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WOOD AND BARK ANATOMY OF *SCALESIA* (ASTERACEAE)

Sherwin Carlquist¹

Introduction

The genus *Scalesia* Arnott is a distinctive Galápagos Island endemic belonging to tribe Heliantheae, subtribe Helianthinae, of Asteraceae. *Scalesia* has received comment from various authors because of two distinctive features. Firstly, the genus has speciated in the archipelago in a rather spectacular way with regard to leaf shape and size. Secondly, although a characteristic shrub of lava pioneer situations in the lowlands, *Scalesia* also occurs as trees in cloud-forest areas of the uplands (*S. cordata* Stewart, *S. microcephala* Robinson, *S. pedunculata* Hook. f.). Woodier than most genera of Heliantheae, *Scalesia* presents a group appropriate for study with respect to wood anatomy. The earlier account of *S. pedunculata* wood (Carlquist 1958) was based on a branch approximately 2 cm in diameter. Eliasson (1974) presented some data on secondary xylem of three species (*S. affinis* Hook. f., *S. cordata*, and *S. villosa* Stewart), compared the data with figures for *S. pedunculata*, and concluded that variation among the materials he studied was not significant. The basis for his study was twigs of limited diameter. I wished to restudy wood anatomy in the genus, using wood samples of more nearly optimal size. This was possible because two collections were supplied to me. One of these, provided by Dr. Charles Rick, was collected by him in 1965, shipped to me shortly thereafter, but not studied until now because of the appearance of Eliasson's study. The second collection was very kindly provided by Dr. Eliasson, who collected woods for the present study at my request during his 1980-1981 visit to the archipelago. These collections are excellent for the central and southern islands. The absence of collections from the remote northern islands is probably not a serious omission, in view of the nature of the results presented here.

The questions to be addressed in wood anatomy of *Scalesia* include whether wood structure is uniform throughout the genus, as Eliasson's data suggested, and whether variation, if present, is correlated with the habit and habitat of the upland tree species as compared to the lowland shrubs. Data obtained in this study are also applicable to questions relating to storied structure, fiber dimorphism, and the significance of fiber length.

Materials and Methods

The specimens studied and their provenance are as follows: *S. affinis*, Rick SAM 1520 (Darwin Station, Academy Bay, Santa Cruz I., el. 10 m, II-

1-1964), *Eliasson 12* (Black Beach, Santa Maria I., el. 10 m, 1.5 m tall, I-8-1981); *S. aspera* Andersson, *Rick SAM 1508* (3 km E of Bahia Conway, Santa Cruz I., el. 5 m, I-27-1964), *Eliasson 16* (Cerro Ballena, Santa Cruz I., el. 50 m, 2.5 m tall, II-13-1981); *S. crockeri* Howell, *Rick SAM 1510* (N side Santa Cruz I., el. 15 m, I-29-1964), *Eliasson 5* (N side Santa Cruz I., el. 70 m, 2 m tall, XII-23-1980); *S. helleri* Robinson, *Eliasson 6* (Santa Fé I., el. 80 m, 2 m tall, XII-28-1980), *Eliasson 7* (S side Santa Cruz I., el. 30 m, 4 m tall, XII-31-1980); *S. pedunculata*, *Rick SAM 1532* (Bellavista, Santa Cruz I., el. 200 m, II-1-1964), *Eliasson 4* (Los Gemelos, Santa Cruz I., el. 630 m, 8 m tall, XII-20-1980); *S. stewartii* Riley, *Eliasson 15* (E of El Sarten, San Salvador I., el. 20 m, 1.2 m tall, I-29-1981); *S. villosa*, *Eliasson 8* (Punta Cormorant, Santa Maria I., el. 30 m, 2.5 m tall, I-7-1981). Eliasson took particular care to obtain specimens of optimal size for each specimen.

