than shrubs makes them look more mesomorphic. Perhaps subshrubs, which tend toward dieback as a drought survival mechanism more than shrubs do, thereby rely less on wood adaptations. Also, one may regard subshrubs as intermediate between shrubs and herbs with respect to xeromorphy of wood features.

The quantitative features for wood of the herbs in the present study are roughly comparable to those reported for annuals earlier (Carlquist, 1975a). Other wood features reported for herbs here are less susceptible to analysis because of the limited number of taxonomic groups represented. One could just as easily have selected families devoid of true tracheids as those which have them (e.g., Polemoniaceae). However, vasicentric tracheids are very rare in herbs (Carlquist, 1985), and the nil figure represented for that feature here is not surprising. The value of a subsidiary conductive system (true or vasicentric tracheids) whereby the plant can survive a dry season is lessened in herbaceous groups. Two of the herbs, *Coreopsis gigantea* and *Turricula parryi*, might be expected to lack growth rings because of their succulent tendencies. Dieback during drought and survival in the form of seeds would be expected to be progressively more prominent, and xeromorphic wood formulations less critical, as life span shortens.

The number of vines is too small to yield analysis as a grouping. Of the two in the present study, *Clematis* tends to characterise chaparral, whereas *Vitis* tends to sprawl in washes. These habitat preferences seem clearly expressed in terms of wood features. *Clematis* has a higher number of vessels per mm², much narrower vessels, a much higher number of vessels per group, and it has vasicentric tracheids; as noted, its wood is much like that of a chaparral shrub except for presence of wide vessels (in addition to narrow ones) and presence of wide rays. *Clematis* has a degree of safety one might think unusual for a vine, although many temperate vines do show appreciable safety in wood construction. *Vitis* is more typical of vines in its relatively lower safety. While vines or lianas occupy a small proportion of any flora, they

(text continued on page 342)

Legends of Figures 1–21 on pages 337–341:

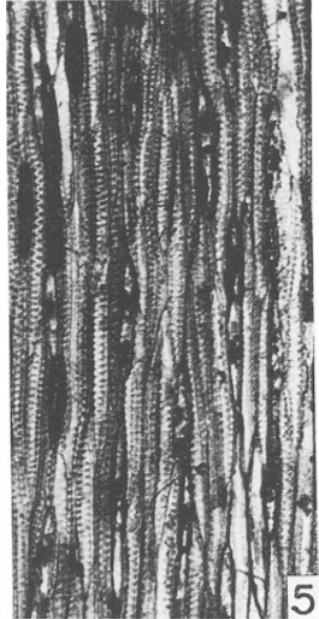
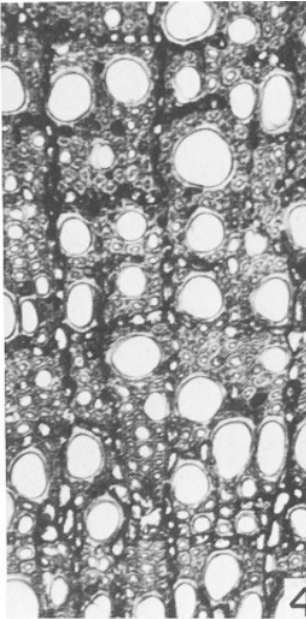
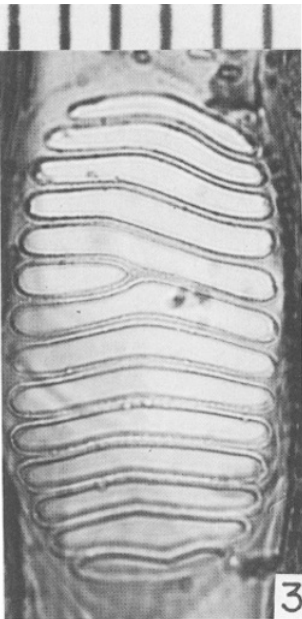
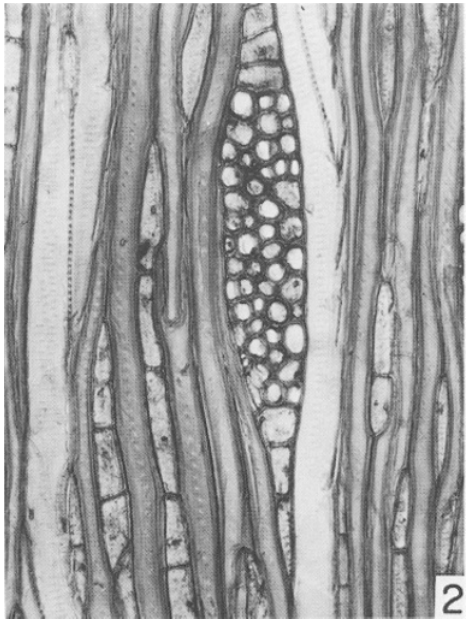
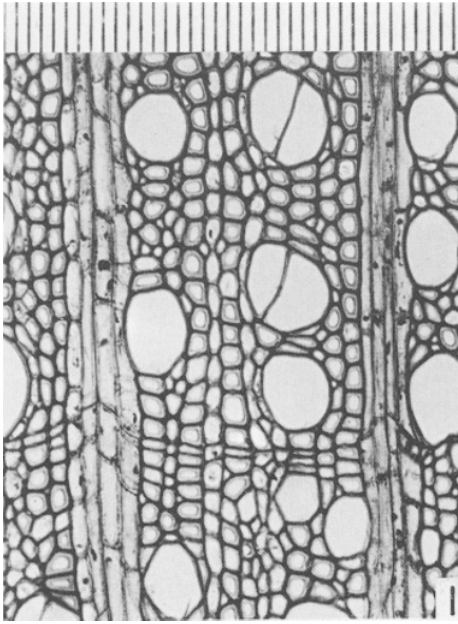
Figs. 1–5. Sections of southern Californian woods that show primitive features. — 1 & 2. *Cornus nuttallii* (Bissing 135, RSA). — 1: Transection, showing solitary nature of vessels. — 2: Tangential section; tracheids are present; vessel with scalariform perforation plate in sectional view, above, to right of centre. — 3. *Alnus rhombifolia* (cult. RSA BG). Perforation plate from radial section. — 4 & 5. *Krameria parvifolia* var. *imparata* (Tilforth 415, RSA). — 4: Transection; vessels solitary, thick-walled. — 5: Tangential section; all imperforate tracheary elements are densely-pitted tracheids. Figs. 1, 2, 4, 5: magnification scale above Fig. 1 (divisions = 10 μm). Fig. 3: scale above Fig. 3 (divisions = 10 μm).

