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COMPARATIVE WOOD ANATOMY OF MALOSMA AND RELATED GENERA (ANACARDIACEAE)

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For the past 135 years a controversy has existed over the taxonomic relationships of Malosma, a monotypic genus [M. laurina (Nutt.) Nutt. ex Abrams] of coastal southern California and Baja California, first named in manuscript by Thomas Nuttall. Torrey and Gray (1838), however, chose not to recognize Nuttall's name and placed his new species in the genus Rhus. Walpers (1842) included M. laurina in Lithrea; however, *Malosma* differs from *Lithrea* in that it is innocuous and possess five rather than ten stamens. Most authors (Munz, 1959; Thorne, 1967; Brizicky, 1963) have followed Torrey and Gray by treating Malosma as a subgenus of Rhus. Barkley (1937), in his comprehensive monograph of North American Rhus and its allies, recognized a number of generic segregates from Rhus (sensu stricto), including Malosma. Heimsch (1940) studied the wood anatomy and pollen morphology of Rhus and its segregates (Actinocheta, Cotinus, Malosma, Metopium, and Toxicodendron) and from his findings supported the classification of Barkley. However, with respect to Malosma, Heimsch's work has two major faults. Firstly, he presented no quantitative data on the wood anatomy of the taxa he investigated. Secondly, he was apparently unable to study in detail those members of Rhus (in particular, R. integrifolia and R. ovata) which are associated with M. laurina in nature. If there is a relationship between Rhus and Malosma, it should be most pronounced in those species which, in terms of habitat, are most closely associated with M. laurina. Brizicky (1963), disagreeing with Barkley (1937) and Heimsch (1940), again relegated two of the segregates, Malosma and Toxicodendron, to subgenera of Rhus. Gillis (1971) in a comprehensive study of Toxicodendron has adequately shown (in my opinion) that it is morphologically distinct from Rhus and should be treated as a separate genus. Gillis also added that Malosma and Lobadium are in need of further investigation. The intent of this study was to reexamine the wood anatomy of *Malosma* and allied genera, and to reevaluate its implications on the taxonomic status of Malosma.

MATERIALS AND METHODS

The taxa investigated are listed in Table 1. The nomenclature used follows that of Barkley (1937) as modified by Brizicky (1963), Gillis (1971),