Wood specimens were prepared by drying. Portions of these were boiled and treated for periods ranging from one to three days in ethylene diamine solution according to the method of Kukachka (1977). In some specimens, adherent bark was sectioned together with the wood. Outermost xylem portions, not wood from near pith, were studied for all species. Sections were stained with safranin. For some sections in which bark was present, fast green was used as a counterstain. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Wood Anatomy

Vessel elements.—Vessel elements of *Scalesia* are round as seen in transection (Fig. 1, 5, 11). They tend to occur in groups often; most collections show an average of about two vessels per group (Table 1), which is near the mean for Heliantheae as a whole, 2.16 (Carlquist 1966). Mean vessel diameter in the genus ranges from 45 to 83 μm , and is thus slightly above the mean for Heliantheae as a whole, 48 μm ; however, the range in *Scalesia* is comparable to vessel diameter for tree Asteraceae (84 μm) or rosette tree Asteraceae (68 μm). The widest vessel diameters occur in the cloud-forest tree species *S. pedunculata* (Fig. 11), the narrowest in *S. aspera* (Fig. 1). In a given section of most *Scalesia* woods studied, some fluctuation in vessel diameter could be observed. These fluctuations are not marked enough to be designated as growth rings; however, weakly differentiated growth rings may sometimes be said to occur (Fig. 5, 11).

Vessel-element length in *Scalesia* ranges from 154 to 324 μm (Table 1); Heliantheae as a whole have somewhat shorter vessel elements, averaging 255 μm (Carlquist 1966). *Scalesia aspera* has the shortest, as well as the narrowest, vessel elements. The fact that vessel elements are notably longer in *S. pedunculata* than in other species is evident from Table 1. Vessel-element length in this species exceeds slightly the mean for mesic Astera-

Figs. 1-4. Sections of *Scalesia aspera* (Eliasson 16)—1. Transection of wood. Fibers relatively thin walled.—2. Transection of bark. Portion of a secretory canal barely visible in cortex, upper left; small secretory canals between fiber bands in secondary phloem.—3. Tangential section of wood. Storied short fibers at extreme left.—4. Portion of vessel wall from tangential section, showing grooves interconnecting pit apertures. (Fig. 1-3, magnification scale above Fig. 2 [finest divisions = 10 μ m]; Fig. 4, scale above Fig. 4 [divisions = 10 μ m].)

Table 1. Features of wood anatomy of *Scalesia* species.

Species	Collection	1	2	3	4	5	6	7	8	9	10
<i>S. affinis</i>	Eliasson 12	62	256	2.5	210	750	1110	135	3.6	0.24	50.5
	Rick SAM 1520	70	213	2.3	196	832	780	136	4.2	0.33	64.4
<i>S. aspera</i>	Eliasson 16	55	236	2.3	153	627	632	79	4.1	0.23	35.9
	Rick SAM 1538	45	770	2.3	180	560	650	85	3.1	0.05	9.0
<i>S. crockeri</i>	Eliasson 5	70	530	1.4	195	670	890	108	3.4	0.13	25.8
	Rick SAM 1510	52	453	1.6	209	673	743	85	3.2	0.11	24.0
<i>S. helleri</i>	Eliasson 6	60	386	2.1	236	766	1240	72	3.2	0.16	36.7
	Eliasson 7	55	506	1.9	205	674	1080	105	3.3	0.11	22.3
<i>S. pedunculata</i>	Eliasson 4	83	328	1.9	320	880	740	103	2.8	0.25	81.0
	Rick SAM 1532	79	434	1.8	324	751	781	48	2.3	0.18	59.0
<i>S. stewartii</i>	Eliasson 15	71	284	1.5	164	720	1190	136	4.4	0.25	41.0
<i>S. villosa</i>	Eliasson 8	55	337	2.0	158	634	1320	98	4.0	0.16	25.8

Legend: 1 = mean vessel diameter, μm ; 2 = mean number of vessels per mm^2 of transection; 3 = mean number of vessels per group; 4 = mean vessel-element length, μm ; 5 = mean libriform fiber length, μm ; 6 = mean height multiseriate rays, μm ; 7 = mean width multiseriate rays, μm ; 8 = ratio of libriform fiber length to vessel-element length; 9 = "vulnerability" (vessel diameter divided by number of vessels per mm); 10 = "Mesomorphy" ("vulnerability" figure multiplied by vessel-element length).