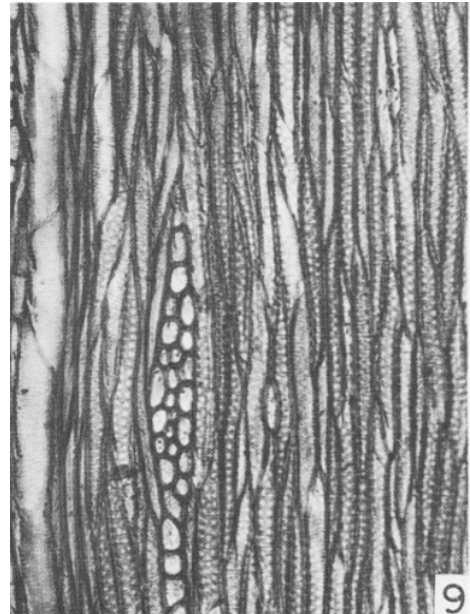
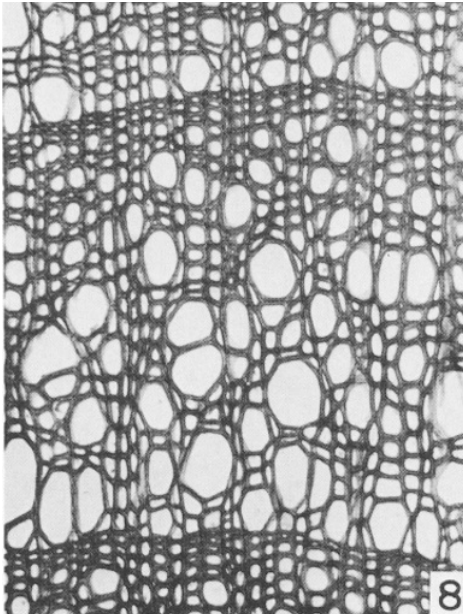
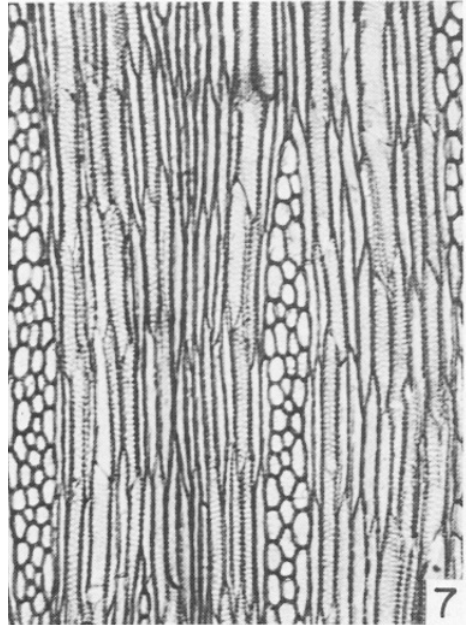
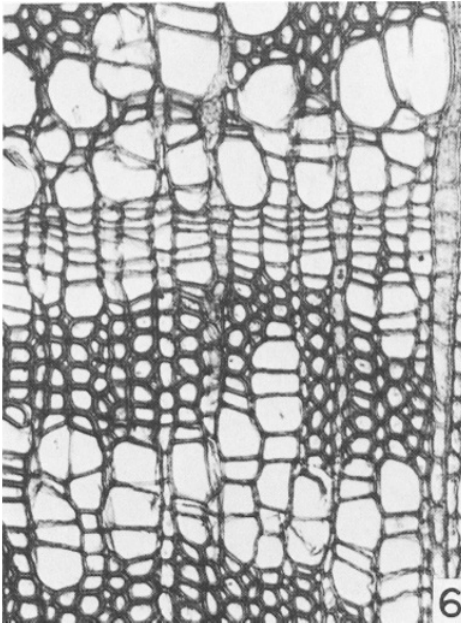
Figs. 6–9. Sections of southern Californian woods with vascular tracheids. — 6. *Sambucus caerulea* (San Antonio Canyon). Transection showing latewood (last-formed cells which appear to be flattened vessels are vascular tracheids). — 7. *Isomeris arborea* (cult. RSA BG). Tangential section through a band of latewood; vessel-like cells shown are mostly vascular tracheids in a storied pattern. — 8 & 9. *Keckiella antirrhinoides* subsp. *microphylla* (Michener 3940, RSA). — 8: Transection, showing two growth rings; vascular tracheids are so narrow that they appear to be fibres in latewood. — 9: Tangential section through latewood; narrow vessel elements are present; vascular tracheids present in last-formed latewood. Figs. 6–9: magnification scale above Fig. 1.