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TAXON	COLLECTION	POROSITY (S ² VESSEL DIAMETER)	$\tilde{\mathbf{x}}$ vessel element Length (range), μ	$\tilde{\mathbf{X}}$ vessel diameter (fange), μ	X NUMBER VESSELS/ MM ²	$\tilde{\mathbf{X}}$ llbriform fiber Llbriform (range), μ Length (range), μ	$\tilde{\mathbf{X}}$ WIDTH MULTISERIATE RAYS (RANGE), μ	$\tilde{\mathbf{X}}$ height multiseriate rays (range), μ	Χ̈́ HEIGHT UNISERIATE RAYS (RANGE), μ	CRYSTALS IN RAYS RAY TYPE (SEE TEXT) HELICAL SCULPTURNG OF VESSEL WALLS RESIN CANALS IN RAYS
Cotinus americanus Nutt.	USw 7418: Maryland (RSA)	RP (2986)	$201 \ (77-319)$	73 (12–160)	427	507 (350–745)	19 (12–27)	280 (154-396)	227 (154-385)	+ wMu
Malosma laurina (Nutt.) Nutt. ex Abrams	Young 1197: Santa Barbara, Calif. (RSA)	DP (428)	$\substack{297\\(169-418)}$	$82 \\ (35-116)$	81	488 (361–689)	$\substack{34 \\ (26-44)}$	$\substack{400\\(215-531)}$	$\substack{221\\(120-470)}$	- + - M
M. laurina	Young 1198: Santa Barbara, Calif. (KSA)	$\begin{array}{c} \mathrm{DP} \\ (517) \end{array}$. ,	26	$\substack{627 \\ (474 - 779)}$	$\substack{39\\(29-55)}$	(/	$240 \\ (110-501)$	- + - M
M. laurina	Young 1001: Yorba Linda, Calif. (RSA)	DP (500)	$317 \\ (169-463)$		46	555 (339–723)	24 (20–29)		$234 \\ (113-565)$	- + - M
M. laurina	Young 1101: Cedros Island Baja Calif. (RSA)	(463)		(/	64	$508 \\ (294-666)$	$\substack{37\\(29-44)}$	$\substack{337\\(226-542)}$	231 (160–360)	- + - wMU
M. laurina	Young 1103: Cedros Island Baja Calif. (RSA)	(145)		. ,	61	$535 \\ (305-632)$		304 (192–463)		- + - wMU
M. laurina	Young 1199: Tres Virgenes Baja Calif. (RSA)	(292)	$317 \\ (237 - 474)$	$\substack{75 \\ (26-102)}$	43	$597 \\ (429 - 847)$	$41 \\ (35-55)$		$\substack{251\\(170\text{-}480)}$	- + - wMU
Metopium toxiferum (L.) Krug & Urb.	USw 4244: Haiti (RSA)	DP (377)	1		20	$962 \\ (632 - 1355)$				+ + - wMU
M. toxiferum	USw 7256: Florida (RSA)	DP (207)	320 (209–418)	$91 \\ (58-116)$	26	$745 \\ (327 - 1129$	55)(35–70)	$505 \\ (192 - 531)$	_	+ + - wMU
M. brownei (Jacq.) Urb.	USw 13551: Mexico (RSA)	DP (584)	430 (237–621)	$125 \\ (73-160)$	21	$\substack{1184 \\ (858 - 1773)}$	37)(26–58)	519 (339–915)		+ + - wMU
Rhus subg. Rhus										
R. lanceolata Gray ex Engler in DC.	Young 1–38: Uvalde, Texas (RSA)	RP (3001)	283 (120–410)	$103 \\ (13-208)$	261	697 (520–891)	$42 \\ (29-57)$	$\substack{430\\(220-751)}$	$166 \\ (100-240)$	+ - + wMu
R. typhina Torner	USw 18991: Illinois (RSA)	RP (4258)	300 (192–452)	97 (15–226)	405	514 (361–632)	$^{22}_{(14-32)}$	353 (113–598)	$244 \\ (158 - 384)$	+ wMu
R. glabra L.	USw 19071: Illinois (RSA)	RP (3324)	$257 \\ (124 - 373)$	90 (17–189)	258	$\substack{530 \\ (395-734)}$	$15 \\ (9-20)$	357 (192–790)	331 (113–632)	+ wMu
R. copallina L.	USw 21724: Virginia (RSA)	RP (3388)	$\substack{268\\(147-384)}$	85 (15–177)	382	630 (418–824)	30 (23–34)	$316 \\ (143-429)$	$165 \\ (113-282)$	+ wMu
R. copallina	USw 9859: Washington, DC (RSA)	RP (3218)	$\substack{264\\(135-406)}$	63 (15–191)	268	599 (373–802)	$\begin{smallmatrix}&23\\(15-32)\end{smallmatrix}$	$236 \\ (135 - 567)$	248 (135–406)	+ wMu
Rhus subg. Lobadium										
R. integrifolia (Nutt. in T. & G.) Brew. & Wats.	Young 718: Santa Barbara, Calif. (MACF)	RP (707)	$\substack{225 \\ (130 - 350)}$	56 (13–96)	137	531 (420–731)	36 (29–44)	371 (220–701)	253 (140–581)	+ - + MU