ceae as a whole (282 μm), and matches very closely the mean length for vessel elements of tree Asteraceae as a whole (312 μm). One possible interpretation is that longer vessel elements correlate with a mesomorphic pattern of wood in *S. pedunculata*. In Asteraceae, as in other groups of dicotyledons, shorter vessel elements seem to correlate with xeromorphy, longer ones with mesomorphy (Webber 1936; Carlquist 1966, 1975). Another possibility is that in the tree species *S. pedunculata* the stems available were larger than in other species, so that more cambial activity has produced longer vessel elements; in the age-on-length curves for most woody plants, length of vessel elements increases with age of stem (Bailey and Tupper 1918; Carlquist 1962). Notably long libriform fibers were recorded for the Rick collection of *S. affinis*, for which a large stem was available; however, the vessel elements in *S. affinis* are not nearly so long as those of *S. pedunculata*. Lengths of libriform fibers would be expected to parallel those of vessel elements rather exactly. That vessel elements in *S. pedunculata* are relatively long compared with libriform fibers in that species seems at present best interpreted as a mesomorphic expression.

Pitting on lateral walls of vessels in *Scalesia* is alternate (Fig. 13). The pit cavities are roughly circular. However, pit apertures are transversely

Figs. 5–10. Wood sections of *Scalesia crockeri* (Eliasson 5)—5. Transection; parenchyma band, center.—6. Tangential section; uniseriate rays, center.—7–9. Multiperforate perforation plates from transection.—10. Ray cells from radial section. (Fig. 5–6, scale above Fig. 2; Fig. 7–9, scale above Fig. 4; Fig. 10, scale above Fig. 10 [divisions = 10 μ m].)

elongate. On most vessels in all species, pit apertures form a continuous groove (Fig. 4, 14). If one obtains a section in which the internal surface of the wall is shaved away from the portion of the wall bearing pit cavities, one can see these coalesced pit apertures, looking somewhat like the pit apertures of scalariform pits except that they are arranged in a spiral fashion. Intervascular pitting always consists of circular bordered pits, but some elongate pits were observed on vessel-parenchyma interfaces, especially in *S. aspera*.

Perforation plates in *Scalesia* are basically simple. However, aberrant multiperforate plates were observed, notably in *S. crockeri* (Fig. 7, 8, 9). However, even in the wood sample in which they were most readily found, multiperforate plates could be seen in fewer than one percent of the vessels. An occasional multiperforate perforation plate, like those figured, was seen in *S. aspera*, *S. stewartii*, and *S. villosa* wood. Multiperforate perforation plates in *Scalesia* range from near-scalariform (Fig. 7) to "fingerprint"-like (Fig. 9); in some, strands of wall material are widely spaced (Fig. 8). These plates are most often nearly transverse in orientation, so that transections of wood samples reveal them best. The presence of numerous bars on a transverse perforation plate would be atypical for a scalariform perforation plate. Likewise, the predominant direction of the bars is inconstant, also suggesting that these plates are not merely altered versions of scalariform perforation plates. In this connection, one should note that Butterfield and Meylan (1975) figure perforation plates of *Vitex lucens* Kirk (Verbenaceae) in which the bars run tangentially in the wood rather than radially. Bars should run radially in true scalariform perforation plates. However, Butterfield and Meylan figure "normal" scalariform perforation plates in *Brachyglottis repanda* J. R. & G. Forst. (Asteraceae); in these plates, bars run radially. The bars are numerous and fine in *B. repanda*, and most plates are simple rather than multiperforate. These two facts suggest that the multiperforate plates of *B. repanda* are not simple vestiges of a scalariform condition. If a vestigial condition were present, one would expect (as is true in a large number of dicotyledons) presence of numerous plates with a few bars along with some simple plates within a given wood sample. The significance of the multiperforate plates in *Scalesia*, as well as in the two other instances mentioned, is not easy to ascertain. One may safely say, however, that such plates do not have a functional explanation, for in those woods, the plates are too infrequent. A wood functions on the basis of the conformation of the majority of cells in it. If fewer than one percent of vessel elements in a species have multiperforate plates, such plates must have an alternative explanation, such as presence of incomplete or faulty genetic information at such a low level of expression as to be functionally harmless.

