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WOOD AND LEAF ANATOMY OF
KECKIELLA (SCROPHULARIACEAE):
ECOLOGICAL CONSIDERATIONS

David C. Michener

INTRODUCTION

Keckiella Straw (Scrophulariaceae) is a genus of seven species of facultatively drought-deciduous, long-lived woody shrubs widespread but only locally common in the cismontane and desert mountains of California (including the Channel Islands) and adjacent Nevada, Arizona, and Baja California. All seven species are native to and centered in the California Floristic Province; two species have disjunct populations in desert ranges well outside this province (Keck 1936; Raven and Axelrod 1978). The genus is distinctive in consisting of strongly woody shrubs 0.5-3 m tall (an anomalous feature in the essentially herbacious Scrophulariaceae) and in having radiated into a wide variety of plant communities over a considerable geographic and elevational range. The species range from rocky sites in the northern Sonoran and Mojave Deserts (*K. antirrhinoides* ssp. *microphylla*) to openings in mixed-evergreen forests in the Coast Ranges and the Klamath Mountains (*K. corymbosa*); the elevational span is from near sea-level (*K. cordifolia*) to over 3000 m in the subalpine forests of the southern Sierra Nevada (*K. rothrockii* ssp. *rothrockii*).

The habitat diversity of *Keckiella* species is not as extreme as the geographic and elevational ranges suggest. Six of the seven species are typically found on such disturbed and exposed sites as steep (often rocky) slopes, rock outcrops, rock scree, and cliff faces. The seventh species, *K. cordifolia*, is often of less xeric sites in southern California; it ranges into riparian woodland margins and is the only *Keckiella* on the Channel Islands. Considerable habitat diversity exists among the species' sites in regularity, amount, and kind (rain vs. snow) of winter precipitation, duration of the growing season, severity of summer drought, summer and winter temperature extremes, and presence of coastal fog. Furthermore, the communities surrounding the typically rocky sites occupied by *Keckiella* differ in fire frequency, although the rockier sites and cliffs may be relatively sheltered from fire. This study presents correlations of wood and leaf characteristics with this habitat diversity, since anatomical characteristics present patterns related to habitat rather than to taxonomic grouping. Descriptive wood and leaf anatomy is presented for all taxa, and trends in shrub, wood, and leaf characteristics are discussed in relation to summer drought severity.

The ecological studies which list *Keckiella* species indicate the species present and provide a scattering of other data (Burk 1977; Hall 1902; Haines 1976, 1977; Mooney et al. 1974; Sawyer et al. 1977; Vasek and Thorne 1977; Vogl 1976; Vogl et al. 1977). These studies verify the wide community range of the genus and the low frequency of most species.

Limited work on wood anatomy of *Keckiella* may have been done; Metcalf and Chalk (1950), Record (1943) and Record and Hess (1943) provide scanty data on *Penstemon* Mitch. without listing the species studied. Only recently has *Keckiella* been recognized as a genus distinct from *Penstemon*. It is not possible to deduce which species were studied as there are over 230 species of *Penstemon*: many are suffrutescent—some to over 1.5 m tall (Straw 1962)—and subgenus *Dasanthera* is primarily of low shrubs (Keck 1951). This diversity may account for the discrepancies between the data of Metcalf and Chalk (1950) and Record (1943).

Earlier work on *Keckiella* was taxonomic. Various generic, specific, and subspecific concepts and names have been used for the taxa considered here. All recent workers agree on the apparently monophyletic origin of this group of taxa, and circumscribe the same larger taxon. Keck (1936) monographed the group as *Penstemon* section *Hesperothamnus* and later (Keck 1951) presented the species as they are now understood. Straw (1966) elevated this section to generic rank, ultimately as *Keckiella* (Straw 1967). A discussion of the reasons for the generic rank and complete synonymy are in Straw (1966, 1967). Nomenclature follows Straw (1967) and is presented in Table 1. Detailed species descriptions, geographic ranges, maps, and notes may be found in Keck (1936).

MATERIALS AND METHODS

Wood and leaf material of all taxa was field collected by the author. Voucher specimens, stock wood samples, and permanent wood and leaf slides are at RSA. A list of collection localities can be obtained from the author. Leaf material of additional populations of *K. antirrhinoides* ssp. *microphylla* was taken from herbarium specimens at RSA. Woods were subdivided and field pickled in FAA and/or air dried. Large, mature branch bases and trunks were sought (Table 1, column 1); large stems ranged to over 5 cm in diameter. Pickled woods were rinsed repeatedly in water prior to softening; dried woods were boiled in water for 1 hr. All woods received the same treatment in subsequent steps. Woods were softened in tightly capped jars of 4% ethylenediamine at room temperature for several weeks, or at 60 C for shorter periods (procedure modified from Kukachka 1977). The ethylenediamine was changed when discolored. Deleting the softening procedure resulted in abysmally poor sections. Sections were made with a sliding microtome at 18–26 μ m, stained by standard procedures in saturated