TAXON	COLLECTION	POROSITY (S ² VESSEL DIAMETER)	$\tilde{\mathbf{X}}$ vessel element Length (range), μ	$\tilde{\mathbf{X}}$ vessel diameter (range), μ	X NUMBER VESSELS/ MM ²	Ř LIBRIFORM FIBER LENGTH (RANGE), μ	$\tilde{\mathbf{X}}$ width multiseriate rays (range), μ	\tilde{X} height multiseriate rays (range), μ	Ř HEIGHT UNISERIATE RAYS (RANGE), μ	CRYSTALS IN RAYS RESIN CANALS IN RAYS HELICAL SCULPTURING OF VESSEL WALLS RAY TYPE (SEE TEXT)
R. integrifolia	Young 1000: Yorba Linda, Calif. (RSA)	RP (641)	233 (124–361)	81 (35–116)	56	567 (361-858)	44(29-87)	432 (135-711)	196 (79–316)	+ - + MU
R. integrifolia	Young 1100: Cedros Island, Calif. (RSA)	RP (1232)	246 (140-320)	62 (18–125)	150	576 (320–651)	29 (23-36)	392 (230–621)	256 (160-410)	+ - + MU
R. ovata Wats.	Young 1002: Claremont, Calif. (RSA)	RP (863)	$210 \\ (113 - 327)$		50	$\substack{450\\(282-565)}$	30 (23–44)	1	183 (90–316)	+ - + MU
R. ovata	Young 682: Warner Springs, Calif. (MACF)	RP (677)	$190 \\ (113-282)$		123	475 (360–651)	$\substack{29\\(23-34)}$	•	$\substack{261\\(150-440)}$	+ - + MU
R. cvata	Young 1200: Riverside Co., Calif. (RSA)	RP (871)	$200 \\ (113 - 282)$	51 (13–99)	197	477 (280–601)	•	289 (120-490)	352 (210–561)	+ - + MU
R. ovata	Young 1201: Tres Virgenes, Baja Calif. (RSA)	(831)	$184 \\ (100-250)$		220	410 (280–490)			356 (190–601)	+ - + MU
R. virens Lindh. ex Gray	Young 1-35: Uvalde, Texas (RSA)	RP (881)	$219 \\ (110-280)$		685	$571 \\ (480 – 701)$				+ - + Wm
R. choriophylla Woot. & Standl.	Young 0636: Cochise Co., Arizona (RSA)	RP (602)	$191 \\ (113-248)$	$\substack{54\\(15-93)}$	365	$377 \\ (226 - 497)$			$287 \\ (135 - 474)$	+ - +WM
R. choriophylla	Young 0634: Santa Cruz Co., Arizona (RSA)	RP (482)	$194 \\ (79-260)$		520	$434 \\ (294 - 587)$	$28 \\ (17 - 38)$		$265 \\ (113-565)$	+ - +WM
R. rubifolia Turcz.	Young 1–23: Monte Alban, Oaxaca, Mexico (RSA)	RP (720)	346 (200–561)	. ,	190	575 (400–761)		486 (180–1271)	476) (310–1001	+ - + wm
R. trilobata Nutt. var. racemulosa (Green) Barkl.	Young 1–31: New Mexico (RSA)	RP (1008)	169 (110–260)	52 (13–104)	858	462 (320–611)	*	_	327 (150–601)	+ + + m ¹
R. trilobata var. racemulosa	Young 1116: Santa Cruz Co., Arizona (RSA)	RP (1246)	$215 \\ (136 - 305)$	$57 \\ (12-104)$	508	$427 \\ (271 - 587)$	*	_	$\begin{smallmatrix}&286\\(124\text{-}452)\end{smallmatrix}$	+++ m
R. microphylla Engelm. ex Gray	Young 1–27: Doña Ana Co., New Mexico (RSA)	RP (1319)	209 (120–370)	$52 \\ (13-135)$	980	547 (380–701)	$\underset{(18-29)}{\overset{24}{\scriptstyle (18-29)}}$	$\substack{295\\(170-420)}$	$\begin{smallmatrix}&273\\(150-501)\end{smallmatrix}$	+ + + m1
R. microphylla	Young 0640: Cochise Co., Arizona (RSA)	RP (1000)	$\begin{smallmatrix}&162\\(77\text{-}242)\end{smallmatrix}$	50 (9–99)	898	368 (220–572)	25 (17–30)	286 (150–500)	$\substack{238\\(113-406)}$	+ + + m
Schinus molle L.	Young 1003: Claremont, Calif. (RSA)	RP (780)	$\substack{272\\(132374)}$	62 (26–119)	473	605 (395–835)	26 (20–38)	$\substack{324\\(169-598)}$	$\begin{smallmatrix}&162\\(102–294)\end{smallmatrix}$	+ - + M
Toxicodendron diversi- lobum (T. & G.) Greene	Wheat s.n.: Claremont, Calif. (RSA)	RP (2213)	292 (181–406)	76 (20–165)	731	$\substack{435 \\ (305-576)}$	46 (32–64)	673 (406–1152)	284) (147–452)	+ WM

*Only multiseriate rays lacking resin canals were measured in this category; R. trilobata var. racemulosa only possessed multiseriate rays with canals.

