Wood anatomy of *Wilkesia* (Asteraceae) with relation to systematics, organography, and habit[1]

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CARLQUIST, S. (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105). Wood anatomy of *Wilkesia* with relation to systematics, organography, and habit. J. Torrey Bot. Soc. 125:261–267. 1998.——Wood anatomy of root, base, and mid-level stems of *Wilkesia gymnoxiphium* is compared with wood of lower stem and root-stem transition of *W. hobdyi*. Wood of *W. hobdyi* is xeromorphic, like that of the base of *W. gymnoxiphium*, and has no unique features not also observable in *W. gymnoxiphium*. Differences among quantitative wood features of collections and portions studied are tabulated. Fiber dimorphism is evident in extensive alternating tangential bands in wood of midlevel stems of wild-occurring *W. gymnoxiphium*, and in short tangential bands in all other collections and portions. Wood of *Wilkesia* is not as xeromorphic as that of *Argyroxiphium*, and is like that of several species of *Dubautia*; recent cladograms that show *Wilkesia* as a sister group to *Dubautia* are thus supported.

Key words: *Argyroxiphium*, Asteraceae, *Dubautia*, ecological wood anatomy, fiber dimorphism, iliau, Madiinae, tarweeds, *Wilkesia*.

Wilkesia, the iliau, is one of the three Hawaiian genera of Asteraceae, tribe Heliantheae, subtribe Madiinae. The others are *Argyroxiphium*, the silversword, and *Dubautia*, the naenae; only Keck (1936), who merged *Wilkesia* with *Argyroxiphium*, has not recognized *Wilkesia* as a distinct genus. Until recently, only a single species, *W. gymnoxiphium* A. Gray, was known; a second species, *W. hobdyi* St. John, is now accepted (Carr 1985).

Molecular evidence, as well as morphology and anatomy, shows that *Wilkesia* is separable from *Argyroxiphium* and *Dubautia* (Carlquist 1957, 1959; Carr 1985; Baldwin et al. 1990). *Wilkesia* appears closer to *Dubautia* on the basis of at least some data (Baldwin et al. 1990), although all authors stress the genetic closeness of the three genera (e.g., Kyhos et al. 1990). Nevertheless, the divergence among and within the genera in terms of habit and ecological adaptation is striking (Carlquist 1970; Carr 1985).

Does wood anatomy exhibit adaptive radiation in *Argyroxiphium*, *Dubautia*, and *Wilkesia*? An early monograph on wood anatomy of Heliantheae (Carlquist 1958) did not address this question. Some data on vessels of *Dubautia* (Carlquist 1974) suggested adaptive radiation with respect to water availability, but were incomplete. A monograph on woods of *Argyroxiphium* (Carlquist 1997) attempted to correlate adaptive

radiation within *Argyroxiphium* with data from wood anatomy by surveying all species. The present paper attempts similar correlations for *Wilkesia*. *Wilkesia hobdyi* is a rare (ca. 350 individuals known) species of dry ridges, 275–400 m (Carr 1985; Carr 1990). The habitats of *W. hobdyi* are at least somewhat more xeric than those of *W. gymnoxiphium*, which occurs in openings in dry to mesic forest but also on ridges (Carr 1985; Carr 1990). Both species are endemic to Kauai.

The habits of the two species are distinctive: *W. gymnoxiphium* is an unbranched and monocarpic rosette plant, to 5 m tall (although lower in open sites). *Wilkesia hobdyi* branches from near the base, and is at most 0.7 m tall (Carr 1985; Carr 1990). The different habits of the two species deserve examination with respect to wood anatomy. In addition, wood anatomy can vary according to height in a monocarpic plant like *W. gymnoxiphium*; such data were given for the monocarpic rosette plant *Echium pininana* Webb & Berth. (Carlquist 1975).

Although the leaves of *W. hobdyi* are smaller than leaves of adult plants of *W. gymnoxiphium*, comparison of sections of both species revealed that leaf features of *W. hobdyi* can all be found in *W. gymnoxiphium* also, and thus reporting of data on leaf anatomy was not undertaken in the present paper.

Materials and Methods. *Wilkesia gymnoxiphium* (Carlquist 575, RSA) was collected in an opening in the Kokee Forest of Kauai. A mature plant and a seedling were collected there. The specimen cited as "cultivated" was grown at my

Table 1. Wood characteristics of *Wilkesia*.