Table 1. Wood features of *Keckiella*.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>K. antirrhinoides</i> (Benth.) Straw	<i>Michener 3660</i> (RSA)	19	41	105	151	16	157	20	234	4.4	2-6	56	403	170	0.24	36
<i>ssp. antirrhinoides</i>	<i>Michener 3668</i> (RSA)	11	29	45	137	17	145	19	242	3.8	2-8	79	361	94	0.31	42
<i>ssp. microphylla</i> (Gray) Straw	<i>Michener 3934</i> (RSA)	33	23	53	129	14	152	18	207	3.7	2-4	46	197	134	0.17	22
<i>K. breviflora</i> (Lindl.) Straw																
<i>ssp. breviflora</i>	<i>Michener 3726</i> (RSA)	24	43	113	174	18	193	21	259	3.2	2-4	42	332	192	0.22	39
<i>ssp. glabrisepala</i> (Keck) Straw																
<i>ssp. glabrisepala</i> (Keck)	<i>Michener 3730</i> (RSA)	12	44	93	136	15	156	19	239	3.3	2-6	48	302	214	0.21	28
<i>K. cordifolia</i> (Benth.) Straw	<i>Michener 3662</i> (RSA)	15	40	90	194	15	233	22	316	3.1	2-9	87	748	151	0.26	51
	<i>Michener 3704</i> (RSA)	15	40	95	188	14	190	21	269	3.5	2-9	79	503	137	0.29	55
	<i>Michener 3932</i> (RSA)	8	45	80	214	18	257	23	337	2.5	2-6	44	429	204	0.22	47
<i>K. corymbosa</i> (Benth.) Straw	<i>Michener 3724</i> (RSA)	18	36	73	170	14	199	17	236	2.3	0	0	0	281	0.13	22
	<i>Michener 3732</i> (RSA)	7	39	73	154	13	180	17	235	2.9	2-5	46	274	183	0.21	33
	<i>Michener 3749</i> (RSA)	15	36	68	140	16	173	17	213	2.6	2-4	49	291	247	0.15	20
<i>K. lemmonii</i> (Gray) Straw	<i>Michener 3763</i> (RSA)	25	40	93	203	14	234	16	277	2.4	2-6	41	308	254	0.16	32
	<i>Michener 3735</i> (RSA)	8	45	120	114	16	144	20	216	3.1	2-7	83	529	98	0.46	52
	<i>Michener 3773</i> (RSA)	7	34	80	177	15	182	23	254	3.5	2-8	67	435	92	0.37	65
	<i>Michener 3778</i> (RSA)	12	41	100	175	19	183	21	267	2.8	2-7	66	368	136	0.30	53
<i>K. rothrockii</i> (Gray) Straw	<i>Michener 3789</i> (RSA)	16	42	85	171	16	209	23	258	3.1	2-5	46	251	158	0.27	45
<i>ssp. jacinensis</i> (Abrams) Straw																
<i>ssp. rothrockii</i>	<i>Michener 3804</i> (RSA)	32	43	83	142	16	184	21	221	2.8	2-7	64	357	158	0.27	39
	<i>Michener 3796</i> (RSA)	40	41	85	133	11	154	17	155	2.8	2-5	72	451	199	0.21	27
	<i>Michener 3798</i> (RSA)	18	39	73	154	15	192	17	221	3.4	2-6	52	371	202	0.19	30
<i>K. ternata</i> (Torr.) Straw	<i>Michener 3800</i> (RSA)	6	30	60	144	14	178	15	202	2.7	2-4	44	370	181	0.17	24
<i>ssp. septentrionalis</i> (Munz and Johnston) Straw																
<i>ssp. ternata</i>	<i>Michener 3689</i> (RSA)	25	22	50	208	15	213	16	261	3.3	2-4	34	250	252	0.09	18
	<i>Michener 3664</i> (RSA)	37	47	95	119	19	139	22	174	2.9	2-6	58	371	206	0.23	27
	<i>Michener 3931</i> (RSA)	4	49	83	214	18	252	20	318	4.0	2-5	38	346	143	0.34	73
	<i>Michener 3933</i> (RSA)	9	42	128	158	19	191	22	244	3.6	2-8	57	308	98	0.43	68