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and Young (1974b). The samples of *Malosma laurina*, *Rhus ovata*, *R. integrifolia*, *R. choriophylla*, *R. lanceolata*, *R. microphylla*, *R. rubifolia*, *R. trilobata* var. *racemulosa*, *R. virens*, and *Schinus molle* were collected by myself and vouchers deposited in RSA or MACF. These samples were dried without artificial heat before being sectioned. Samples of *Metopium toxiferum*, *M. brownei*, *Cotinus americanus*, *R. copallina*, *R. typhina*, and *R. glabra* were from the RSA wood collection. Sections and macerations of the samples were prepared using standard techniques and the slides deposited in the RSA slide collection.

For each quantitative measurement the mean (\bar{x}) and range were calculated (n = 50 for vessel-element and libriform fiber lengths; n = 25 for vessel diameter; n = 20 for ray height and width; n = 10 for number of vessels per mm²). The sample variance (s^2) of vessel diameter was calculated as a means of comparing diffuse-porous (DP) and ring-porous (RP) woods. Standard deviation (s) and standard error of the mean (SE) were calculated for selected characteristics such as vessel-element length and vessel diameter.

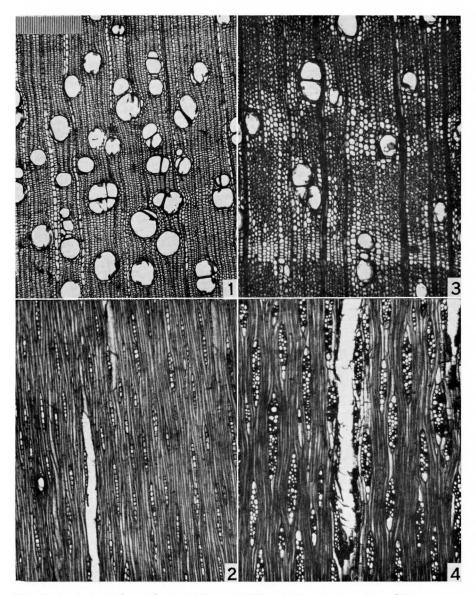
Several symbols were arbitrarily chosen to designate ray types (M = multiseriate; U = uniseriate; W = winged multiseriate). A capital letter denotes that the particular characteristic in question predominated, whereas a lower case letter denotes a lesser or weaker occurrence. For example, wMu signifies that slightly winged multiseriate rays occurred most commonly but that uniseriate rays were also present.

RESULTS AND DISCUSSION

TAXONOMIC CONSIDERATIONS

Quantitative and qualitative features considered to show significant differences or similarities between the woods of the taxa investigated are summarized in Table 1. Several features are shared by all taxa: (1) libriform fibers (no tracheids); (2) alternate pitting on lateral vessel walls with more or less elliptical pits (Fig. 12); (3) simple perforation plates (Fig. 13); and (4) heterogeneous rays (both multiseriate and uniseriate), with an abundance of upright, procumbent (predominated), and square cells, were uniformly present.

When the remainder of the characteristics are compared a striking feature emerges: *Malosma* and *Metopium* have a number of characteristics in common and differ considerably from the remaining genera. Only *Malosma* and *Metopium* include species that are diffuse porous (Figs. 1 and 3) and lack helical sculpturing on their vessel elements. Also, members of both possess resin canals in their rays (Figs. 2 and 4). Resin canals have been reported in the rays of species of *Toxicodendron* (Record, 1939), *Schinus* (Heimsch, 1942), and *Rhus* [e.g., *R. trilobata*, *R. aromatica* Ait., and *R. viminalis* Ait. (Heimsch, 1940)], although they were not observed in this study in the first two genera. Heimsch (1940) also failed to detect resin canals in the rays of *Toxicodendron* and it is likely that they do not occur in the rays of species of this genus. Heimsch (1942) did not indicate the



Figs. 1–4.—1–2. Malosma laurina (Young 1103).—1. Transection. Note diffuse-porous condition.—2. Tangential section. Note resin canal in ray.—3–4. Metopium brownei (USw 13551).—3. Transection. Note abundant (aliform and terminal) axial parenchyma.—4. Tangential section. Note lack of uniseriate rays and resin canals.—(Each line in the scale in Fig. 1 = 0.01 mm, and applies to Figs. 1–10.)