Collection	1 VG	2 VD	3 VM	4 VL	5 FL	6 MH	7 MW	8 MR
W. gymnoxiphium								
Carlquist 575 (RSA)								
midlevel stem								
cultivated	1.7	32	51	240	682	1195	3.5	151
midlevel stem	1.5	28	70	187	501	1517	7.6	75
base	1.9	26	42	142	408	1142	8.5	88
root	1.6	42	45	239	591	719	4.4	214
W. hobdyi (cult. NTBG)								
stem	1.4	15	44	171	401	967	4.5	58
lower stem	2.0	16	30	136	503	1919	7.2	73

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean lumen diameter of vessels, μm; 3 (VM), mean number of vessels per mm^2; 4 (VL), mean vessel element length, μm; 5 (FL), mean nonstoried libriform fiber length, μm; 6 (MH), mean height of multiseriate rays, μm; 7 (MW), mean width of multiseriate rays, cells; 8 (MR) Mesomorphy Ratio.

home in Santa Barbara, California, from seeds collected in August, 1992 on the Iliau Loop Trail, Waimea Canyon, Kauai. This plant likely experienced conditions more xeric than individuals of this species would in their native habitats. The plants of *W. hobdyi* were cultivated at National Tropical Botanical Garden (stem, accession number 880474; lower stem, 930205). Two plants of this species were harvested shortly before they died at maturity. Wood samples were dried. The term "lower stem" as used here denotes the stem–root transition below the branches and approximately at ground level. "Stem" in *W. hobdyi* applies to wood taken near the bases of branches; in *W. gymnoxiphium*, it refers to the stem 0.5 to 0.7 m above the ground.

Woods of *Wilkesia* are neither excessively hard nor soft in texture, and were sectioned successfully on a sliding microtome. Portions of specimens were prepared for sectioning by boiling in water and storing them in 50% aqueous ethanol. Sections were stained with safranin (Carlquist 575) or a safranin-fast green combination (other collections). Macerations were prepared with Jeffrey's Solution and stained with safranin.

Quantitative data are reported in Table 1. Vessel diameter is measured as mean lumen diameter (widest and narrowest dimensions of a lumen averaged). Vessel grouping is measured as a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. The terms used conform to the IAWA Committee on Nomenclature (1964), except for the terms "fiber dimorphism" (Carlquist 1961) and "vasicentric tracheid" (Carlquist 1985). For all features in Table 1, 25 measurements were used as the basis for the means. Ranges in dimensions are not given because ex-

ceptionally large or small cell sizes or other quantitative features are occasional in most woods and do not help to present an image of what is characteristic of a wood. The Mesomorphy Ratio presented in Table 1 is calculated as mean vessel lumen diameter times mean vessel element length divided by mean number of vessels per mm^2.

Statistical treatments other than calculation of means have not been used for several reasons. Because of rarity of individuals of *Wilkesia* and because of their protected status, a number of individuals large enough to justify statistical procedures could not be obtained. Standard deviation is typically high in quantitative wood features. More importantly, site of sampling within a plant is a source (usually unexplored by most workers) of much greater source of diversity in measurements than differences among individuals of woody species when similar portions of these individuals are sampled (e.g., stem base 10 cm above ground level). Although typical mature individuals could be obtained for *W. gymnoxiphium*, the plant of *W. hobdyi* was a default collection: senescent cultivated specimens that could be donated because they were no longer of value for display at National Tropical Botanical Garden.