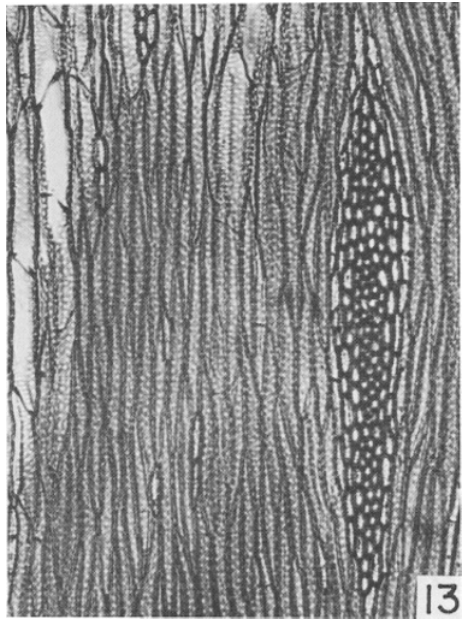
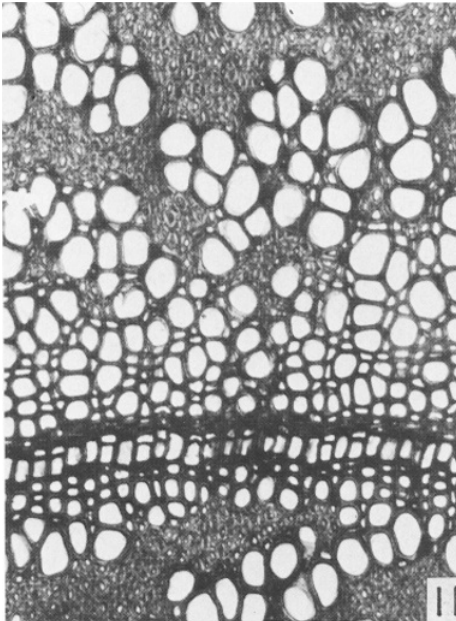
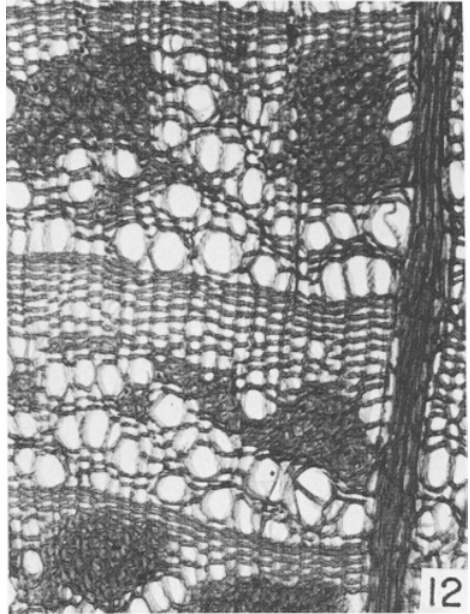
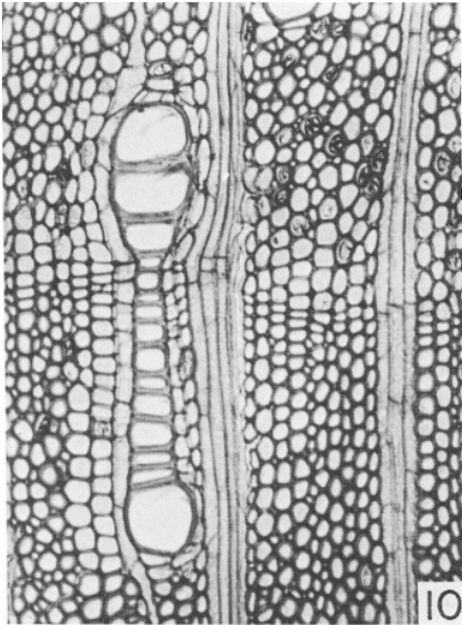
Figs. 10–13. Sections of southern Californian woods with growth ring phenomena. — 10. *Cercidium floridum* (Bissing 231, RSA). Transection showing progressive narrowing of vessels (last-formed latewood contains vascular tracheids) which are in radial clusters. — 11. *Artemisia tridentata* (cult. RSA BG). Transection showing latewood demarcated by interxylary cork layer; earlywood above cork begins with narrow vessels. — 12 & 13. *Chrysothamnus parryi* var. *monocephalus* (Peterson 498, RSA). — 12: Transection, showing that vessels and vascular tracheids are more abundant than the thick-walled libriform fibres. — 13: Tangential section of latewood; vascentric tracheids mixed with narrow vessels are present abundantly. Figs. 10–13: magnification scale above Fig. 1.