The number of vessels per mm² of transection ranges between 213 and

Figs. 11–15. Wood sections of *Scalesia*.—11–14. *S. pedunculata* (Eliasson 4)—11. Transverse section; poorly defined growth ring evident.—12. Tangential section; libriform fibers are storied.—13. Vessel wall from tangential section, showing circular pit cavities.—14. Vessel wall from tangential section, showing grooves interconnecting pit apertures.—15. *S. stewartii* (Eliasson 15), tangential section. Rays tall and wide. (Figs. 11, 12, 15, scale above Fig. 2; Figs. 13, 14, scale above Fig. 4).

770 in *Scalesia* (Table 1). A range this great suggests that one might expect variation in number of vessels according to species, individual, or portion of the wood within an individual. Perhaps all three sources of variation occur in *Scalesia*. However, one may note marked differences between the two collections of *S. aspera* (Table 1), and one can see fluctuation within a single section also, related to vessel diameter fluctuations, as in *S. crockeri* (Fig. 5) and *S. pedunculata* (Fig. 11).

Libriform fibers.—As shown in Table 1, libriform fibers range from 560 to 880 μm in length in *Scalesia*. Within the genus as a whole, libriform fibers are relatively long compared to vessel elements. If one constructs a ratio of libriform fiber length to vessel element length (Table 1, column 8), one finds a range from 2.3 to 4.4 in the genus. *Scalesia pedunculata* has the lowest ratio, *S. stewartii* the highest. The most important fact which emerges is that longer libriform fibers do not correlate clearly either with arborescence or with greater stature. This point, made earlier (Carlquist 1975, 1980) is worthy of mention because some (Baas 1976; Zimmermann 1978) have questioned the reasons I advanced why vessel elements tend to become shorter with phylesis, namely that shorter vessel elements are more adaptive in drier regimes. However, phylesis leading to shorter fusiform cambial initials is not directed by the selective value of short imperforate elements, nor is phylesis leading to longer fusiform cambial initials directed by the selective value of longer imperforate elements in most cases. If one hypothesizes that long imperforate elements have the advantage of greater strength (Wardrop 1951; Wellwood 1962), longer libriform fibers ought to be found in arborescent members of a group as opposed to shrubby species. This is not supported in *Scalesia*, in which the libriform fibers are not appreciably longer in the species with long vessel elements, *S. pedunculata*, than they are in the shrubby species. The ratios of libriform fiber length to vessel-element length are from 2.3 to 4.4 in *Scalesia*, as noted. This is noteworthy in that Asteraceae as a whole have a lower ratio, 1.7 (Carlquist 1966). Heliantheae have a ratio somewhat higher (1.9), but this is still below the ratio found in *Scalesia*. Tree Asteraceae have a notably low ratio, 1.5 (Carlquist 1966), which seems to demonstrate that longer vessel elements but not proportionately longer libriform fibers are basic to tree Asteraceae; this is shown by *S. pedunculata*. One can hypothesize that the high libriform fiber to vessel-element length ratio has no significance in *Scalesia*, although I suspect a reasonable explanation can be found.