Key to columns: 1, Number of growth rings.—2, Vessel diameter, mean, μm .—3, Vessel diameter, maximum, μm .—4, Vessel-element length, mean, μm .—5, Vascular tracheid diameter, mean, μm .—6, Vascular tracheid length, mean, μm .—7, Fiber diameter, mean, μm .—8, Fiber length, mean, μm .—9, Imperforate-element wall thickness, mean, μm .—10, Multiseriate ray width, number of cells.—11, Multiseriate ray width, mean, μm .—12, Multiseriate ray height, mean, μm .—13, Number of vessels per sq. mm of transection, mean.—14, Vulnerability ratio (vessel diameter divided by vessels per sq. mm).—15, Mesomorphy ratio (vulnerability ratio multiplied by vessel-element length).

safranin in absolute alcohol, and mounted in Coverbond. Some sections were counterstained with fast green to highlight parenchyma cells and non-lignified secondary walls in fibers. Macerations were made from unsoftened material with Jeffry's solution (Johansen 1940) and stained with safranin as above. Growth rings were counted from transverse sections or from sanded and oiled stem butts. Leaves were sliced and field pickled in FAA or 50% alcohol. The alcohol was used in later collections to avoid the macerating effects of FAA on the outer epidermal walls. Pickled leaf material was rinsed in water, moved to 50% alcohol, aspirated, and embedded by standard paraffin methods. Dried leaves were relaxed in 2% NaOH at 60 C for 1–2 hr, rinsed in water, and then treated as the pickled materials. Leaves were sectioned at 10 μm and stained with safranin and fast green according to Northen's modification of Foster's tannic acid-iron chloride method (Johansen 1940). Few of the leaf sections were entirely satisfactory as the pickling and relaxing solutions slightly expanded or even macerated the outer epidermal walls. Accurate measurements of total leaf and outer wall thicknesses could not be made consistently. Leaves were cleared to see venation patterns by being soaked in 2% NaOH at 60 C, rinsed in water, moved to 50% alcohol, and stained with safranin as for the woods. Leaf terminology follows Hickey (1973).

All anatomical observations were made with a light microscope. Quantitative wood data of Table 1 are based on 50 counts per sample except for vessels per sq. mm ($N = 10$) and imperforate-element wall thickness ($N = 25$). The number of vessels per group was not calculated as it is difficult to distinguish narrow vessels from vascular tracheids in transections. Leaf measurements are from 10 counts per sample.

No habitat parameters were measured quantitatively in the field. Microhabitat features and surrounding community type were subjectively determined. Gross soil characteristics were determined when excavating root systems.

ANATOMICAL DESCRIPTIONS

Woods

Wood measurements are presented in Table 1. *Keckiella* woods are stereotyped in basic construction, and highly specialized in their paedomorphic phenomena, vessel features, presence of vascular tracheids, and extremely short fibers.

Two paedomorphic features are evident. The age-on-length curve for vessel elements of *K. corymbosa* (3749) is similar to that of *Aster spinosus* Benth. (Carlquist 1975:219) except that the age span is 15 years. The initially rapid and then continuing decline in vessel element length throughout the life of the stem is clearly a paedomorphic phenomenon. Age-on-length

curves were not made for the other taxa. The second paedormorphic feature is the nearly rayless condition of the 18-year-old stem of *K. corymbosa* (3724) in which the erect ray cells approach the fibers in shape (Fig. 12). The origin of variation in intervascular lateral wall pitting during secondary growth is probably not a paedomorphic feature. Intervascular pitting is primarily alternate (Fig. 16), but irregular and opposite to pseudoscalariform-transitional types occur (Fig. 17). Since the vessels have tertiary helical thickenings (Fig. 15), lateral wall pits are restricted to areas between the gyres. Shifts in gyre angle and irregularities in the gyres can cause the opposite to irregular pitting, and lateral fusion of pits (the only fusion possible due to the gyres) results in pseudoscalariform pits. The paedomorphic origin of such pitting types in woods other than *Keckiella* is by retention in the primary xylem and subsequent continuation into the secondary xylem (Carlquist 1962). In *Keckiella*, by contrast, these pitting types appear to be de novo features in the secondary xylem.

Vessel elements are very specialized in having simple, predominantly transverse perforations on end walls, prominent tertiary helical thickenings, nearly circular transectional profiles, and in being very narrow and short (Table 1). The mean vessel-element width ranges from 22 μm (*K. ternata* ssp. *septentrionalis*) to 49 μm (*K. ternata* ssp. *ternata*), and the average length : width ratio is 4:1, with a range of means from 2.5:1 (*K. ternata* ssp. *ternata*) to 9:1 (*K. ternata* ssp. *septentrionalis*). The intervascular lateral wall pitting is primarily of circular-bordered alternate pits, with variation as described above. Vessel-ray pitting is similar to the intervascular pitting: it is alternate, opposite, or sometimes irregular and is typically strongly bordered.