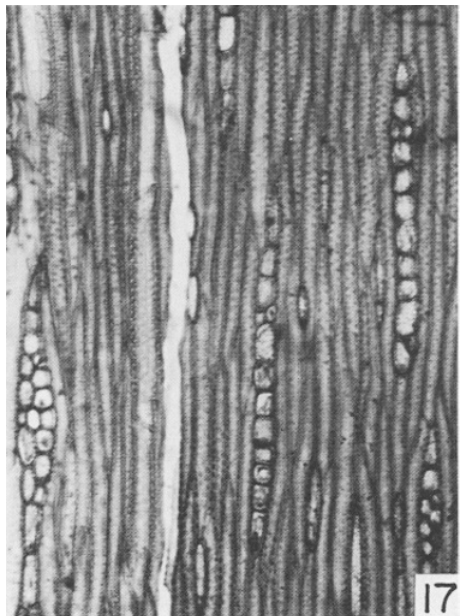
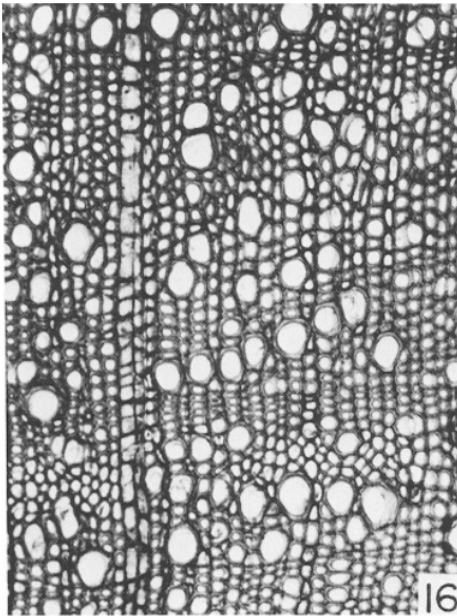
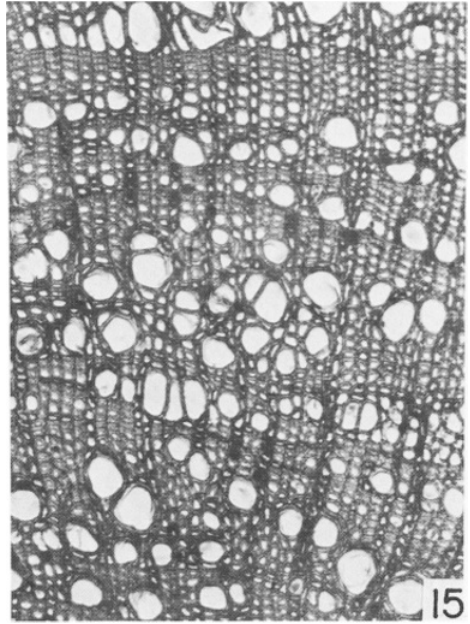
Figs. 14–17. Sections of southern Californian woods with vasicentric tracheids. — 14. *Rhamnus crocea* (Claremont). Showing diagonal aggregations of vessels mixed with vasicentric tracheids. — 15. *Salvia dorrii* (Carlquist 15860, RSA). Transection with several growth rings; the majority of the imperforate tracheary elements are vasicentric tracheids. — 16 & 17. *Trichostema lanatum* (cult. RSA BG). — 16: Transection; the vessels in the centre of the photograph are intermixed with vasicentric tracheids. — 17: Tangential section; two vessels are present, left of centre; most other fibriform cells in the photograph are vasicentric tracheids. Fig. 14: magnification scale above Fig. 14 (finest divisions = 10 μm). Figs. 15–17: magnification scale above Fig. 1.