Variation in wall thickness of libriform fibers occurs prominently in *Scalesia*. In some instances this accords with species lines. Libriform fibers of *S. stewartii* are uniformly thick walled (Fig. 15). Variation may be seen within a single stem, as in *S. crockeri* (Fig. 5) and *S. pedunculata* (Fig. 11). These two examples differ in synchronization of thick-walled fibers with vessel diameter. The thick-walled fibers are produced along with wide ves-

sels in the section shown for *S. pedunculata*, but thick-walled fibers are produced simultaneously with narrow vessels in the *S. crockeri* section shown. The patterns of these variations are probably of no functional significance. However, the fact that both thin- and thick-walled libriform fibers are produced in a species does have significance. The thin-walled fibers appear to be shorter, often storied (Fig. 3, left; Fig. 12), whereas thick-walled fibers appear longer and nonstoried (Fig. 3, right; Fig. 6, 15) in *Scalesia*. The difference between the two kinds of fibers is not always marked, and intergrading libriform fibers may be found. However, *Scalesia* seems clearly to represent an opening stage in the phenomenon of fiber dimorphism. The concept of fiber dimorphism originated in a study of woods of Heliantheae (Carlquist 1958; see Carlquist 1980 for a review). The shorter fibers show the storied pattern because their lessened intrusiveness reflects in a less modified way the storied nature of fusiform cambial initials. The shorter fibers may serve to some extent as a parenchyma substitute; clearly they do when fiber dimorphism is further advanced than it is in *Scalesia*. However, a band of parenchyma (Fig. 5, center) was observed in *S. crockeri*, and this band probably owes its origin to fiber dimorphism.

Parenchyma.—Axial parenchyma in all species of *Scalesia* is of the type known as vasicentric scanty. The strands consist chiefly of two cells. The band of parenchyma of *S. crockeri* (Fig. 5), as noted in the preceding paragraph, has a different origin.

Multiseriate rays are more abundant than uniseriate rays in all species of *Scalesia*. Uniseriate rays are moderately abundant in *S. crockeri* (Fig. 6) and *S. pedunculata* (Fig. 12), uncommon in *S. affinis* and *S. aspera* (Fig. 3), and very rare in *S. helleri*, *S. stewartii* (Fig. 15), and *S. villosa*. According to the criteria of Kribs (1935), *Scalesia* should be considered in transition to a highly specialized condition in this respect.

The tallest and widest rays (Table 1, columns 6 and 7) occur in *S. affinis*, *S. stewartii* (Fig. 15), and *S. villosa*. The shortest, narrowest rays occur in *S. pedunculata*. In Asteraceae as a whole, height of multiseriate rays parallels vessel-element length (Carlquist 1966, and the papers on which that study was based). However, this is not true in *Scalesia*. The explanation seems to be that the stems of *S. pedunculata*, the largest trunks in this study, have had more time in which areas of ray initials in the cambium could be subdivided into smaller segments by intrusion of fusiform cambial initials. *Scalesia stewartii*, with notably tall, wide rays (Fig. 15) came from the smallest "tree" of the species collected by Eliasson. The rays in *S. stewartii* also bulk large with relation to fascicular tissue in comparison to what one finds in other species of *Scalesia*. Of the two collections of *S. affinis*, the shorter rays are found in the larger wood sample (Rick SAM 1520).

With respect to ray histology, erect ray cells predominate by far in most

species of *Scalesia* (Fig. 10). Procumbent cells were observed to be common only in *S. affinis* (Rick SAM 1520), both collections of *S. pedunculata*, and *S. villosa*. These wood samples also happen to be the largest in diameter, coming from plants of greater stature than tend to characterize the remaining species. Thus one may conclude that ray initials are horizontally subdivided over time, and that larger and older trunks will have more procumbent cells at their peripheries than smaller and younger ones. This phenomenon is widespread in dicotyledons (Barghoorn 1941). However, one should note that procumbent cells are missing or rare at the outset of secondary xylem production in *Scalesia*. This absence of procumbent cells might be considered an aspect of herbaceous structure, or paedomorphosis (Carlquist 1962).

Ray cell walls are not notably thick in any species (Fig. 3, 5, 12, 15). Ray cells are generally lignified. In *S. aspera*, some nonlignified thin-walled ray cells were observed. Deposits of resinlike compounds were seen in ray cells in the form of small droplets in most species (Fig. 10). Occasionally carbonized intercellular deposits of these in rays were seen. No crystals were observed.