Vascular tracheids are vessel-element derivatives which are much narrower and longer than vessel elements (Table 1); they are too narrow for end-wall pore formation, and are thus imperforate. Vascular tracheid proportions are modally distinct from the vessel-element proportions, but a few cells intergrade in size and shape. All vascular tracheids are easily distinguished from fibers by their tertiary helical thickenings. The mean vascular tracheid width ranges from 13 μm (*K. corymbosa*) to 19 μm (*K. lemmonii*, *K. ternata* ssp. *ternata*) and the average length : width ratio is 12:1 with a range of means from 7:1 (*K. ternata* ssp. *ternata*) to 17:1 (*K. corymbosa*). Exceedingly narrow vascular tracheids are present and range from 20 to 30 times longer than wide. Lateral wall pitting is restricted by the tertiary helical thickenings, and borders are often much reduced.

Fibers are thick-walled, elongate, and narrow, but wider than the vascular tracheids. The mean fiber width ranges from 15 μm (*K. rothrockii* ssp. *rothrockii*) to 23 μm (*K. cordifolia*, *K. lemmonii*) and the average length : width ratio is as for the vascular tracheids; 12:1. Length : width ratios range from 8:1 (*K. ternata* ssp. *ternata*) to 17:1 (*K. corymbosa*). The fibers

are surprisingly short in relation to the other cells, averaging 1.3 times the length of the vascular tracheids. The mean proportional increase in fiber length over the vascular tracheid length varies from none (*K. rothrockii* ssp. *rothrockii*) to 1.7 (*K. antirrhinoides* ssp. *antirrhinoides*). Relatively long fibers (over 400 μm) are consistently present in *K. cordifolia* (which has a novel sprawling shrub habit) and are occasionally found in *K. corymbosa*, *K. lemmonii*, and *K. ternata*. Lateral wall pitting is simple.

Axial parenchyma is scanty vasicentric with the strands divided into only a few cells (Fig. 15). Rays are primarily multiseriate and heterocellular. Multiseriate rays vary in abundance and proportions, being prominent in *K. cordifolia* (Fig. 2) to almost absent in one sample of *K. corymbosa* (Fig. 12). No wood studied was truly rayless. Most multiseriate rays are not extremely tall; mean length : width ratios range from 4:1 (*K. antirrhinoides* ssp. *microphylla*) to 10:1 (*K. cordifolia*). Ray walls are relatively thick except in some materials of *K. lemmonii* and *K. rothrockii*. Pits between ray cells are simple or bordered.

Most growth rings have distinct earlywood with relatively wide vessels, and latewood with few or no wide vessels (but vascular tracheids are usually present). All woods have a terminal band of thick-walled fibers (prominent in Fig. 9); the secondary walls of these fibers may be poorly to nonlignified. Considerable variation exists in the width of earlywood vessels, width of the entire earlywood, and in the abruptness of the change to latewood. Dry-site samples of *K. antirrhinoides* ssp. *microphylla* (Fig. 13) and *K. rothrockii* ssp. *rothrockii* (Fig. 9) have vessels few and narrow and an abrupt shift to latewood. Earlywood with wide vessels and a rather abrupt transition to latewood occurs in the desert-margin material of *K. ternata* ssp. *septentrionalis* (Fig. 14). A gradual transition to latewood occurs in the chaparral-margin material of *K. breviflora* (Fig. 7) and *K. ternata* ssp. *ternata*. The mesomorphic extreme, with wide vessels in the earlywood only gradually tapering in diameter through the season, is found in *K. cordifolia* (Fig. 1), a species of relatively mesic habitats.

Leaves

Leaf architecture and anatomy are fairly stereotyped throughout the genus, and leaves of all taxa are facultatively drought-deciduous. Changes in

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Figs. 1–4. Wood sections of *Keckiella*.—1–2. *K. cordifolia* (Michener 3704). Mesomorphy ratio is 55.—1. Transection: vessels wide, numerous; latewood indistinct.—2. Tangential sections: rays tall, wide.—3, 4. *K. lemmonii* (Michener 3735). Mesomorphy ratio is 52.—3. Transection: earlywood vessels wide.—4. Tangential section: rays tall, wide. (Figs. 1–4, magnification scale above Fig. 6. Divisions = 10 μm .)

leaf characteristics, including those represented by the data of Table 2, are related (sometimes weakly) to leaf size.