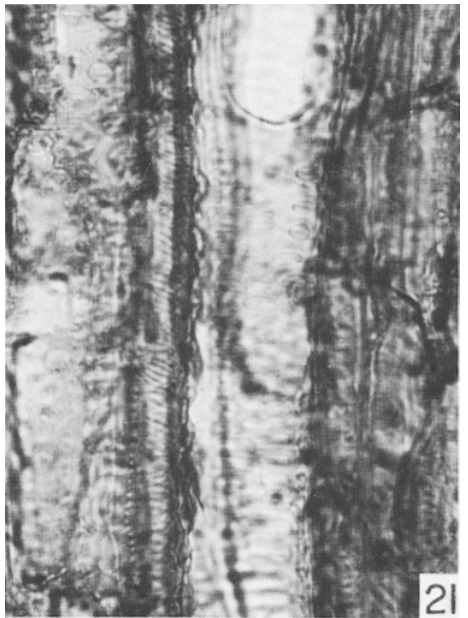
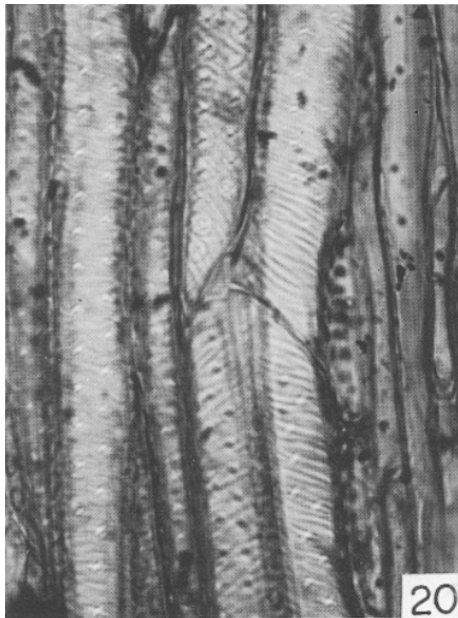
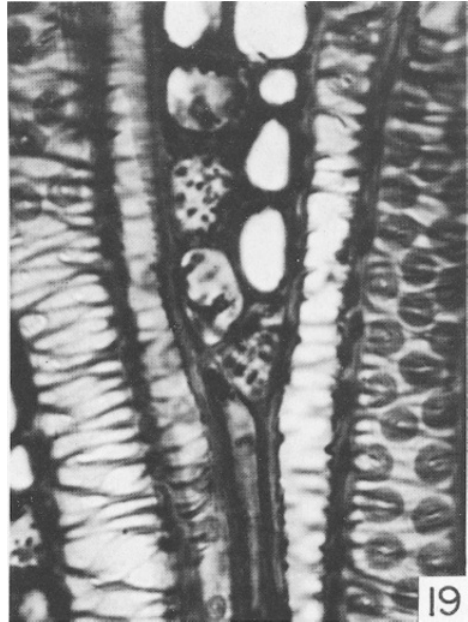
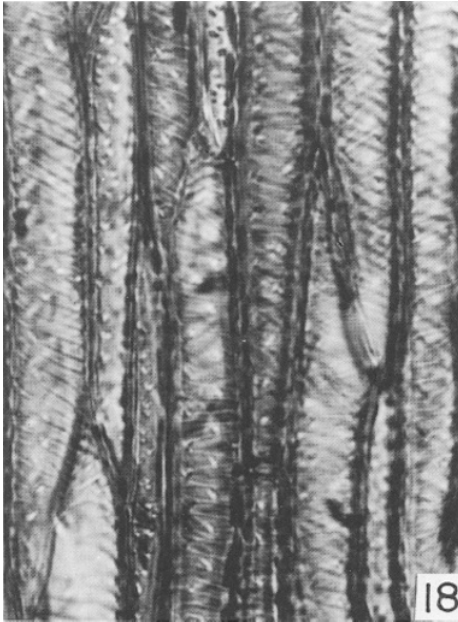
Figs. 18–21. Sections of southern Californian woods showing helical sculpture. — 18. *Keckiella antirrhinoides* subsp. *microphylla* (Michener 3940). Tangential section showing helical bands in latewood vessels. — 19. *Ceanothus thyrsiflorus* (cult. RSA BG). Tangential section showing coarse bands in vessels and vasicentric tracheids. — 20. *Trichostema lanatum* (cult. RSA BG). Tangential section showing fine helical bands on vessel walls. — 21. *Symphoricarpos mollis* (Mt. San Jacinto). Radial section; fine helices are present in the tracheid to the left of the vessels, centre. Figs. 18–21: magnification scale above Fig. 3.











are notably few in southern California. The advantage of the vining habit is diminished when an arboreal canopy is infrequent and when water abundance is low over much of an area.

Wood features (see Figs. 1–21). – Number of vessels per mm² is generally high in southern California, matching the predominantly dry conditions of the area. The figure for the flora studied, 251 (Table 2), or 257 if pro-rated to all 512 species, is in marked contrast with such figures as 47.2 for 'primitive mesic species' (Carlquist, 1975a). The mean 251 lies midway between the figures for two of the predominant vegetation types, chaparral (299) and coastal sage (212). There can be little doubt of the value of high vessel density to desert scrub (361) and the alpine species (442). The southern Californian succulents have a figure (44.6) much like that reported for a world sample (64.2: Carlquist, 1975a); such a low figure suggests that safety drops when plant structure provides water indefinitely to conductive cells; the single parasite studied also represents this condition.

Vessel diameter is by no means a perfect inverse of vessel density; packing considerations are not severe in most ranges for vessel density and vessel diameter, so that considerable deviation from a linear relationship between these two can and does occur. The ratio between these two, termed Vulnerability (Carlquist, 1977b) ranges widely in such groups as Hydrophyllaceae (Carlquist & Eckhart, 1984) or Polemoniaceae (Carlquist et al., 1984). In mesomorphic species, vessel diameter advances numerically as vessel density drops, providing a loss in safety with a gain in conductivity. Table 3 shows that riparian, desert wash, succulents, and especially woodland species show this trend, whereas the reverse is true in chaparral, desert scrub, halophytes, and especially alpine species.

Vessel element length is a curious feature in the evolution of dicotyledons. The patterns uncovered by Bailey and Tupper (1918) and Frost (1930) show that vessel element length steadily decreases in the phyletic of dicotyledons. The mechanism for this differs, of course, from the factors which govern vessel density or vessel diameter. Short vessel elements may localise air bubbles (Carlquist, 1982). From the present study, one can see that vessel element length does relate to ecology. Elements appreciably longer than the mean are found in riparian, moist, and woodland species (Tables 2 & 3); elements shorter than the mean typify coastal sage, desert scrub, desert wash, halophytes, and

parasites. Webber (1936) noted shortness of vessel members in dryland habitats of southern California. Vessel element length is longer than the flora mean in two associations where one would expect xeromorphy to predominate, chaparral and alpine. Chaparral comes close to the flora mean in a number of respects; in alpine species, vessel element length perhaps is longer than one might expect because shortening of vessel elements appears slowed in phylads with true tracheids. Certainly various elements of the southern Californian flora prove that vessel element length is not directly related to vessel diameter. If one computes a ratio between these for coastal sage (0.183), for example, and calculates for other ecological categories what vessel element length ought to be based upon that ratio, one obtains some remarkable discrepancies, as follows (observed value in parentheses): riparian, 276 (418); moist, 199 (338); alpine, 114 (266); succulent, 292 (245); halophyte, 158 (100); parasite, 185 (53.1); woodland, 424 (454); vine, 561 (156). Vessel element length does not appear unambiguously related to habit. If one compares column 4 of Table 3 to the habit categories, one finds a progression from tree to shrub to subshrub, but that seeming progression is countered by the figure for herbs, which lies between that for trees and that for shrubs. The fact that vessel element length in such comparisons varies independently of diameter would seem to argue against a morphogenetic connection between the two to any close degree. A relationship of some kind between vessel element length and ecology is certainly not ruled out.