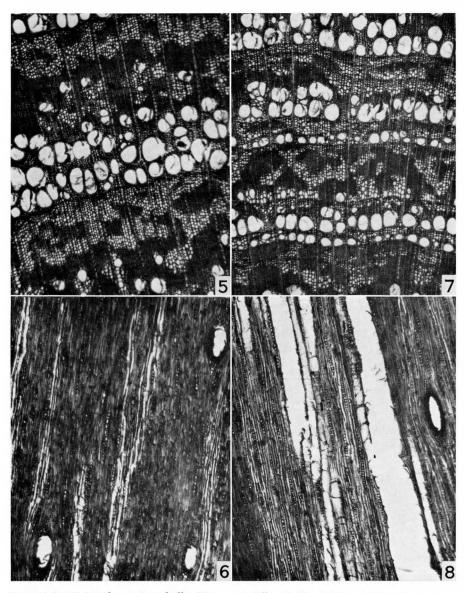
species of *Schinus* he investigated; the occurrence of resin canals may vary among species of *Schinus*. *Rhus viminalis*, of the subgenus *Thezera* [or the genus *Searsia* according to Barkley (1965)], is just one of approximately 50 species from the Cape region of South Africa. Unfortunately, material of this group was unavailable for study. Further study is needed on these species.

Heimsch (1940) indicated that R. trilobata and R. aromatica are the only American species of Rhus having resin canals in their rays (see Fig. 8), and he felt it significant that both species belong to the same section (Lobadium) of the genus. However, I have found resin canals in the rays of R. microphylla (Fig. 6). Rhus microphylla is also similar to R. aromatica and R. trilobata in possessing flamelike clusters of small vessels in the late wood (Figs. 5 and 7). At present, R. microphylla is placed in a separate, monotypic section (Rhoeidium) of the genus. However, the unique clustering of vessels in the late wood and resin canals in the rays suggests a close relationship between R. microphylla, R. trilobata, and R. aromatica. On the basis of wood anatomy, R. microphylla would be better placed in the section Lobadium, rather than in a section of its own.

Because resin canals occur in the rays of certain species of *Rhus*, their presence or absence, by itself, cannot be used to distinguish *Malosma* from *Rhus*. However, the presence of resin canals in the rays of *M. laurina* in combination with other features of its wood anatomy does distinguish *Malosma* from all species of *Rhus* investigated to date. In this regard, both Heimsch (1940) and Brizicky (1963) have pointed out that very little is known of the wood anatomy of the Mexican species of *Rhus*. At present, I am investigating the wood anatomy of these species and have included one of them, *R. rubifolia*, in this study. My preliminary investigations of *R. standleyi* Barkl., *R. kearneyi* Barkl. ssp. virginum Moran, *R. lentii* Kellogg, and *R. oaxacana* Loes. show that none possesses resin canals in its rays and in their wood anatomy they appear to be very similar to *R.* ovata, *R. choriophylla*, and *R. virens*.

Metopium spp. differ from M. laurina and members of the remaining genera in their longer libriform fibers ($\bar{x} = 939\mu$ vs. $\bar{x} = 590\mu$ in Schinus molle), lack of uniseriate rays, and abundant vasicentric (often aliform and terminal in M. brownei) axial parenchyma (Fig. 3). Representatives of all other genera have scanty paratracheal parenchyma (see Fig. 1). Toxicodendron diversilobum is distinctive only in its longer ($\bar{x} = 655\mu$ vs. $\bar{x} = 506\mu$ in Metopium brownei), distinctly winged multiseriate rays (Fig. 11).

As stated in the introduction, if *Malosma* is closely related to *Rhus* then one would expect the most similarities in wood anatomy to exist in those *Rhus* species associated in nature with *M. laurina*. However, when the latter is compared with *R. integrifolia* and *R. ovata*, two closely related species (Young, 1974a) which also occur in the southern California chaparral, they differ markedly. Of most significance, *R. integrifolia* and *R. ovata* are ring porous, as are all species of *Rhus* investigated to date (see Figs. 9 and 10). The ring-porous condition appears to be highly specialized



Figs. 5–8.—5–6. Rhus microphylla (Young 1–27).—5. Transection. Note ring-porous condition and flamelike clusters of small vessels in late wood.—6. Tangential section showing resin canals in rays.—7–8. Rhus trilobata var. racemulosa (Young 1–31).—7. Transection. Note distinct ring-porous condition and flamelike clustering of vessels.—8. Tangential section. Note resin canal in ray and abundant uniseriate rays.