Ecological Summary of Wood

Differences among the species appear to be related to habit and to ecology, as noted above. The relatively long vessel elements of *S. pedunculata*, which are not accompanied by proportionately long libriform fibers, may be related to mesomorphy in that upland species. The vessel-element length and vessel diameter of the remaining species fall within ranges typical for Asteraceae, a family the majority of which are adapted to dry conditions. Libriform fibers in *Scalesia* are notably long. Although the length of fibers in the genus may be related to the "miniature tree" habit of *Scalesia* species, that explanation does not seem wholly satisfactory. Rays of *S. pedunculata* are relatively short and wide, and are richer in procumbent cells than those of the other species. These tendencies are explained by the fact that the *S. pedunculata* stems studied were larger than those of the other species, so that more time in which breakup of ray initial areas by intrusion of fusiform cambial initials and subdivision of ray initials horizontally could occur was available. These tendencies could also be seen in *S. affinis*: the larger of the two samples had shorter rays with more numerous procumbent cells. The vessel elements in *S. pedunculata* evidently become longer with age of stem; they are reported here to average 320 and 324 μm in the two collections; the smaller stem in my 1958 study had vessel elements 246 μm in length. The figure 246 lies within the range of vessel-element lengths found in three species of *Scalesia* other than *S. pedunculata* by Eliasson (1974).

Figures have been presented in Table 1 for the indices termed vulnerability (column 9) and mesomorphy (column 10). The range within the genus

in the mesomorphy index is 9.0–81.0. As might be expected, the two collections of the upland tree species *S. pedunculata* have the highest mesomorphy value, owing to vessel-element length and vessel diameter. However, the other species trail closely behind *S. pedunculata*. The wood of *S. pedunculata*, if slightly more mesomorphic than that of the other species, is still rather xeromorphic. We can see this if we compare, for example, the range in mesomorphy figures for *Scalesia* with the range in Pittosporaceae (Carlquist 1981), in which only a few species have values below 100. These ranges correlate with the probable moisture availability of sites where the various *Pittosporum* Banks ex Soland apud Gaertn. and *Scalesia* species grow.

The fact that the wood of *S. pedunculata* is not greatly more mesomorphic than that of the other *Scalesia* species probably can be interpreted as meaning that the *S. pedunculata* forest is not a true mesic habitat. Although covered with clouds during the wet season, the precipitation is probably not great, judging from the lack of truly mesic genera and species. More importantly, the Galápagos uplands experience a dry season. Wood patterns of dicotyledons may be expected to evolve in accordance not so much with the most favorable portion of a year, but more in accordance with the least favorable.

Anatomy of Bark

Transections of bark were studied for several species of *Scalesia*. All proved to be essentially identical, so a description for only a single species, *S. aspera* (Fig. 2), will suffice. Secretory canals are present in outer bark which represents a remnant of the cortex of a primary stem (Fig. 2, upper left). Such secretory canals are present in stems of many Heliantheae (Carlquist 1957). Strands of protophloem fibers (Fig. 2, upper right) are present, as with other Heliantheae. The cells at the periphery of the fiber strand may be designated as endodermis, for they bear a Casparian strip, best demonstrated with counterstaining. This feature, although rare in stems of dicotyledons at large, is frequent in stems of Heliantheae (Carlquist 1957).

Two features present in *Scalesia* bark are not common in Asteraceae, however: the production of strands of fibers in the secondary phloem, and of secretory canals, formed among parenchyma cells in phloem no longer actively conducting. The bands of fibers and the bands of inactive phloem containing secretory canals alternating with the fiber bands may be seen in Fig. 2. Most Asteraceae have neither secretory canals nor fibers in secondary phloem.

The exudate of secretory canals in Asteraceae, as well as in other families, protects the plant against insect attack in all likelihood. This may be the significance of the canals in *Scalesia* bark. However, a second possibility

might also be considered in *Scalesia*: sealing of the plant against desiccation. Dried bark of *Scalesia* wood samples is often permeated with the resinlike materials these secretory canals contain.

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Footnote

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