Keckiella leaves are usually short petiolate and elliptic to weakly cordate. Leaf bases may be broadly cordate in *K. cordifolia*, and narrowly ovate to cordate-clasping in some material of *K. rothrockii*. Leaf apices are typically acute, but vary to rounded in *K. antirrhinoides*, *K. cordifolia*, *K. corymbosa*, and *K. rothrockii*. Leaf margins are typically toothed, but teeth are often absent in *K. antirrhinoides* and scattered materials of all other taxa. Erode margins are restricted to *K. rothrockii*; revolute margins are sometimes present in *K. cordifolia* and *K. corymbosa*. Leaf lamina are typically plane, but may be folded upwards along the main vein into a 'v' in *K. breviflora* and *K. ternata*. Higher venation is eucamptodromous with a definite primary vein and usually few (<10) secondary veins except in some leptophylls of *K. antirrhinoides* and *K. rothrockii*. In these the venation is not always strongly developed. Areoles are imperfectly developed, randomly oriented, irregular in shape, and with no to several veinlets. Veinlets are simple to erratically twice branched. Major vein support is related to leaf size (Table 2). Vein support consists of protophloem fibers (Fig. 18) and parenchyma-sclerenchyma arcs (Fig. 20–21) between the phloem and the lower epidermis. Neither type of support is well developed in the leptophylls of *K. antirrhinoides* (Fig. 19) or *K. rothrockii*. The remaining taxa, with the exception of *K. cordifolia*, usually have one type better developed than the other. None of the microphylls and few of the larger nanomicrophylls have well-developed protophloem fibers. Leaves are dorsiventral with 2–4 palisade layers except for the isolateral leaves of some plants of *K. antirrhinoides* ssp. *microphylla* (Fig. 19), *K. corymbosa*, and *K. rothrockii* (Table 2). Plants with isolateral leaves are from some of the most exposed and xeric sites that these species enter.

Leaf primordia of all taxa are pubescent, although the mature leaves are glabrous to glabrescent in *K. breviflora*, *K. cordifolia*, *K. corymbosa* (glabrous form), and *K. ternata*. Two trichome types occur: single-celled nonglandular hairs, and glandular hairs with a typically two-celled gland and a one- or two-celled stalk (Fig. 22).

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Figs. 5–8. Wood sections of *Keckiella*.—5–6. *K. antirrhinoides* ssp. *antirrhinoides* (Michener 3668). Mesomorphy ratio is 42.—5. Transection: vessels wide, scattered.—6. Tangential section: ray height modest.—7. *K. breviflora* ssp. *glabrisepala* (Michener 3730). Mesomorphy ratio is 39. Transection: gradual transition from earlywood to latewood.—8. *K. breviflora* ssp. *breviflora* (Michener 3726). Tangential section: rays short, narrow. (Figs. 5–8, magnification scale above Fig. 6. Divisions = 10 μ m.)

Table 2. Leaf features of *Keckiella*.

Species	Collection	1	2	3	4	5	6
<i>K. antirrhinoides</i>	Michener 3660 (RSA)	n-l	12.9	0	0	21	0
ssp. <i>antirrhinoides</i>	Michener 3668 (RSA)	n-l	11.8	0	0	16	0
ssp. <i>microphylla</i>	Michener 3934 (RSA)	l	6.5	0	0	33	0
	Henrickson 1999 (RSA)	l	8.2	0	0	32	+
<i>K. breviflora</i>	Michener 3696 (RSA)	n	9.8	+	++	44	0
ssp. <i>breviflora</i>	Michener 3720 (RSA)	n	26.0	+	++	35	0
	Michener 3726 (RSA)	n	36.6	+	++	34	0
ssp. <i>glabrisepala</i>	Michener 3730 (RSA)	n-m	46.6	+	++	27	0
	Michener 3783 (RSA)	n-m	27.4	+	++	29	0
	Michener 3793 (RSA)	n	20.2	+	++	29	0
<i>K. cordifolia</i>	Michener 3704 (RSA)	n-m	20.7	+	+	0	0
	Michener 3710 (RSA)	n-m	20.4	+	+	0	0
<i>K. corymbosa</i>	Michener 3724 (RSA)	n	18.1	+	++	29	+
	Michener 3732 (RSA)	n	17.1	+	++	26	0
	Michener 3749 (RSA)	n	19.5	+	++	23	0
	Michener 3763 (RSA)	n-m	31.8	+	+	4	0
<i>K. lemmonii</i>	Michener 3773 (RSA)	m	37.4	++	+	12	0
	Michener 3778 (RSA)	m-n	32.2	++	+	11	0
	Michener 3789 (RSA)	n-m	25.1	++	+	9	0
	Michener 3790 (RSA)	n-m	28.7	++	+	15	0
<i>K. rothrockii</i>							
ssp. <i>jacintensis</i>	Michener 3804 (RSA)	n-l	9.0	0	0	33	+
ssp. <i>rothrockii</i>	Michener 3796 (RSA)	n-l	8.0	0	0	47	+
	Michener 3798 (RSA)	n-l	10.3	0	0	39	+
	Michener 3800 (RSA)	n-l	8.2	0	0	39	+
<i>K. ternata</i>	Michener 3689 (RSA)	n	23.5	+	+	29	0
ssp. <i>septentrionalis</i>	Michener 3692 (RSA)	n	24.5	+	+	34	0
	Michener 3722 (RSA)	n-m	34.5	++	+	36	0
ssp. <i>ternata</i>	Michener 3708 (RSA)	n-m	37.3	++	+	33	0
	Michener 3709 (RSA)	m	57.3	+	+	24	0
	Michener 3711 (RSA)	n-m	48.0	++	+	37	0