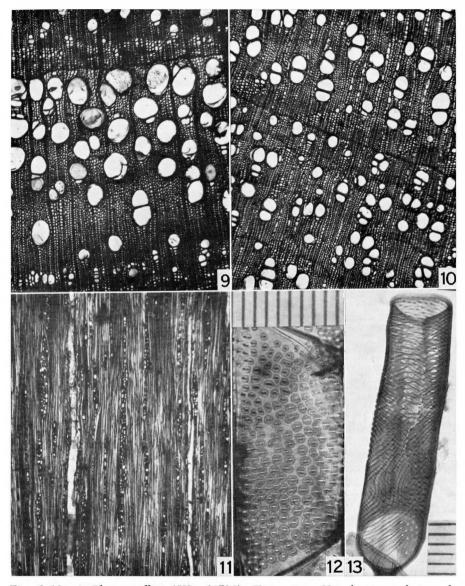
and occurs in comparatively few woods, many of which are species of the north temperate zone (Gilbert, 1940; also see Carlquist, 1957). Of the 30 genera of the tribe Rhoeae studied by Heimsch (1942), species of only four (Cotinus, Pistacia, Rhus, and Toxicodendron) were ring porous and, with the exception of certain species of Rhus subg. Lobadium, this feature is concomitant with deciduousness. For the Anacardiaceae in general, diffuse porosity is characteristic (Heimsch, 1942). Distributions of M. laurina, R. integrifolia, and R. ovata in the Miocene were very similar (see Young, 1974a) for the species occurred throughout central and southern California and into west-central Nevada (Axelrod, 1967). The general tendency in the woods of chaparral species is towards diffuse porousness (Webber, 1936), yet R. integrifolia and R. ovata have retained the ring-porous condition. Ring porosity in Rhus appears rather fixed genetically. If species of Malosma and Rhus are derived from a common ancestor (i.e., closely related) then this ancestor must have been diffuse porous and the divergence must indeed be ancient in terms of geologic time. The same argument would seem to apply when comparing M. laurina, in terms of wood anatomy, with species of Cotinus, Schinus, or Toxicodendron.

ECOLOGICAL CONSIDERATIONS

Carlquist (1966), in his study of the wood anatomy of the Asteraceae, found a number of correlations between wood anatomy and ecological conditions, particularly with regard to the amount of rainfall. With increased aridity he found in xeromorphic woods a sharp decrease in vesselelement length, an increase in helical sculpturing of vessel elements, and more numerous, narrow vessels per unit area. With regard to the latter, Carlquist concluded that numerous, narrow vessels would provide for greater capillarity per unit volume of wood than would few, wide vessels. That is, in a xeric situation where water is a limiting factor, numerous, narrow vessels would be more efficient in translocating water and thus be of selective advantage to a woody plant. Habitats of the various species investigated in this study are numerous, ranging from the more or less subtropical regions of southern Florida and the West Indies to the arid desertlike parts of Baja California and northern Mexico (for the distributions of each species refer to Barkley, 1937). Thus, it seemed useful to compare the various species studied and, using Carlquist's findings as an indication of xeromorphy, to determine whether or not the same anatomical trends are present in woods of Anacardiaceae.

Several authors (Carlquist, 1966, 1970a, 1970b; Stern and Green, 1958) have stressed the difficulty of making comparisons of the wood anatomy of different species because of inherent variability, not only in the woods but in sampling techniques. This is especially true when a limited sample is available, as was true for most species used in this study. Thus, the statistics presented here are applicable only for the samples that I have studied and may differ from other samples of the same species.