Results. Vessel groupings in the genus are relatively small (Fig. 1, 3, 5, 7), averaging from 1.4 to 2.0 vessels per group (Table 1, column 1). This contrasts with *Argyroxiphium* and xeric species of *Dubautia* (Carlquist 1997), in which groups of several very narrow vessels are often associated with wider vessels. Vessel diameter (Table 1, column 2), on the other hand, varies
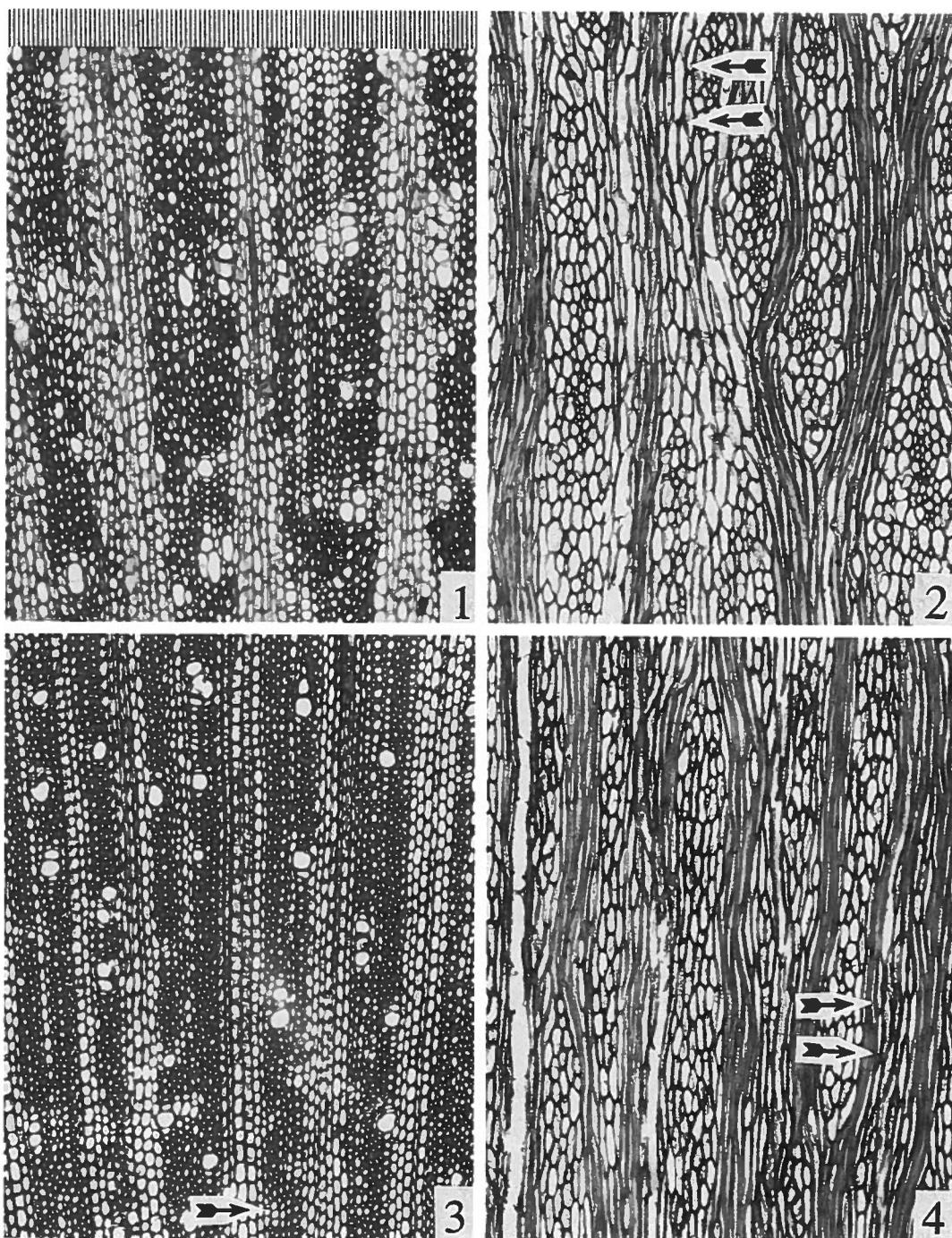
Figs. 1–4. Wood sections of *Wilkesia*. Figs. 1–2. *W. gymnoxiphium* (cultivated), sections from base of stem. Fig. 1. Transection; growth rings are absent. Fig. 2. Tangential section; rays are wide and contain numerous procumbent cells; arrows indicate shorter thin-walled fibers. Fig. 3–4. *W. hobdyi* (cultivated at NTBG), sections from stem. Fig. 3. Transection; vessels are narrow in diameter; arrow indicates patch of thin-walled fibers. Fig. 4. Tangential section; rays