Key to columns: 1, Raunkiaer's leaf size class: l = leptophyll; n = nanophyll; m = microphyll.—2, Leaf length, mean, mm.—3, Parenchyma-sclerenchyma arc on main vein relative size: 0 = absent or weakly developed; + = developed; ++ = massive.—4, Protophloem fibers, relative abundance: 0 = absent or rarely present; + = consistently present, few; ++ = consistently present, numerous.—5, Stomates on upper surface, percent.—6, Leaf symmetry: 0 = dorsiventral; + = isolateral.

DISCUSSION

The habitats of all species of *Keckiella* are similar in having either a mediterranean or desert climate in which the spring growing season is terminated by summer drought (unstudied populations of *K. antirrhinoides* ssp. *microphylla* in the Sonoran Desert of Arizona may receive significant summer rain). The basic similarities among all species in wood and leaf

anatomy reflect this climatic pattern. All species have earlywood with relatively wide vessels, and facultatively drought-deciduous leaves. These features are functionally linked, as during the spring growing season the fairly mesomorphic leaves are produced and active when the earlywood vessels are neither limited by lack of water nor disabled by embolisms. As the summer drought progresses, the leaves are progressively shed, leaving the wood unbuffered from the now arid environment. The shrub must still maintain the cambium and wood parenchyma, and in some cases the green stems (presumably photosynthetic) may lose water. The latewood, composed primarily of the imperforate vascular tracheids and fibers, apparently forms an embolism-resistant conductive system during the summer drought. In short, most species produce relatively mesomorphic leaves which are progressively abscised through the summer drought; simultaneously the shrub shifts to an embolism-resistant latewood for its limited water conduction. One consequence of this arrangement is that woods and leaves are exposed to different climatic regimes, and thus show somewhat different patterns in relation to summer drought severity.

The wood mesomorphy ratios of Table 1 are the most informative single measure of structural mesomorphy. The ratio reflects vessel-element proportions and abundance. A potential measurement error is present in the vulnerability and mesomorphy ratios: in these paedomorphic woods vessel-element length, diameter, and the number of vessels per sq. mm can all change with age. The data of Table 1 are average figures of several years, while the ratios are calculated using the vessel per sq. mm values of later years. These figures were checked for *K. corymbosa* (3749) for years 2–3 and 12–15. Vulnerability and mesomorphy ratios shifted from 0.09:23 to 0.15:20, respectively. The values for years 12–15 are used in Table 1. The range of mesomorphy values among the samples of *K. ternata* ssp. *ternata* may be partially due to the limited age of two samples.

Photographs of wood sections showing trends in wood characteristics related to habitat severity are presented in Fig. 1–13. The sequence is of decreasing mesomorphy ratio values and increasing drought severity. Figure 14 shows the wood having the lowest mesomorphy ratio (18)—a desert-margin sample of *K. ternata* ssp. *septentrionalis*, from a habitat judged slightly less severe than the desert sample of *K. antirrhinoides* ssp. *microphylla* (Fig. 13).

Keckiella cordifolia enters the most mesic sites of any *Keckiella* species. This represents a secondary radiation into mesic habitats, and the novel sprawling shrub habit (branches scandent to 3 m long) is a form of ecological release. Sample 3704 (Fig. 1–2) is from the interface of riparian and oak woodland communities in the Santa Ana Mountains; subsurface water may be present well into the summer. Mesomorphic wood features include the novel shrub habit, earlywood vessels wide and abundant, average vessel