Vessel diameter: Of all the characters studied, vessel diameter may be the most important in influencing the conduction of water. However, a problem



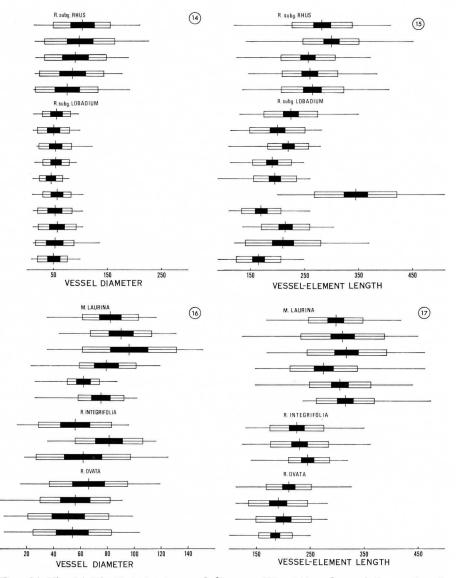
Figs. 9–13.—9. Rhus copallina (USw 21724). Transection. Note large vessels in early wood.—10. Rhus ovata (Young 682). Transection. Note smaller vessels in early wood.—11. Toxicodendron diversilobum (Wheat s.n.). Tangential section showing very long winged multiseriate rays.—12. Rhus lanceolata (Young 1–38). Lateral vessel wall showing alternate arrangement of pits. (Each line in scale = 0.01 mm).—13. Rhus virens (Young 1–35). Vessel element; note simple perforations and helical sculpturing of vessel wall. (Each line in scale = 0.01 mm.)

inherent in comparing the woods of *Cotinus*, *Rhus*, *Toxicodendron*, and *Schinus* with those of *Metopium* and *Malosma* is that the former are all ring porous, whereas the latter are diffuse porous. Some anatomists (Esau, 1967, pg. 257) considered the zone containing the larger pores in ring-porous woods as an additional tissue with no equivalent in diffuse-porous woods. This difference is apparent when comparing vessel diameter variance in ring-porous and diffuse-porous woods (see Table 1). Thus, a mean vessel diameter of 125μ in *M. brownei* is indicative of the entire wood, whereas a mean of 102μ for *R. lanceolata* is not. The mean vessel diameter in the early wood of *R. lanceolata* is 143μ compared with 34μ in the late wood. Even though *M. brownei* is characteristic of a more mesic habitat, larger vessels are produced in the early wood of *R. lanceolata*.

Differences in habit may affect overall vessel diameter. This is especially noticeable when comparing Rhus subg. Rhus, whose species are deciduous, with Rhus subg. Lobadium, many of whose species are evergreen (Fig. 14). Mean vessel diameter appears to be significantly wider in Rhus subg. Rhus than in Rhus subg. Lobadium. This is direct result of the much wider vessels produced in the early wood of the deciduous species (see Fig. 9). This difference in vessel diameter appears to be a direct response to habit and genetically fixed; it appears little influenced by environment. For example, the samples of R. lanceolata (subg. Rhus) and R. virens (subg. Lobadium) were collected growing next to each other. Yet, there appears to be a significant difference in vessel diameter in the two species (see Fig. 14). Gibson (1973), in his study of the wood anatomy of the Cactoideae, also found that habit seemed to influence wood anatomy more than habitat. However, R. microphylla, which is deciduous and probably the most xeric species (in terms of habitat) studied, does appear to have significantly smaller vessel diameters than the deciduous species of Rhus subg. Rhus (see Figs. 6 and 14).

Just as vessel diameter was difficult to analyze in the strongly ringporous species, so was the number of vessels per mm². For example, in the early wood of *R. lanceolata* the mean was 30 vessels per mm² compared with a mean of 495 vessels per mm² in the late wood. However, two general trends were evident. Diffuse-porous species tended to have fewer vessels per unit area than did ring-porous species; and the species of *Rhus* subg. *Rhus* had fewer than those of *Rhus* subg. *Lobadium*. However, this is only true when comparing the mean for the entire wood and may not be true if one compared only late or early wood in the ring-porous species.