consist mostly of upright cells; arrows indicate shorter thin-walled fibers. Magnification scale for all figures above Fig. 1 (divisions = 10 μm).
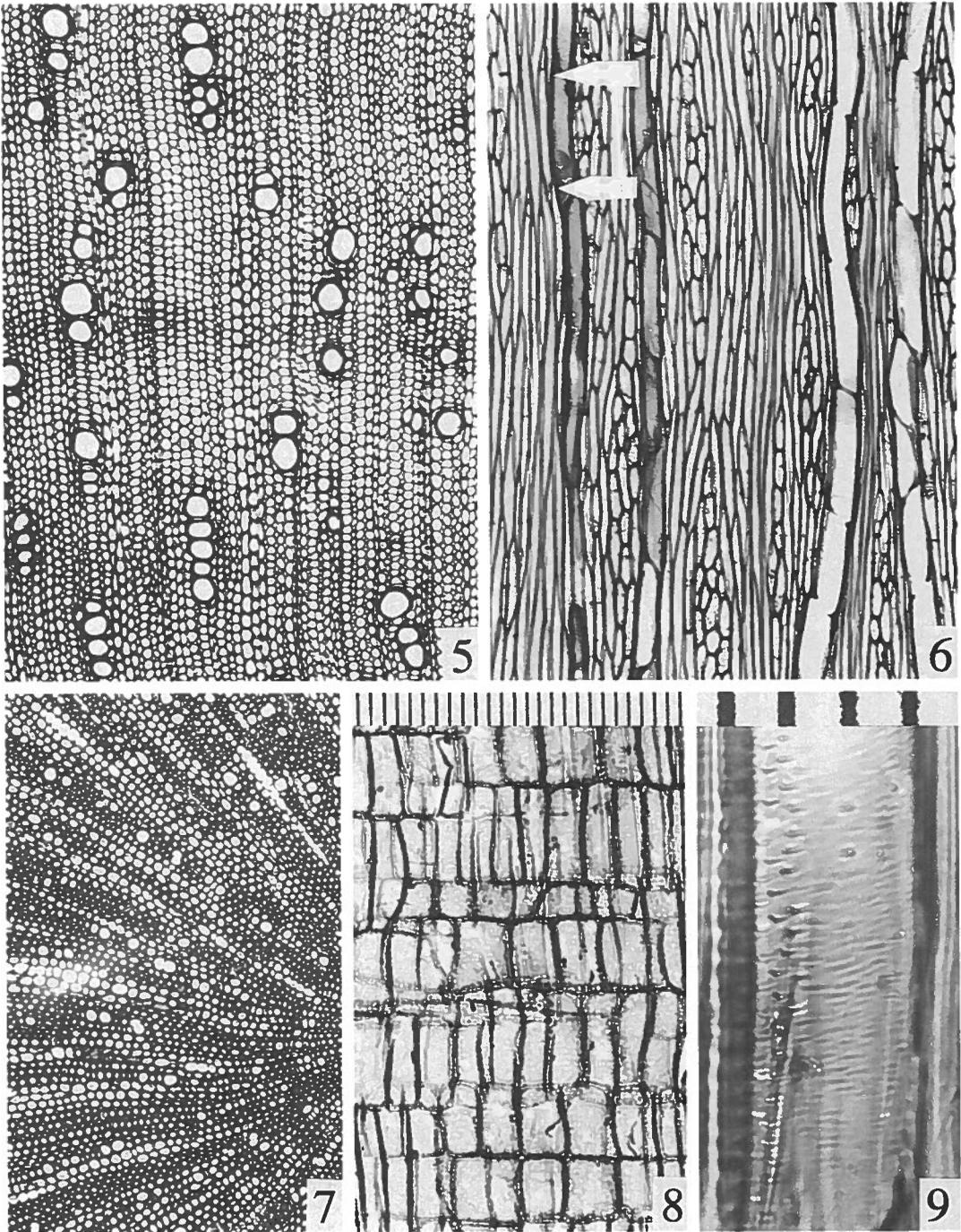
Figs. 5–9.   Wood sections of *Wilkesia gymnoxiphium* (Carlquist 575), a naturally-occurring specimen. Fig. 5. Transection from midlevel of stem; vessels are wide, Fig. 6. Tangential section from midlevel of stem; arrows indicate storied nature of the shorter thin-walled fibers, which predominate in the area shown in the photograph. Fig. 7. Transection from lower stem of seedling to show narrowness of vessels. Fig. 8. Radial section; all cells are upright except for the file indicated by the arrow. Fig. 9. Vessel wall with sparse pitting; the secondary wall is striate. Figs. 5–7, scale above Fig. 1; Fig, 8, scale above Fig. 8 (divisions = 10 μm); Fig. 9, scale above Fig. 9 (divisions = 10 μm).