width relatively wide ($40\text{ }\mu\text{m}$), rays relatively tall ($503\text{ }\mu\text{m}$) and wide ($79\text{ }\mu\text{m}$), and mesomorphy ratio high (55). Leaves are mesomorphic in their dorsiventral construction and lack of stomates (0%) on the upper surface. *Keckiella antirrhinoides* ssp. *microphylla* grows in some of the most xeric habitats in the genus: from the desert slopes of the Peninsular Ranges, across the Mojave Desert, and into the Sonoran Desert of Arizona. Sample 3934 (Fig. 13) is from a north-facing boulder slope at the lower elevational limit of piñon-juniper woodland in the Little San Bernardino Mountains. Xeromorphic features include the shorter shrub size (branches self-supporting to ca 1.2 m tall), earlywood vessels narrower and relatively scarce, average vessels narrow ($23\text{ }\mu\text{m}$), rays short ($197\text{ }\mu\text{m}$) and narrow ($46\text{ }\mu\text{m}$), and mesomorphy ratio low (22). Leaves are xeromorphic in their small size (leptophylls), isolateral construction in some materials (Fig. 19; this material collected several km from sample 3934), and relatively high proportion of stomates on the upper surface (32%). A very similar pattern is found by comparing *K. lemmonii* (shrubs to 1.5 m tall) of relatively mesic sites of northern California with the high-elevation, short-statured shrubs (ca 0.5 m tall) of *K. rothrockii* of the southern Sierra (3798), the desert ranges of the southwestern Great Basin (3796, 3800), and the San Jacinto Mountains (3804). Leaves of *K. rothrockii* are distinctively xeromorphic in their isolateral construction and abundant stomates on the upper surface (33–47%).

Keckiella breviflora, *K. corymbosa*, and *K. ternata* range through a gamut of sites in the chaparral and chaparral: coniferous forest boundary. The species' geographic ranges overlap, but are substantially different. *Keckiella breviflora* encircles the Central Valley of California, *K. corymbosa* is primarily of the Coast Ranges and the Klamath Mountains, and *K. ternata* is restricted to the mountains of southern California and northern Baja California. The three species present a plexus of xeromorphic, intermediate, and some mesomorphic features that do not resolve by species or by community type, but which do correspond to microhabitat features. *Keckiella breviflora* (3730), *K. corymbosa* (3724, 3749), and *K. ternata* (3689) all have very low mesomorphy ratios and usually have the narrowest vessels and shortest rays within each species. These samples represent all the exposed or severe sites that these species entered. *Keckiella corymbosa* (3724) is an

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Figs. 9–12. Wood sections of *Keckiella*.—9. *K. rothrockii* ssp. *rothrockii* (Michener 3698). Mesomorphy ratio is 30. Transection: vessels narrow; terminal fiber band prominent.—10. *K. rothrockii* ssp. *rothrockii* (Michener 3800). Tangential section: rays narrow, height modest.—11, 12. *K. corymbosa* (Michener 3724). Mesomorphy ratio is 22.—11. Transection: vessels in narrow bands; growth rings narrow, outer rings erratic.—12. Tangential section: rays apparently absent, possible ray just left of center. (Figs. 9–12, magnification scale above Fig. 6. Divisions = $10\text{ }\mu\text{m}$.)

extreme case for both wood and leaf xeromorphy. It is from exposed rock scree and cliff faces on the inland side of the Santa Lucia Mountains, the southern limit of the species. This sample has very xeromorphic woods (Fig. 11–12) and leaves for the species: vessels are relatively narrow and essentially restricted to the narrow earlywood, mesomorphy ratio is low (22), and rays are indistinguishable from the fibers. Leaves are isolateral with numerous stomates on the upper surface (29%).

Fire adaptation.—The rocky sites occupied by *Keckiella* species may be relatively fire-free, and the typical occurrence of the nondesert species in these sites may indicate that the species are somewhat fire intolerant. *Keckiella antirrhinoides* ssp. *antirrhinoides* and *K. cordifolia* can stem sprout after being burned, although severe fires can be lethal (pers. obs.). Both species enter lower elevational (<1500 m) chaparral margin and coastal sage-scrub communities off of rocky sites where fire is an important ecological factor. Some samples of *K. antirrhinoides* ssp. *antirrhinoides* and *K. cordifolia* are distinctive in having enlarged gnarled roots just below soil level (a slightly thickened stem: root transition region is usually present in the other species). Originally, this may not have been a fire adaptation, as desert material of *K. antirrhinoides* ssp. *microphylla* sometimes root perenniates and forms a small ring of stems. An enlarged root gnarl may have evolved as a water and photosynthate storage device for surviving the summer drought, and then served as a preadaptation for fire survival. Wells (1969) proposed that the fire response strategy of a genus is an important factor in speciation in the California chaparral. Genera which recolonize by seed are more speciose than those which reestablish the parental plants by stem or crown sprouts. The nondesert species of *Keckiella*, even if somewhat fire intolerant, may be similar to *Rhamnus* L. (7 sp.), *Garrya* Dougl. (6 sp.), and *Lonicera* L. (5 sp.) in having some ability to resprout, and consequently not having speciated at the increased tempo of truly fire intolerant species (Wells 1969).