The number of vessels per group was signalled as an indicator of xeromorphy earlier (Carlquist, 1966a). However, groups that possess true tracheids or an abundance of vasicentric tracheids (e.g., *Quercus*) do not show vessel grouping (Carlquist, 1984a). This is shown clearly by the data of the present study (Table 2): the number of vessels per group is 4.67 in species with libriform fibres or fibre-tracheids, 1.37 in species with tracheids. Thus one must consider vessel grouping and tracheid presence correlatively. As shown in Table 3, 24% of the flora does have true tracheids. Thus, portions of the flora above that level (riparian, moist, alpine, desert scrub) might be expected to show some depression in vessel grouping below what otherwise might obtain, and that apparently is indeed the case (note for example the percentages less than 100 for vessel grouping of alpine and desert scrub). If, however, one does take this into account, vessel grouping can be predictive of xeromorphy, that is to say, one should consider it a factor in groups which have fibre-

tracheids or libriform fibres. The reader may wonder why in species in which true tracheids are present there are 1.37 vessels per group rather than 1.00. The answer might lie partly in random nature of vessel–vessel contacts, so that the figure 1.00 should not be realised in actuality. However, other factors may be more operative. In vessel-bearing species with growth rings, vessels are often crowded at the beginning of earlywood (where by virtue of packing constraints, they tend to be in contact more), and are less frequent, often absent, in latewood. The type V growth ring (Carlquist, 1980) is based upon this phenomenon, in which absence of vessels in latewood results in the optimally safe configuration of an all-tracheid conductive system. If growth rings are extremely narrow, vessels tend to be in contact more than if growth rings are wider. The above conditions may be seen, for example, in taxa with true tracheids in which number of vessels per group does exceed 1.00 (Table 1): *Symphoricarpos* (Caprifoliaceae), *Leptodactylon* (Polemoniaceae), and *Fendlerella* (Saxifragaceae). In a family in which true tracheids do not occur, such as Asteraceae, vessel grouping is in exact proportion to dryness of habitat (Carlquist, 1966a, 1984a). Vasicentric tracheids depress vessel grouping only if they are very abundant, and in the present study (Table 1) candidates for that effect certainly include Cactaceae, Fagaceae, Frankeniaceae, Verbenaceae, and Zygophyllaceae; to a lesser extent, lowered vessel grouping can be said to occur in Ericaceae (*Arbutus*, *Arctostaphylos*), Rhamnaceae (*Colubrina*, *Condalia*, *Rhamnus*, *Zizyphus*), Rutaceae (*Thamnosma*), and Solanaceae (*Solanum*). The intricate interrelationships between vessel grouping, true tracheid presence, and vasicentric tracheid presence demonstrate the multifarious methods of achieving safety. Solitary vessels are correlated with mesomorphy in four features, as can be seen in the horizontal lines ('Grouped', 'Solitary') of Tables 2 and 3 (1.15 vessels per group or less is the criterion for 'Solitary' in that line).

The distribution of simple versus scalariform perforation plates, as noted before, is indicative of both historical and ecological factors: scalariform perforation plates can be said to occur relictually in wet habitats (Carlquist, 1975a), and to represent unbroken history of such occupancy. Attention has been called before to the low proportion of species with scalariform perforation plates in southern California (Carlquist, 1975a). Scalariform perforation plates characterise a high number of species in riparian, moist, and alpine environments (Tables 2 & 3), confirming this tendency. A positive correlation between scalariform perforation plates

(Tables 2 & 3) and vessel element length is to be expected on the basis of the data of Frost (1930). A similar correlation between scalariform perforation plate presence and occurrence of true tracheids is evident in these tables and parallels the finding of Metcalfe and Chalk (1950: xlv). Association of scalariform perforation plates with diffuse-porous wood is not surprising because growth rings are less marked in wet habitats than in dry ones in southern California. Likewise, when the flora studied is prorated to 512 woody species (last line, Tables 2 & 3), the number of bars per plate drops, indicating relictual presence of bars and their characteristic occurrence in wet habitats. Wet habitats are small in extent in southern California and offer few opportunities for speciation in comparison with dryland habitats of this area.