markedly in *Wilkesia*. Vessels in adult plants of *W. hobdyi* (Fig. 3) average approximately half the diameter of those of adult plants of *W. gymnoxiphium* (Fig. 1, 5,), even though Fig. 1 suggests that vessel diameter in the base of *W. gymnoxiphium* is similar to that in stems of *W. hobdyi* (note should be taken of the dry conditions under which the cultivated *W. gymnoxiphium* was grown. Vessel diameter is very narrow in the stems of young seedlings of *W. gymnoxiphium* (Fig. 7), in which mean lumen diameter = 16 μm, a figure identical to that of the midlevel stems of *W. hobdyi*; vessels increase in diameter as the stem grows in diameter. In no case were growth rings based on fluctuation on vessel diameter (or on other criteria) observed.

Vessel density (Table 1, column 3) is similar in *W. hobdyi* and *W. gymnoxiphium*. However, vessel density in the cultivated *W. gymnoxiphium* is greater than in the naturally-occurring plant of that species.

Vessel element length is relatively uniform in the genus (Table 1, column 4). Radial sections of the midlevel stem of *W. gymnoxiphium* (Carlquist 575) showed steady decrease in vessel element length, corresponding to a paedomorphosis curve (Carlquist 1962) from pith to cambium.

Vessel wall thickness of 2.2–2.5 μm characterizes all of the collections except the midlevel stem of *W. gymnoxiphium* (Carlquist 575), in which vessel wall thickness is approximately 3.5 μm.

All vessels have simple perforation plates. All lateral wall pitting of vessels is alternate (Fig. 9, top). Pits are mostly oval, with slitlike pit apertures. Pit cavity diameter in an axial direction is about 3 μm. A few pits are laterally elongate. On wall surfaces of *W. gymnoxiphium* midlevel stems that are less densely pitted, striations are present (Fig. 9); because these are faint, terming them "helical thickenings" would be misleading, although they are a form of helical sculpturing.

Imperforate tracheary elements are all libriform fibers with small pits. Within a specimen, libriform fibers are not uniform in length and morphology. The darker tangential bands (Fig. 5) are libriform fibers that are thicker-walled (ca. 2.3 μm), longer, and nonstoried, like those between the vessels at right in Fig. 6. The lighter bands of libriform fibers in Fig. 5 are shorter, storied to various degrees, and thinner walled (ca. 1.5 μm), like the majority of libriform fibers in Fig. 6 (arrows indicate where storying is clear.

Such diversity in libriform fibers was cited as an incipient example of fiber dimorphism (Carlquist 1958, 1961). In the other collections of *Wilkesia*, fiber dimorphism takes a different form. In the basal stem of *W. gymnoxiphium*, as well as in the stem of *W. hobdyi*, there are short tangential bands of thin-walled storied fibers (arrows, Figs. 2, 3, 4). This condition was also observed in the root and midlevel stems of the cultivated *W. gymnoxiphium* and the basal stem of *W. hobdyi*. The length of libriform fibers given in Table 1, column 5, is the length of nonstoried thick-walled fibers. These lengths exceed the length of associated vessel elements by a factor of almost three in *Wilkesia*. Both nonstoried and storied libriform fibers are dead at maturity, judging from lack of contents, and lack of septa or other cellular subdivision within them.

The shorter, thinner-walled storied fibers of *Wilkesia* differ from axial parenchyma. As in other Asteraceae, axial parenchyma is scanty vasicentric, not banded. As in *Argyroxiphium* (Carlquist 1997), the vasicentric parenchyma consists of few strands (1–3) per vessel; the strands consist of two cells (a single cell in collections where cambial initials are shorter) and contain cytoplasm, whereas libriform fibers in *Wilkesia* do not.

Rays are both multiseriate and uniseriate in *Wilkesia*, but height of uniseriate rays is not given in Table 1 because uniseriate rays are infrequent and most commonly are a single cell in height. Multiseriate rays consist chiefly of upright cells (Fig. 8), but where multiseriate rays are wider (*W. gymnoxiphium* base, Fig. 2, and *W. hobdyi* lower stem: Table 1, column 7), procumbent cells are more common. In all collections and portions, upright cells are not confined to a single sheathing layer; rays either consist mostly of upright cells or are sheathed by a minimum of two layers of upright cells. Perforated ray cells were observed in both *W. gymnoxiphium* and *W. hobdyi*.

Amorphous deposits often termed "oleoresins" in Asteraceae may be observed in woods (e.g., two vessels at left in Fig. 6). A large quantity of such deposits was observed in the lower stem of *W. hobdyi*; this may be indicative of trauma or ageing in this plant. No secretory canals or crystals were observed in wood, although secretory canals are common in cortex of stems and roots in *Wilkesia*.