Comparison with other studies.—Correlations of shifts in dicot wood features with shifts in habit or habitat features are presented in several studies. Gibson's (1973) study of Cactoideae wood reports that vessel-element pro-

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Figs. 13–17. Wood sections of *Keckiella*.—13. *K. antirrhinoides* ssp. *microphylla* (Michener 3934). Mesomorphy ratio is 22. Transection: vessels few, narrow.—14, 15. *K. ternata* ssp. *septentrionalis* (Michener 3689). Mesomorphy ratio is 18.—14. Transection: transition to latewood relatively abrupt, compare with Fig. 7.—15. Axial parenchyma strand of two cells; helical thickenings prominent in vessel.—16. *K. cordifolia* (Michener 3704). Intervascular pitting alternate.—17. *K. rothrockii* ssp. *rothrockii* (Michener 3798). Intervascular pitting pseudoscalariform-transitional. (Figs. 13, 14, magnification scale above Fig. 6; Fig. 15–17, magnification scale by Fig. 16. Divisions = 10 μ m.)

Figs. 18–22. Leaf sections of *Keckiella*.—18. *K. corymbosa* (Michener 3749). Protophloem fibers prominent.—19. *K. antirrhinoides* ssp. *microphylla* (Henrickson 1999). Leaf isolateral; main vein lacking protophloem fibers.—20–21. *K. ternata* ssp. *septentrionalis* (Michener 3722).—20. Leaf dorsiventral; main vein with massive parenchyma-sclerenchyma arc.—21. Detail of main vein, protophloem fibers reduced.—22. *K. cordifolia* (cult. RSA 10,151). Leaf primordia with glandular trichome and simple hairs. (Figs. 18, 19, 21, magnification scale by Fig. 21; Fig. 20, scale above Fig. 6; Fig. 22, scale by Fig. 16. Divisions = 10 μm .)

portions are related to plant habit: longer and wider vessels are from species with taller plants. Other authors correlate wood features with various measures of habitat severity. Versteegh (1968) studied 68 Indonesian woods representing 31 families. Woods with "less specialized" features are of montane (i.e., less water stressed) areas; phylogenetic ranking of the taxa does not group these woods. Bass (1973), in a study of *Ilex* L., found some features relate to latitudinal and elevational distribution, rather than to subgeneric classification. For vessel-elements, the longer elements are from tropical lowland species, the shorter ones from temperate region species. The data of Dickison et al. (1978) on *Hibbertia* Andr. shows that vessel-element length and diameter decrease from mesic to xeric habitats. Carlquist and Debuhr (1977) found species of Peneaceae from xeric habitats to have vessel elements narrower and shorter. A floristic approach to wood trends (Carlquist 1977) revealed the same pattern: the mean vessel-element diameter and length (as well as mesomorphy value) decreased in the same sequence as did the rainfall in five communities of Western Australia.

Two studies including North American taxa (but not *Keckiella*) compare woods of plants from desert and dry regions. Carlquist (1966) provided a desert : dry : mesic array in his summarization of woods of Asteraceae. Plants of desert species differed from dry-site species in having vessel elements narrower and shorter, fibers shorter, but little difference in ray height. *Keckiella* woods present a similar pattern except that rays are reduced in height in populations from dry or desert sites. Webber (1936) presented wood characteristics of sclerophyllous chaparral and various desert dominants of California. She found (data reported as ranges) desert woods to have vessel elements slightly larger and shorter. This seemingly contradictory trend in vessel-element diameter is probably due to the comparison of sclerophyllous taxa with a heterogenous assemblage of desert shrubs. Over half of the desert shrubs listed may have paedomorphic woods; many of these have drought-deciduous leaves. These latter species are probably similar to the xeromorphic *Keckiella* woods in having wider earlywood vessels which are not representative of growing conditions through the year. The sclerophyllous chaparral taxa, in contrast, have woods buffered by the leaves throughout the year.

SUMMARY

Detailed descriptions of the range of variation in woods and leaves of *Keckiella* species are presented. *Keckiella* woods are very specialized and have several paedomorphic features. Because *Keckiella* leaves are facultatively drought-deciduous, the woods and leaves are exposed to different environmental regimes. Shrub habit, shrub size, and anatomical characteristics of woods and leaves are all related to habitat severity. Xeromorphic features of dry-site and desert species include: vessel elements narrower

(and usually shorter), mesomorphy ratio lower, rays shorter (if present); leaves smaller (often leptophylls), isolateral, with abundant stomates on the upper surface. One species, *K. cordifolia*, has secondarily entered more mesic sites; the novel sprawling shrub habit is a form of ecological release. Correlated with this increased shrub size are increased length of vessel elements, vascular tracheids, and fibers. The potential role of fire as a factor in microhabitat preference and in speciation is considered.

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