Presence of true tracheids ('T' in Tables) is related to presence of primitive vessel elements in some species but, as noted above, in mapping the significance of this feature, one must take into account other factors. Primitive vessels do not have a positive selective value in habitats with dry seasons, but true tracheids do, and thus true tracheids have been retained in many groups whereas scalariform perforation plates characterise a more limited number in the southern Californian flora. By virtue of the definition followed (see Materials and Methods), true tracheids, vasicentric tracheids, and vascular tracheids are mutually exclusive, and only one type per species can be claimed. True tracheids and vasicentric tracheids are similar by surrounding vessels, to which they form a subsidiary conductive system, whereas the latewood positioning of vascular tracheids potentially renders their function different, one of maintaining water supply to the cambium or limited stem portions rather than to an entire foliar system. If true tracheids and vasicentric tracheids are equivalent, the combination of the two types can be cited as representing a functional capability. Alpine plants here thus have 100%: the safety of tracheids is evidently mandatory where water stress conditions owing to drought and cold are so severe. The next highest proportion would be found in desert scrub (74%), which certainly is a category one would choose in terms of water stress, followed by chaparral (68.3%). The role of true tracheids or vasicentric tracheids in desert and chaparral situations was signalled earlier (Carlquist, 1985), and the role of both kinds of tracheids in tropical alpine habitats has been stressed (Carlquist, 1986); certainly both true tracheids and vasicentric tracheids may be found abundantly in shrubs of all of the five Mediterranean-type re-

gions of the world (Carlquist, 1985), as well as in some dry scrub portions of zones with rather more rainfall (Carlquist, 1985). If one looks at the figure for true tracheids in the southern Californian flora studied, 23.7% (projected to 15.3% for all 512 woody species, Table 2), that figure is not particularly large; indeed, it probably is somewhat below the world figure. Metcalfe and Chalk (1950: xlv) seem to give 33% for the world flora, although their definition very likely includes what would be considered fibre-tracheids here. The sharp drop (23.7 to 15.3) as one projects for the entire southern Californian flora demonstrates that genera bearing true tracheids are mostly represented by one or a few species in California (the rosaceous genera are typical in this regard). Genera which have been able to speciate better do not have true tracheids. Phylads with vascentric tracheids have speciated well; the proportion of species with vascentric tracheids rises slightly in the projection for the 512 species.

Certainly the proportion of species studied that have vascentric tracheids is indeed spectacular (33.3%; 37.8% in the pro-rated flora). One should note that by deducting true tracheids (15.3%) and vascular tracheids (11.7%) from the flora, one finds that the maximum percentage in which vascentric tracheids could ever be present is 73%; one could legitimately deduct 7% for the herbs included in the present study, because herbs lack vascentric tracheids (Table 2). Thus, of the roster of taxa in which vascentric tracheids could possibly develop, they have developed in 51.8% (pro-rated value), a remarkably high percentage. In segments of the flora, one can make similar calculations and obtain even more striking results. For the alpine flora, 100% of the species which could have developed vascentric tracheids have done so; in desert scrub, 77%; in chaparral, 75% (no subtraction for herbs is made for these categories because herbs were omitted from calculations for the ecological categories). These high percentages show dramatically the selective value for vascentric tracheids in these ecological zones. In passing, one might mention an important vessel-bearing shrub with true tracheids not included in the figures because only dicotyledons have been studied here: *Ephedra*, which forms a conspicuous element in dry areas of California and the Southwest.

Vascular tracheids are not common in the southern Californian flora. They bulk large only in three groups: coastal sage, desert wash, and vines. The latter two represent too few species to be significant. The coastal sage tends to include plants with drought-deciduous foliage (e.g., *Toxicodendron diversilobum*, *Eriophyl-*

lum confertiflorum, *Lotus scoparius*, and *Eriogonum fasciculatum*), in which not merely leaves but branch tips and various portions of branches also are sacrificed during severe drought. These habits may be related to vascular tracheid presence. These are plants of open habitats which can die back to a base, not losing canopy status, whereas evergreen shrubs like those of the chaparral, would lose canopy status should dieback occur. Vascular tracheid presence seems related to loss of leaves during drought, since the latewood-only distribution of vascular tracheids (as defined here and elsewhere) would not be a distribution ideal for leaf maintenance, but it would be favourable for maintenance of the cambium.

Helical sculpture is represented in both horizontal and vertical columns in Tables 2 and 3 in order to show as many interfaces of this character as possible. Occurrence of sculpture in earlywood (SE) as well as latewood (SL) have been recorded. The fact that helical sculpture occurrence increases in latewood suggests correlation with xeromorphy. Webber (1936) noted correlation of helical sculpture with habitat in southern Californian shrubs, and here we see that in fact, it characterises 39.6% of the 207 species studied; if pro-rated to the 512 species, the percentage would be 43.9. More significant even than the total percentage is the distribution of helical sculpture among the groupings of the flora. Appreciably elevated values for helical sculpture presence are found in chaparral and (at least in latewood) desert scrub, as well as shrubs in general. The low number of vines studied renders that category moot. Categories that fall below the flora average in percentage of helical sculpture presence include riparian, moist, desert wash, succulents, trees, subshrubs, and herbs. Other categories contain too few species to be significant. The categories that fall below the flora average can be said to range from strongly (riparian) to moderately (desert wash) mesophytic. The alpine shrubs are slightly below the flora average in sculpture presence, perhaps because the fewer of the taxonomic groups in that grouping tend to possess helical sculpturing on vessels. Strong correlation exists with simple perforation plates and vascentric tracheid presence. These seem related to xeromorphy (although see above with respect to scalariform perforation plates). Helical sculpture is strongly correlated with narrow vessels, high vessel density, and is weakly correlated with short vessel element length. Thus there is a very strong correlation between presence of helical sculpture and a low Mesomorphy ratio. Helical sculpture thus appears clearly an indicator of xeromor-

phy, as well as other factors (e.g., cold, which may be merely physiological drought when freezing occurs, in North Temperate woody plants). Helical sculpture has very likely evolved numerous times independently; a discussion has been offered elsewhere (Carlquist, 1984c). Baas et al. (1983) found that a low proportion of shrubs from arid regions of Israel and adjacent regions have helical sculpture, but 44% of the Mediterranean species are reported to have helical sculpture, a finding in agreement with those of the present paper (43.9% for the pro-rated flora). The low proportion found by Baas et al. (1983) in the arid-land species may be related to the near-absence of the character in the family which represents the dominant shrubs of that region, Chenopodiaceae. Families that characteristically do not have helical sculpture may have other devices of greater significance (C_4 photosynthesis is common in Chenopodiaceae).