Conclusions. In *Echium pininana*, vessel element length is greater in roots than in the stem

base, then becomes progressively greater at higher levels in the stem (Carlquist 1975). The same pattern is evident in *W. gymnoxiphium*, which is a very close analogue to *E. pininana* in habit, monocarpy, and in tending to flower as it reaches the canopy of a low forest in which it begins growth in the shade of trees (Carlquist 1974).

In *W. gymnoxiphium*, rays are wider in stem bases than in roots, and narrowest in wood of midlevel stems. Starch storage in rays of the base may be significant in this regard. A smaller proportion of ray tissue could be correlated with mechanical strength of the midlevel and upper stem, the wood of which is present as a much thinner cylinder than is wood at the base of the plant.

Vessel diameter increases from inside the base of a seedling to the outside in *W. gymnoxiphium*. Because *W. hobdyi* does not have an upright, unbranched stem as does *W. gymnoxiphium*, the wood of *W. hobdyi* is comparable to wood at lower levels of *W. gymnoxiphium*, as the similarity between Fig. 1 and Fig. 3 indicates. The vessel diameter in wood of a seedling of *W. gymnoxiphium* is about the same as that in *W. hobdyi* wood samples. Both a seedling of *W. gymnoxiphium* and the adult plant of *W. hobdyi* draw water from soil levels relatively close to the surface (compared to the deepr taproots of mature individuals of *W. gymnoxiphium*). Thus, similar wood xeromorphy as indicated by narrow vessel diameter in *W. gymnoxiphium* seedlings and in adult plants of *W. hobdyi* is to be expected. Water availability fluctuates more markedly close to the soil surface, so xeromorphic wood features are potentially of greater selective value in plants with shallow roots. The figures for the Mesomorphy Ratio (Table 1, column 8) confirm that *W. hobdyi* has wood more xeromorphic than wood of *W. gymnoxiphium* adult plants. The tendency for root wood to be more mesomorphic than that of stem wood, noted elsewhere (Patel 1965; Carlquist 1975), is evident in *W. gymnoxiphium*. At the base of *W. gymnoxiphium*, vessels are much narrower and denser close to the pith (seedling wood, Fig. 7) than in wood at the periphery of a mature plant (Fig. 1). The Mesomorphy Ratio figures increase from pith to cambium in the base. The Mesomorphy Ratio for midlevel stems of *W. gymnoxiphium* is similar to that for roots in that species, but the difference between the two collections for midlevel stems suggests that this feature is environmentally modifiable depending on the

habitat. The figure for the cultivated plant is lower than that for the naturally-occurring plant. The habitat of the latter was likely more mesic than the relatively sunny, dry, garden locality in which the cultivated plant was grown. Although one often assumes that areas of cultivation offer greater water availability for a given species than the natural habitat does, and therefore the wood would be more mesomorphic in comparisons for two such collections of a particular species, the reverse can be true and has been reported for a number of species (Bissing 1982).

There are no qualitative anatomical features in the wood of *W. hobdyi* not also found in *W. gymnoxiphium*. This would support the closeness of the two species indicated in cladograms of the Hawaiian Madiinae (Baldwin et al. 1990; Baldwin & Robichaux 1995; Kyhos et al. 1990). The paedomorphosis curve in vessel element length supports the idea that *Wilkesia* is derived from a phylad that is not strongly woody.

The process of fiber dimorphism is incipient in *Wilkesia*. A similar degree of fiber dimorphism is evident in such species of *Dubautia* as *D. laxa* Hook. & Arn.; other species of *Dubautia* show either less differentiation into two kinds of fibers or a greater degree of differentiation (Carlquist 1958, 1994). The presence of tangential strands of short, storied libriform fibers (as opposed to bands of indefinite tangential extent) in both *W. gymnoxiphium* and *W. hobdyi* is a feature newly reported here.

Argyroxiphium and species of *Dubautia* from more xeric habitats have large groupings of narrow vessels plus a few vasicentric tracheids (Carlquist 1958, 1994, 1997). *Wilkesia* lacks large vessel groupings and vasicentric tracheids. Because a greater degree of vessel grouping and the presence of vasicentric tracheids are indicative of wood xeromorphy (Carlquist 1984, 1985), *Wilkesia* wood qualifies as less xeromorphic than that of *Argyroxiphium* or species of *Dubautia* such as *D. menziesii* (A. Gray) Keck. However, qualitative features of *Wilkesia* wood lie within the range of character state expressions found in *Argyroxiphium* and *Dubautia*. Although wood indicates close relationship among the three genera, diversification with respect to quantitative features clearly indicates adaptive radiation by component species of the three genera.

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