Vessel-element length: The average vessel-element length for each of the species studied is less than that of dicots ($\bar{x} = 500\mu$; Metcalf and Chalk, 1950) in general. Metopium brownei, the most mesic species studied, in terms of habitat, had the longest vessel elements ($\bar{x} = 418\mu$; s = 84; 2SE = 24) and members of Rhus subg. Lobadium the shortest. Vessel-element lengths of the species of Rhus studied are compared in Fig. 15. Again, members of the subgenus Rhus appear to be distinct from those of the subgenus Lobadium, with the exception of R. rubifolia. Rhus rubifolia was the only



Figs. 14–17.—14–15. Variation in vessel diameter (Fig. 14) and vessel-element length (Fig. 15) in *Rhus*. The species included are arranged in the following order in both figures: *Rhus* subg. *Rhus*—*R. lanceolata*, *R. typhina*, *R. glabra*, *R. copallina* (USw 21724), *R. copallina* (USw 9859); *Rhus* subg. *Lobadium*—*R. integrifolia* (Young 718), *R. ovata* (Young 1200), *R. virens*, *R. choriophylla* (Young 0636), *R. choriophylla* (Young 0634), *R. rubifolia*, *R. trilobata* (Young 1–31), *R. trilobata* (Young 1116), *R. microphylla* (Young 1–27), *R. microphylla* (Young 0640).—16–17. Geographic variation (northsouth) in vessel diameter (Fig. 16) and vessel-element length (Fig. 17) in *Rhus integrifolia*, *R. ovata*, and *Malosma laurina*. Species are arranged in the same order as listed in Table 1.—(Scale in each figure is in microns.)

species of the section *Pseudosumac* studied. Other species of this section will have to be investigated before any conclusions about its relationships to the other sections can be made. As was true of vessel diameter, two species (*R. lanceolata* and *R. virens*) growing right next to each other differ rather significantly in vessel-element length (see Fig. 15).

ALISO

Thus, species of *Rhus* subg. *Lobadium* tend to fit Carlquist's findings for the Asteraceae. In general, they have shorter, narrower, more numerous vessel elements than the other species studied and are typical of xeric habitats. However, the predicative value of this set of characteristics, for the species studied in this investigation, is limited because other species (e.g., *R. lanceolata*) have been able to adapt to the same habitats by a completely different mechanism, i.e., deciduousness, which is only reflected in their wood anatomy as a markedly ring-porous condition. For the species of Anacardiaceae studied in this investigation, it would appear that wood anatomy alone cannot be used to characterize a species as to the type of habitat to which it is adapted.

Intraspecific variation: Geographic variation (north-south) in vessel diameter and vessel-element length for *M. laurina*, *R. integrifolia*, and *R. ovata* is compared in Figs. 16 and 17. Over the range studied, there appears to be no significant difference in either vessel diameter or vessel-element length in *R. integrifolia* or *R. ovata*. In *M. laurina* there is a slight decrease in vessel diameter in one of the Cedros Island samples; however, the difference is probably not significant. Vessel diameter in the three species is very similar (all three are chaparral species), but *M. laurina* appears to have significantly longer vessel elements compared with the other two species.

In conclusion, it is my opinion that the data presented in this paper adequately demonstrate that at least in terms of wood anatomy *Malosma* is not closely related to *Rhus* and should be treated as a distinct genus, as first proposed by Nuttall in 1838 and supported by Barkley (1937) and Heimsch (1940). If anything, *M. laurina* is more closely allied in its wood anatomy to the subtropical species of the genus *Metopium*. Fruit, flower, and pollen morphology (Young, unpubl. data) also tend to support the recognition of *Malosma* as a distinct genus.

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SUMMARY

The wood anatomy of *Malosma laurina* was compared with species of *Rhus* and four other genera of Anacardiaceae. *Malosma laurina* is most

like species of *Metopium* in that they are diffuse porous, lack helical sculpturing of vessels, and have resin canals in their rays. The most important feature distinguishing Malosma from Rhus is that the former is diffuse porous, whereas all species of the latter studied to date are ring porous.

The wood anatomy of *Rhus microphylla* is reported on for the first time, and it is very similar to R. trilobata and R. aromatica in the presence of resin canals in its rays and flamelike clustering of small vessels in its late wood. It is suggested, that on the basis of wood anatomy, R. microphylla should be treated as a member of the section Lobadium.

Several correlations between wood anatomy and habitat were attempted. It was found that some species of Anacardiaceae agree with the correlations found by Carlquist in the Asteraceae, but that others did not.

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