Three degrees of growth ring occurrence are recorded in the horizontal lines of Tables 2 and 3; a proportionate figure is given in the vertical columns (0 = absent or diffuse-porous; 50 percentile value is given to semi-ring-porous, 100 to ring-porous). Because of the percentile values represented, none of the figures in the vertical column could be expected to approach 100 very closely. For example, all three woodland trees have (semi-ring-porous) growth rings, and thus rate 50 (Table 2). Interestingly, species that lack growth rings have appreciably wider vessels (Tables 2 & 3); growth rings are, as noted earlier, less common in riparian species. This correlation derives from the tendency, in southern California, for growth rings to occur in more highly xeromorphic plants. The percentage spreads shown for this feature in Table 3 are more significant than equivalent ones for other features because of the 50% value assigned to semi-ring-porous.

Comparison of features related to xeromorphy can be done using Tables 2 and 3. Growth rings are much more common than are other features indicating xeromorphy, followed by helical sculpture, followed by vascentric tracheids; vascular tracheids are a weak fourth. The former two features can occur in plants with any kind of tracheid, and so one would expect those features to be more common than are vascular tracheids or vascentric tracheids, which cannot occur in plants with true tracheids by definition.

If one looks at how vessels per mm^2 and vessel diameter differ from the flora mean in the categories chaparral, alpine, and desert scrub (Table 3), one can total the percentages by which each feature differs from the total flora.

The combined percentages thus obtained are 139 for vessels per mm^2 , 84 for vessel diameter. One could thus say that vessel density changes more rapidly (at least as a numerical quantity) than vessel diameter by roughly a factor of 2. Vessel element length does change with respect to xeromorphy, but its changes are not as strongly correlated with vessel diameter or vessel density as those features are with each other, and vessel element length is also influenced by tracheid presence.

True tracheid presence or absence and number of bars per perforation plate are not simple indicators of xeromorphy, since relictual phenomena are involved as noted above. Disappearance of bars from perforation plates does accompany entry into seasonally dry environments, although one can cite exceptions (the alpine plants of the present study, most of which retain primitive woods). Alpine plants very likely experience shorter and less severe dry periods than do desert scrub plants or chaparral shrubs. There is a loose linkage between long vessel elements, scalariform perforation plate presence, and tracheid presence (Tables 2 & 3) in a few such primitive woods of this study. This linkage of primitive features is evidently not disadvantageous because the plants concerned are basically in moist habitats and have adapted to seasonal drought or cold with respect to vessel diameter, vessel density, presence of helical sculpture, and presence of growth rings. True tracheid presence is basically valuable in dry conditions, but it is distinctive among the primitive features in this respect. Vessel elements longer than one might expect may be present in such groups as desert scrub because tracheids are present to such a high degree in such associations; a linkage of sorts between these two features apparently does occur. The fact that scalariform perforation plates are so scarce in southern Californian habitats other than alpine and riparian whereas true tracheids characterise nearly a quarter of the flora studied shows that true tracheids have been retained preferentially at the same time that bars on perforation plates have been lost and great length of vessel elements has been lost.

The projection for the 512 woody species of the southern Californian flora (Tables 2 & 3, last lines) shows that there is a slightly greater degree of xeromorphy in all pertinent features compared to that of the 207 species actually studied. The differences are not statistically significant, but the fact that all features (except for vascular tracheids) tend toward xeromorphy rather than mesomorphy in the pro-rated flora is no chance occurrence. Note

should be taken of the fact that the more common a feature is in the flora studied, the less one should expect it to advance in the projected figures. Consequently, growth rings are only slightly more common in the projected flora, vascentric tracheids much more common. Two features do show statistical significance in the pro-rated flora: scalariform perforation plates ('bars') and presence of true tracheids. These dip sharply in the projected flora. That can be explained on the basis that these features are associated with primitive woods, and that species with such woods have speciated little within southern California, whereas phylads with more specialised woods have speciated far more.

The Mesomorphy figures for the flora as a whole require comment: how can the 217 species studied have a Mesomorphy figure of 123, whereas only the few representatives of five groupings (riparian, desert wash, succulents, woodland, and herbs) exceed that figure? The answer is that those few with large Mesomorphy figures (e.g., the woodland trees) raise the average inordinately. If one derives a Mesomorphy figure instead based on the last two lines of Table 2, one finds $M = 32.7$ for the 207 species, 30.1 for the projected species. These figures rank as rather strongly xeromorphic compared with the ratios found in other groups, and should leave no doubt that wood anatomy has indeed played a significant role in adaptation by the southern Californian flora to the ecology of this area. Clearly, one cannot disregard wood anatomy when considering adaptations of plants to ecology in this or any other area.

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